Observations on the ecology and life-history of *Chrysaora fulgida* (Reynaud 1830) (Scyphozoa: Semaeostomeae) and other pelagic cnidarians in the inshore waters off central Namibia

by

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A thesis submitted in fulfilment of the requirements for the degree of Philosophiae Doctor in the Faculty of Natural Science, Department of Biodiversity and Conservation Biology, University of Western Cape.

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DECLARATION

I declare that: **Observations on the ecology and life-history of *Chrysaora fulgida* (Reynaud 1830) (Scyphozoa: Semaeostomeae) and other pelagic cnidarians in the inshore waters off central Namibia**, is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Heidi Skrypzeck November 2018

Signed……

"…*Immensely powerful though we are today it is equally clear that we are going to be even more powerful tomorrow. And what's more there will be greater percussion to use our power as a number of human beings on earth increases still further. Clearly we could devastate the world. If we not to do so, we must have a plan. And such a plan has been formulated by environmental scientists. They call it – the World Conservation Strategy – and it rest on three very simple propositions. One, that we should not so exploit natural resources that we destroy them. Common sense you might think? And yet, look what we have done to the European herring, the South American anchovy and are still doing to the whales. Two, that we should not interfere with the basic processes of the earth on which all life depends in the sky, on the green surface of the earth and in the sea. And yet, we go on pouring poisons into the sky, cutting down the tropical rainforest, dumping our rubbish into the oceans. And third, that we should preserve the diversity of life, that's not just because we depend upon it for our food – though we do – nor because we still know so little about it that we won't know what we are losing – although that is the case as well. But, it is surely that we have no moral right to destroy other living organisms with which we share the earth. As far as we know the earth is the only place in the universe where there is life. Its continued survival now rests in our hands*." – David Attenborough, The Living Planet (1984)

DEDICATION

Ek dra hierdie tesis op aan my ouma, Anna M.J. Skrypzeck. Dankie vir jou onvoorwaardelike liefde en vir die mens wat ek vandag is. Daar is ‘n leemte in my lewe met jou afwesigheid – ek mis jou elke dag!

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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ABSTRACT

Although jellyfish are recognised recently as key components that can influence ecosystem functioning and trophic flows in the northern Benguela upwelling ecosystem, the number of published studies on their abundance, seasonality, life history and ecological roles off Namibia is strictly limited. *Chrysaora fulgida* is one of the most common and conspicuous medusae in the plankton off Namibia, and has flourished in the region, following the decline of the pilchard fishery at the end of the 1960s. It is said that their biomass (together with *Aequorea forskalea*) exceed that of the commercially important fish stocks off Namibia. In addition, this species is also capable of forming large swarms in northern Benguela where they are a nuisance to fisheries operations. The objective of this study is to try and fill gaps regarding our knowledge of the biology and ecology of *Chrysaora fulgida* off Namibia, with a view to improve our understanding of its success in the northern Benguela ecosystem.

In the Chapter 1, a general overview on the current knowledge and population dynamics of jellyish blooms and their ecology is compiled. Other key topics of the thesis such as jellyfish life cycles and their reproduction are also introduced.

Chapter 2 investigates the temporal changes in the jellyfish community in Walvis Bay over a 23-month period from biweekly plankton samples. All twelve of the recovered taxa were characteristically neritic, and included meroplanktonic Hydrozoa and Scyphozoa, as well as cydippid ctenophores and shallow water siphonophores. Whilst, ephyrae of *Chrysaora fulgida* were dominant overall, and peaked in abundance during mid-spring (Year 2012: 168 933 ind. 100 m^{-3}) and late winter (Year 2013: 23 389 ind. 100 m^{-3}), they were not present all year round, being replaced (in part) by *Obelia* in summer and autumn, *Bougainvillia* in spring and summer, and *Muggiaea atlantica* in summer. Seasonal changes in the composition and structure of the community were driven primarily by bottom water temperature and day length (explaining 24% of the variability in community structure), with wind speed and moon illumination playing a secondary role. The recruitment of ephyrae of *C. fulgida* to the plankton off Walvis Bay is confirmed not to be continuous throughout the year.

Chapter 3 present the first detailed investigation on the identification, morphological development and growth of wild caught “ephyrae” of the scyphozoan *Chrysaora fulgida* and *Chrysaora africana* in

Walvis Bay, off Namibia. Concrete morphological dissimilarities are documented to distinguish *C. africana* from *C. fulgida*, despite the limited sample size of *C. africana*: coloration differences and the presence/absence of branched canals on the periphery of velar and rhopalial canal tips. In the case of *C. fulgida* the morphological development from an ephyra (Stage 0) to a juvenile medusa could be described successfully in six stages, whilst missing stages were noted for *C. africana*. In general, the development of ephyrae described here agrees with patterns described for other species in the genus from elsewhere. The ephyrae stages of *C. fulgida* illustrated a low overall growth rate (4.33 and 3.45% d^{-1}, respectively) and longer ontogenic development (~164 days), respectively, than most other jellyfish species.

Through the histological examination of medusa gonads, Chapter 4 investigates the sexual reproduction and maturation of both *Chrysaora* species, collected off Walvis Bay, Namibia. Both species were non-brooding, gonochoristic, displayed a 1:1 sex ratio and exhibited no clear sexual dimorphism features. Gametogenesis in both species was similar to that displayed by other Discomedusae, whilst some differences in gonad maturity were evident between them – *Chrysaora fulgida* displayed aseasonal, reproductive heterogeneity (maturing at ~300 mm diameter) and individuals were semelparous, whilst *C. africana* appeared strongly seasonal but iteroparous.

Through stable isotope analysis (δ^{13}C, δ^{15}N and C:N ratios), Chapter 5 examines the presence of tissue, ontogenetic, seasonal, spatial and interspecific variability in medusae of *Chrysaora fulgida* and *Chrysaora africana* off Walvis Bay, in the northern Benguela, Namibia. This study did not only illustrate size-associated shifts in trophic ecology, but also revealed spatial, inter-species and some tissue differences in the northern Benguela upwelling system. Size would appear to be the over-riding factor that influences the isotope signatures of *Chrysaora fulgida*; size being linked in turn to space. A clear negative relationship is illustratred between δ^{15}N and individual size for two scyphozoans (*C. fulgida* and *C. africana*) off central Namibia, indicating that larger jellyfish feed lower down the food chain than smaller ones in both species. This is explained by the need and ability of ephyrae and small medusae to access the microbial food web which consists of many trophic steps and hence numerous opportunities for enrichment of nitrogen isotopes, resulting in higher δ^{15}N values of smaller individuals.

Chapter 6 provides a synthesis of the main findings of the thesis, and makes recommendations on ways that the research can be carried forward.

Jellyfish bloom in Walvis Bay.

PICTURE

CHAPTER 1

GENERAL INTRODUCTION

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Until fairly recently, research into zooplankton has largely been focused on crustaceans owing, in part (Gibbons & Richardson 2013), to their abundance and importance as a food source for commercial fish resources: jellyfish have been comparatively neglected (Fransz et al. 1991; Verity & Smetacek 1996; Haddock 2004; Gibbons & Richardson 2013). Aside from problems associated with their quantitative sampling and fragile nature (Hamner et al. 1975, Weisse et al. 2002, Purcell 2009; Frangoulis et al. 2017), the neglect of jellyfish has been fostered by a perception that they are trophic dead ends and that they play a limited role in pelagic ecosystems (Omori & Hamner 1982; Boero & Mills 1997; Boero et al. 2008; Pauly et al. 2009; Richardson et al. 2009; Brotz et al. 2012; Laakmann & Holst 2014). This situation has been reversed in the past two decades and jellyfish have received considerable attention due (again) to perceptions that they have increased in abundance, and that blooms are being reported with greater frequency and for a longer duration (Mills 1995, 2001; Link & Ford 2006; Lynam et al. 2006; Jackson 2008; Richardson et al. 2009; Brotz et al. 2012; Condon et al. 2012, 2013; Purcell et al. 2012). When present in large abundances, jellyfish can have negative repercussions for marine ecosystem dynamics and human activities in coastal waters (reviewed in Purcell et al. 2007; Richardson et al. 2009; West et al. 2009a, 2009b; Schrope 2012; Bayha & Graham 2014). Further, some species have expanded their range into new habitats (Mills 2001; Graham et al. 2003; Graham & Bayha 2007; González-Duarte et al. 2016 and references within).

Jellyfish blooms are a natural phenomenon, and reflect the intersection between population dynamics and life cycles of individuals and hydrological processes that serve to concentrate individuals (Hernroth & Gröndahl 1983; Gröndahl 1988a; Lynam et al. 2005a; Purcell 2005; Fuentes et al. 2011; Schnedler-Meyer et al. 2018). Fossilised mass strandings of medusae date back to more than 500 million years ago (Hagadorn et al. 2002), indicating that the blooming phenomenon is not new. There is at present a controversy about whether the recent increases in jellyfish blooms reflect their response towards the human-induced alteration of global ocean ecosystems (Mills 2001; Purcell et al. 2007; Jackson 2008; Lo et al. 2008; Richardson et al. 2009; Purcell 2012) or whether they are “apparent

blooms" (Graham et al. 2001). The latter being linked to natural oscillations in populations associated with seasonal, climatic and oceanographic forcing (Hernroth & Gröndahl 1983; Lynam et al. 2005a; Purcell 2005; Fuentes et al. 2011; Condon et al. 2013; Purcell 2012; van Walraven et al. 2014; Schnedler-Meyer et al. 2018).

Despite natural inter-annual fluctuations in jellyfish densities, several human-induced factors can be linked locally to the underlying causes of their increased bloom frequencies, especially in coastal waters (Mills 2001; Purcell 2012) (as discussed in Section 1.8). These factors (natural fluctuations and/or human-induced) might act synergistically with each other, which complicates the determination of the exact nature of jellyfish blooms (Purcell et al. 2007; Richardson et al. 2009). The majority of recent studies and syntheses have focused on understanding the causes (and consequences) influencing the population variability of the medusa component (pelagic) of the jellyfish assemblage (see Lucas et al. 2012 and references therein). However, in order to gain an understanding of patterns in coastal systems, research should be focused on the complete life cycle pattern and life history, community interactions of both the benthic and pelagic phase (benthic-pelagic coupling) and how these vary with the abiotic environment (Marcus & Boero 1998; Boero & Bonsdorff 2007; Lucas & Dawson 2014).

In order to establish any cause-effect relationship behind the dynamics and ecosystem role of jellyfish blooms, a number of issues need to be considered (Pauly et al. 2009; Gibbons & Richardson 2013; Lucas & Dawson 2014). Fundamental biological information is required on the life cycle dynamics, life history traits, behaviour, physiological rate processes, trophic interactions (diet, trophic level, biodiversity) and taxonomy of local species. Standardised protocols for field and laboratory methods need to be created in order to establish quantitative and comparable long-term time series covering all temporal and spatial scales. This would permit local and regional comparisons of jellyfish numbers, their distribution and diets. Then, their physiological responses to environmental variability need to be identified so that the potential drivers behind their blooms are fully grasped. Finally, all these abovementioned data are parameterized into population and ecosystem models in order to understand the dynamics of jellyfish populations and the ecological role of jellyfish; and potentially forecast and manage their blooms (Pauly et al. 2009; Purcell 2009; Gibbons & Richardson 2013; Goldstein & Steiner 2017; Goldstein et al. 2018; Henschke et al. 2018; Schnedler-Meyer et al. 2018).

1.1 What are jellyfish?

Jellyfish are members of the phyla Ctenophora and Cnidaria, and are free-swimming gelatinous animals (Richardson et al. 2009). Ctenophores and pelagic cnidarians share a number of characteristics. They are mostly transparent; they have a soft, gelatinous body composed of ~95% water content (Lucas et al. 2011); some can reach high population densities (blooms) during favourable conditions; most of them are carnivorous and feed on prey ranging in size from protists to fish larvae; they are common in coastal and shelf seas; they have a similar impact on humans (except for stings and human health) and their likely reactions to anthropogenic drivers are convergent (Alvariño 1985; Purcell & Mills 1988; Richardson et al. 2009; Lucas et al. 2011; Gibbons & Richardson 2013).

The phylum Ctenophora consists of ~130 recognised marine species that are carnivorous (Mills Internet 1998–2018). They are characterised by a gelatinous body, eight bands of cilia known as 'comb rows' and general sticky cells (colloblasts) that adhere to prey (Mianzan 1999). The cilia rows are used for locomotion and are often responsible for the iridescent appearance of the animal (Mianzan 1999). Many species are bioluminescent (Gershwin et al. 2014) and some are capable of blooming in huge numbers to the detriment of wider ecosystems (Shiganova et al. 2001; Kideys 1994, 2002; Kideys et al. 2005). Most ctenophores are concurrently hermaphroditic, have a simple life cycle with a single generation: eggs are fertilized externally and the larvae develop directly into juveniles (Gershwin et al. 2014). Ctenophores are divided into four classes (Mills Internet 1998–2018): Ctenophora incertae sedis (fossils), Nuda (order: Beroida), Scleroctenophora (fossils) and Tentaculata (with orders: Cambojiida, Cestida, Cryptolobiferida, Cydippida, Ganeshida, Lobata, Platyctendida, Thalassocalycida, Tentaculata incertae sedis).

The phylum Cnidaria includes corals, hydroids, jellyfishes, sea anemones, and sea fans and contains ~11 000 recognised species (~13 000, if the Myxozoa are included: Lom & Dyková 2006). They are aquatic, being primarily marine. Cnidaria is divided into two clades, Anthozoa (subclasses: Hexacorallia and Octocorallia) and Medusozoa. There are four classes within Medusozoa: Hydrozoa, Cubozoa, referring to box jellyfish; the Scyphozoa, or true jellyfish; and Staurozoa, the stalked jellyfish (Arai 1997; Dawson 2004; Marques & Collins 2004). There are ~200 species of Scyphozoa, 50 species of Staurozoa, 41 species of Cubozoa, and 3 702 Hydrozoa species (Mayer 1910; Kramp 1961; Russell

1970; Bouillon et al. 2006; Mills & Hirano 2007; Kingsford & Mooney 2014). Three of the modern Medusozoa have a fossil record dating back over 500 million years: Cubozoa, Hydrozoa and Scyphozoa (Cartwright et al. 2007). Medusozoans are found in all aquatic environments: from the sea through brack- to freshwater; from the poles to the tropics; from the bottom of the ocean floor to the surface (Arai 1997; Jankowski 2001; Dawson 2005).

Medusae can obtain nourishment through the capture of prey organisms, absorption of dissolved organic matter or from organic compounds derived from symbioses with zooxanthellae (Arai 1997; Pitt et al. 2009a, 2009b). Many species of pelagic cnidarians and ctenophores are predominantly carnivorous and prey on a variety of zooplankton, ichthyoplankton (fish eggs and larvae), benthic organisms and other medusae but infrequently on phytoplankton (Mills 1995; Arai 1997; Purcell & Arai 2001; Flynn & Gibbons 2007; Purcell 2009). Some species, for instance the scyphozoan *Drymonema larsoni,* specialize in preying exclusively on other medusae and it is morphologically adapted to its unique diet (Bayha et al. 2012). A recent study indicated that jellyfish display similar clearance rates as fish (if compared on a carbon basis) due to their evolutionary trait of having a large, water-loaded body that promotes increased prey encounter and feeding rates (Acuña et al. 2011). Predation rates of medusae increase with prey densities though satiation does not appear to occur at natural prey densities (Arai 1997).

Different jellyfish taxa respond at different times to certain environmental conditions: this could result in seasonal medusae blooms in coastal waters (Mills 1981; Buecher & Gibbons 1999; Boero et al. 2008; Bravo et al. 2011; Petrova et al. 2011; van Walraven et al. 2017). The combination of high predation rates by jellyfish coupled with their blooming capability (Hamner & Dawson 2009) can enable jellyfish to be the dominant pelagic carnivore in coastal marine ecosystems (e.g. Feigenbaum & Kelly 1984; Möller 1984; Cowan & Houde 1993; Behrends & Schneider 1995; Omori et al. 1995). By this means, jellyfish can lead to the restructuring of marine food webs both via top-down (predation) and bottom-up (acquisition of resources) during their periodic dominance (Verity & Smetacek 1996; Purcell et al. 2001; Shiganova et al. 2001; Boero et al. 2008).

1.2 Population dynamics – life history – life cycles

Populations comprise individuals having a life cycle involving a series of chronological and recognised states of development that can be defined by age, stage/phase or size (cohorts) (Cortés 2004). Population dynamics seeks to describe fluctuations in the cohort-specific abundance of a population over space and time owing to various sources of variability that are governed by both ecological and genetic processes (Cortés 2004). The cohort-specific abundance of individuals in space and time is regulated by the key vital rates – birth, growth and death – and the demographic processes of emigration and immigration, which are affected by genetic, demographic, environmental and anthropogenic randomness (Cortés 2004).

The life history of an organism comprises its life pattern from birth to death, describing the age-size-, or stage-specific patterns of its development by growth, maturation, reproduction, survival and lifespan (Braendle et al. 2011; Fabian & Flatt 2012). The key characteristics of life are shaped by demographic traits – size at birth, growth pattern, reproductive maturity age and size, specific reproductive investments, reproductive schedule, number and size of offspring produced, age and size specific mortality and lifespan – interlinked by constraining trade-offs (Stearns 1976, 1992; Ramirez Llodra 2002; Braendle et al. 2011; Edward & Chapman 2011). Life history research seeks to understand the causes and consequences of genetic and environmental variation in life history traits across environments, individuals, populations and both within and among species. It also focuses on strategies that have an effect on the survival and reproduction at individual -, populations - or species levels. Hence, life histories represent unique biological outcomes to the opportunities and challenges presented by the ecosystems and environments that the organisms inhabit. Each outcome comprises of complex life-history traits responsible for allocations of limited resources of energy, biomass and time among various competing attributes that may influence survival and reproduction (Stearns 1976, 1992; Ramirez Llodra 2002; Braendle et al. 2011; Edward & Chapman 2011).

A common oversight when evaluating life history traits and plankton community dynamics is to consider marine taxa only on the basis of morphological and functional features of the pelagic stage, failing to recognise that many marine organisms have complex life cycles consisting of a pelagic - and a benthic stage (Marcus & Boero 1998). In such cases, the benthic life cycle stage may buffer population reductions during poor environmental conditions and provide the key to understanding fluctuations in the

abundance of the pelagic stage (medusae). Therefore, a knowledge of the linkages between benthic and pelagic environments, combined with the interdependence between life histories, life cycle and population dynamics are essential in understanding population fluctuations (short and long term), population blooms and the importance of a species in the ecosystem (Giangrande et al. 1994; Marcus & Boero 1998; Boero & Bonsdorff 2007).

The majority of scyphozoans exhibit metagenetic life cycles (Hamner & Dawson 2009): they have an asexual, sessile polyp phase, which alternates with a dispersive, sexually reproducing pelagic medusa (Arai 1997). The polyp is the benthic, solitary or colonial, cylindrical-shaped form that is crowned by a ring of tentacles around the mouth opening. The other form, the medusa, is the movable, bell-shaped organism that actively swims by means of rhythmic subumbrellar muscle contraction (Arai 1997). Eggs and sperm are produced by medusae, which develop after fertilisation into motile planulae (on completion of embryogenesis) that characteristically settle on hard substrata to metamorphose into sessile polyps (Lucas et al. 2012 and references therein). These benthic polyps can reproduce through various modes of asexual reproduction (e.g. Schiariti et al. 2008; Adler & Jarms 2009; Arai 2009a; Han & Uye 2010; Fuentes et al. 2011). The transition from the sessile polyp benthic stage to the dispersive medusa pelagic stage transpires through the process of strobilation (Arai 1997). This specific asexual mode describes the entire developmental process of the polyp that gives rise to ephyrae (Arai 1997). An ephyra is the most basic pelagic and immature stage of the scyphomedusa, which is sequentially: released in the water column (from the parental polyp), grows in size, takes on the morphology of the adult medusa and initiates sexual reproduction (Arai 1997). After the release of the last ephyra, the strobila reverts to a polyp, which, under the appropriate conditions, can again propagate through various modes of asexual reproduction (Arai 1997). Strobilation may result in the release of a single ephyra (monodisc) or multiple ephyrae (polydisc) per polyp (Arai 1997).

For a scyphozoan to be prone in forming high numerical populations that potentially could result in ‘blooms’ or ‘outbreaks’ during suitable environmental conditions, it requires life-history, morphological and behavioural traits that facilitate the rapid production of vast numbers of individuals, with the assumption of high survivorship through to the adult (asexual and sexual reproductive) phase (Dawson & Hamner 2009; Lucas & Dawson 2014). Accordingly, a number of life history traits have been identified

although this may not be applicable to all blooming species (Dawson & Hamner 2009; Lucas & Dawson 2014 and references within; Schiariti et al. 2014, 2015). 1) Asexual reproduction is responsible for generating the size of the source (polyps) and supply (ephyrae) of new recruits to the medusa population. 2) Podocyst formation to ensure population survival during harsh environmental conditions while 3) polydisc strobilation and 4) multi-mode asexual propagation are also associated with “blooming” species. 5) Large sized medusae, with high predation rates, that ensures rapid growth (increase in population biomass) with associated high fecundity, 6) short generation times and life spans are also considered as “blooming” characteristics. The above listed life history traits enable jellyfish populations to respond quickly to highly variable environments and to exploit temporarily abundant resources (Boero et al. 2008; Dawson & Hamner 2009; Richardson et al. 2009; Lucas et al. 2012). This opportunistic habit may sometimes lead to a dramatic localized population increase termed a “true” bloom (Graham et al. 2001). This response is reflected in the pulsed nature of their populations, which makes the dynamics of their populations a chaotic phenomenon (Boero et al. 2008). In order to deal with seasonal resource availability, populations can alternate between being extremely abundant in some years, common in others and even rare or absent in yet others only to reappear in numbers again at some time subsequently (Boero et al. 2008). These population dynamics can be achieved, from a reproduction viewpoint, by way of two strategies: qualitative adjustments to the life cycle or quantitative life history adjustments. In the case of life cycle adjustments, a species maintains its presence locally at different times during its different life cycle stages. In the case of life history adjustments, a species may undergo alternate and seasonal peaks of rarity and abundance in its adult population (Boero et al. 2008). Scyphozoa are capable of adopting both strategies, depending on whether they are holoplanktonic (life history) or meroplanktonic with a benthic stage (life cycle) (Boero et al. 2008). These two strategies are not mutually exclusive since they denote the extremes of a continuum. Species continuance is achieved by alterations in either the life cycle (benefiting the most appropriate developmental stage: resting stage, larva, juvenile or adult) or the life history (with shifts in population sizes, distribution ranges and life history traits) or both (Boero et al. 2008).

1.3 Factors influencing the abundance of medusae (blooms) – spatial and temporal (natural perspective)

In order to understand the factors that influence the abundance of medusae, the term “jellyfish bloom” needs to be defined. A “true bloom” is the outcome of population increases (production and growth of new medusae) resulting in part from seasonal life cycles, while an “apparent bloom” is the outcome of the redistribution of an existing medusa population (Graham et al. 2001; Hamner & Dawson 2009; Lucas & Dawson 2014). In an “apparent bloom”, individuals in a population will often originate (e.g. via migration, emigration; Lucas & Dawson 2014) from a different place – a place that itself may display a “true bloom”. As noted previously, jellyfish blooms are natural features of healthy ecosystems and reflect seasonal, climatic and oceanographic forcing (Arai 1997; Graham et al. 2001; Mills 2001; Purcell 2005, 2012) that interact with jellyfish biology, behaviour and life cycles (Dawson et al. 2015; Lucas & Dawson 2014). However, the ability for jellyfish to bloom seems to be predetermined by the species, yet only a subset of jellyfish taxa have the set of traits that predispose them to appear often at vast densities (Lucas & Dawson 2014; Schiariti et al. 2014, 2015).

Lucas & Dawson (2014) illustrated (fig. 2.4(b); p. 20) the sequence whereby life history leads to population biomass changes over time which translates the dynamics of a “true” bloom into four stages (I–IV) for scyphozoans having a metagenetic life cycle, as following: Stage I represents a vast increase in the abundance (frequency) of ephyrae, yet a nominal increase in population biomass, as a consequence of strobilation. Stage II represents a rapid increase in the biomass of medusae due to growth surpassing the numerical increase of medusae (stemming from Stage I) whereas strobilation recedes. However, growth is so rapid that it overwhelms the loss of mass due to mortality or advection (emigration) of ephyrae and medusae. Stage III corresponds to the onset of the demise of the bloom and, although still spectacular, the biomass starts to decrease/disperse due to declining growth rates of large medusae that cannot counteract the numerical losses anymore caused by mortality and advection (or diffusion). Stage IV is typified by the medusa population becoming inconspicuous, absent and inconsequential resulting from degrowth, senescence and advection. Hence, Stages I and II are seen as the ‘critical stages’ required for bloom formation. The primary stage of a ‘true bloom’ is Stage II since rapid medusae growth can escalate their biomass by many orders of magnitude more than can strobilation. Stage III may

possibly be vital in maintaining blooms as a result of oceanographic factors (giving rise to an “apparent bloom”) and the biological responses of large natatory medusae. The collapse of a bloom is also associated with senescence after spawning, parasite infestations, food limitation, disease, low salinity, extreme water temperatures, predation and intertidal strandings (see Pitt et al. 2014).

The transition from one life form to another is triggered by biotic and abiotic signals (see Sections 1.4 and 1.5), hence to understand the mechanisms underlying jellyfish blooms, it is necessary to return to the basis – the jellyfish life cycle. The local recruitment of jellyfish depends on the success of each part of their life cycle and, as a result, greatly determines adult (reproductive) abundance (Colin & Kremer 2002; Lucas & Dawson 2014). Basically, recruitment success encompass the ability of the planulae to settle and metamorphose; the polyps to survive, mortality and reproduce; ephyrae to feed survive and grow; and adult medusae to feed, grow, survive and produce gametes that can be fertilized. Furthermore, the success of each individual stage is reliant on its interaction with biotic (food availability, predators, competitors, parasites) and abiotic (suitable substrate availability, dissolved oxygen content, temperature, tides, currents, winds) factors (Kikinger 1992; Kingsford et al. 2000; Lucas et al. 2012; Lucas & Dawson 2014).

The causes (and consequences) of blooms are the outcomes of interactions between a suite of abiotic and biotic factors, which take place within populations over a specific time line and route (or in a single location) (Lucas & Dawson 2014 and references within). The relative intensities of, and interactions between, these factors varies over time and space (Lucas & Dawson 2014). There are no individual causes (or consequences) of mass incidences, blooms or ‘outbreaks’ of jellyfish (Lucas & Dawson 2014). To discern which causes are critical in each case, it is required that the techniques of population biology and population genetics be combined and integrated (Lucas & Dawson 2014). In so doing, this would allow research to encompass multiple populations over a diversity of species through a range of localities, repetitively over years, permitting a broad view of the relative frequencies, biological - and environmental causes of mass occurrences and the differentiation between accumulations, aggregations, blooms, swarms and outbreaks (Lucas & Dawson 2014).

1.4 Polyps and factors affecting polyps

Generally, in coastal jellyfish taxa that feature a bipartite life cycle, embryos develop from fertilised eggs into free-swimming planula larvae. These planulae attach to hard, shaded substrata and metamorphose into sessile polyps (Boero et al. 2008). Ultimately, the polyps develop into juvenile medusae (as Cubozoa), or they strobilate (asexual segmentation) to liberate ephyrae (as Syphozoa) (Arai 1997). The benthic polyp stage is responsible for the production of the seeding stock of medusae by asexual reproduction (Colin & Kremer 2002). Although, metagenesis and strobilation are not preconditions for jellyfish characterised as blooming taxa (such as *Pelagia noctiluca*; Dawson & Hamner 2009), asexual reproduction is an "efficient, effective and inexpensive" (Crow 1994) process of reproduction which facilitates blooming by multiplying the source (polyps) and supply (ephyrae) of new recruits to the medusa population (Lucas & Dawson 2014). Polyps are the long living part of the population that can stay possibly alive for decades or centuries (Da Silveira et al. 2002; Jarms 2010): they have remarkable regeneration capabilities (Kakinuma 1975), they can survive starvation for up to a month (Hiromi et al. 1995) and produce many generations of juvenile medusae (Lucas et al. 2012). In order to determine the local distribution and abundance of medusa, knowledge of the distribution, abundance and survival of the polyp stage is crucial. Boero et al. (2016, p. 218) summarized this concept with their statement that "the consistency of the polyp reservoir, in fact, is the premise for the onset of the blooms for species with a benthic stage".

Jellyfish polyps can be found on natural (e.g. algae, mussel shells, barnacles, polychaete tubes, ascidians, hydroids, stones) and artificial substrata (various underwater structures like pier pilings, floating docks, etc.) (Da Silveira et al. 2002; Miyake et al. 2004; Holst & Jarms 2007; Hoover & Purcell 2009; Han & Uye 2010; Di Camillo et al. 2010; Duarte et al. 2013). Studies have shown that while the planulae of six scyphozoan taxa preferred to settle on artificial substrata (Holst & Jarms 2007; Hoover & Purcell 2009), others either exhibited no preference, or selected natural substrata for settlement (Astorga et al. 2012; Duarte et al. 2013). Polyps are typically located in shallow (0 to 15 m) coastal areas but can occur to depths of 120 m (Hernroth & Gröndahl 1983; Miyake et al. 2002; Toyokawa 2011). A key barrier that challenges the identification of the underlying causes of jellyfish blooms is the difficulty of pinpointing the habitat of the polyps owing to their cryptic nature, small size and fragility (Mills 2001; Boero et al. 2008).

Temporal (and spatial) patterns in polyp population abundance is maintained by the offset between colony growth (recruitment of newly settled planulae and asexual proliferation) and mortality (predation, physiological stress, inter- and interspecific completion for space and food); all influenced by phylogenetics, density-dependent factors and environmental conditions (Lucas et al. 2012 and references within; Schiariti et al. 2014, 2015). In response to certain natural and artificial environmental triggers (Thiel 1962; Sugiura 1964; Spangenberg 1968; Cargo & Shultz 1966; Purcell et al. 1999b; Lucas 2001; Colin & Kremer 2002; Willcox et al. 2008 Arai 2009a; Lucas et al. 2012; Sukhoputova & Kraus 2017), the benthic polyp can propagate through various modes of asexual reproduction (e.g. Schiariti et al. 2008; Adler & Jarms 2009; Arai 2009a; Han & Uye 2010; Fuentes et al. 2011) which depends on its phylogenetics (Schiariti et al. 2014). In addition to strobilation, creating podocysts and stolon budding; there are several other documented asexual processes such as *Sanderia*-type budding, developing stolons, bud like particles, pedal laceration, tentacles tips/pieces, longitudinal fission, gastric constrictions, forming planuloid buds or cysts (Berrill 1949; Schiariti et al. 2008; Adler & Jarms 2009; Arai 2009a; Han & Uye 2010; Fuentes et al. 2011; Schiariti et al. 2014). It is proposed that the quantity of food available may directly influence the allocation of energy to the different reproductive strategies of the polyp. During periods of high food availability, both budding and stolonation increase, whilst during periods of reduced food availability, energy allocation shifts from budding to strobilation: during periods of extreme food shortage, animals survive by forming podocysts (Arai 2009a; Lucas et al. 2012; Lucas & Dawson 2014).

Water temperature, nutritional status, light intensity, day length, lunar cycles, salinity, the presence of zooxanthellae, polyp density and various chemicals, or interactions of multiple factors (e.g. temperature and salinity; upwelling) have been found to affect the onset and extent of strobilation in Scyphozoa, as well as medusa budding in Hydrozoa (Elmhirts 1925, Thiel 1962; Boero 1984; Gröndahl & Hernroth 1987; Carré & Carré 1990; Brewer & Feingold 1991; Arai 1992a; Byrne 1995; Purcell et al. 1999b; Bullard & Myers 2000; Lucas 2001; Colin & Kremer 2002; Willcox et al. 2008; Lucas et al. 2012; Baumsteiger et al. 2017; Sukhoputova & Kraus 2017). These factors are discussed in full detail in Chapter 2. Depending on the species, region and environmental conditions, polyps can strobilate once or numerous times during the year/season (Lucas & Dawson 2014). A single large, well-fed polyp of *Aurelia labiata* (a prolific strobilator) may produce up to 42 ephyrae per strobilation cycle (Purcell 2007), whereas

Lychnorhiza lucerna (a low strobilator) may yield by repeated strobilation cycles 50–60 ephyrae over a four-month period (Schiariti et al. 2008). The number of ephyrae produced by multi-disc strobilating polyps depends on factors such as species, age, size and their nutritional status (Spangenberg 1968; Holst 2008; Lucas et al. 2012; Lucas & Dawson 2014).

A state of dormancy is also associated with some scyphistomae through the formation of podocysts (Arai 1997, 2009a). Podocysts are dormant cysts, armoured with chitin, that develop beneath the pedal discs of scyphozoan polyps and possess organic-rich reserves (Arai 1997, 2009a; Thein et al. 2012). During excystment, a very small four-tentacled (*Nemopilema nomurai*, *Rhopilema esculenta*, *Rhizostoma octopus, Rhizostoma pulmo*, *Aurelia aurita* and *Chrysaora quinquecirrha*) or two-tentacled (*Chrysaora fuscescens*) polyp is typically produced from the internal tissue that exits the podocysts through its degraded top (see Arai 2009a). Such polyps grow into fully developed scyphistomae capable of asexual propagation through the various modes.

These dormant cysts provide a mechanism for polyp populations to increase their number and survive through adverse conditions such as low food availability, hypoxia, sediment burial and extreme temperature (Arai 2009a; Lucas et al. 2012; Lucas & Dawson 2014). They also provide protection against predators (Arai 1997, 2009); act as temporal seeding outposts (Thein et al. 2012) and can stay potentially viable for years (3.2 years for *Aurelia aurita* s.l., Thein et al. 2012). Temperature, salinity and food availability are the environmental factors indicated to influence podocyst production rates, however the mixed literature findings suggest that species- or site-specific differences may also play an important role (see Lucas et al. 2012; Hubot et al. 2017). Although Jiang et al. (1993) agreed that podocysts are capable of resisting adverse conditions, these authors indicated that adverse conditions are not essential for podocyst formation, and indeed podocysts appear to be a general mode of asexual propagation for *Rhopilema esculenta*. This contrasts with Thien et al. (2012), who indicated that podocyst formation facilitates the maintenance of the *Aurelia* spp. population against adverse environmental conditions and predator attacks since starvation was the primary cause of polyp encystment, while rising temperatures hastened podocyst production rates. This finding is corroborated for both *Aurelia coerulea* and *Aurelia relicta,* which did not exhibit significant difference in podocyst production rates under different experimental feeding regimes (9.3, 18.6, 27.9 µg C ind^{-1} $week^{-1}$) (Hubot et al. 2017). Han & Uye (2010)

recorded the production of podocysts by *Aurelia* sp. polyps kept under low food rations (1.7 and 3.3 µg C $polyp^{-1}$ day^{-1}) and high temperature (≥26°C), however all pododcysts remained encysted during their experiment. Although podocysts are regularly regarded as a mode for surviving periods of low food conditions, their production rates in fact can elevate at higher food levels for *Chrysaora quinquecirrha* and *Rhopilema esculenta* (Arai 2009a; Lucas et al. 2012). Although, inter-specific differences between podocyst production rates of *Aurelia coerulea* and *Aurelia relicta* were significant; the podocyst production rates per *A. coerulea* polyp were affected by temperature, salinity and the interaction between temperature and salinity, whereas in the case of *A. relicta,* rates were only affected by temperature (Hubot et al. 2017). Podocysts of both *Chrysaora quinquecirrha* and *Aurelia aurita* exhibited resilience towards predators such as nudibranchs *Coryphella verrucosa* and *Cratena* sp. (Cargo & Schultz 1967; Hernroth & Gröndahl 1985b). A single polyp of *Chrysaora quinquecirrha* yielded 52 podocysts and six polyps in <3 months (Cargo & Schultz 1966) while *Chrysaora fuscescens* yielded 53 podocysts and 51 polyps in 8 months (Widmer 2008a). Podocyst formation can thus act as a mechanism to increase the population numerically. Podocysts are associated with bloom-forming species and may therefore play a significant role in the capacity of several species of scyphozoans to establish, spread out and bloom successfully (Arai 2009a; Thein et al. 2012; Dawson & Hamner 2009).

A new developmental mode equated “as an additional strategy to the benthic podocyst as a stress-survival mechanism” was described for *Aurelia relicta* (Hubot et al. 2017). This species is endemic in the Mljet lake (living usually below isotherms up to 19–20 °C) with a very narrow ecological valence: cold, marine environmental optimal preferences with salinity 37 ppt and temperature ranges 14–19℃ (Hubot et al. 2017). By subjecting *A. relicta* polyps to a minor increase in temperature (21 °C), the sessile polyp regressed into a dispersive, temporarily unattached and tentacle-less, non-feeding propagule, followed by the restructure of a tentacled feeding polyp.stage after a dormant period (Hubot et al. 2017). Food availability also triggers the onset of this resting mode since a previously well-fed polyp is implied to have an improved ability to activate the dormant cycle during warm temperature (21 °C) (Hubot et al. 2017). As a result, zooplankton prey might boost the ability of polyps to go through a dormant state and thus enhance their capacity to endure subsequent, extended stressful conditions (Hubot et al. 2017). The reversible transformation stage could not be associated with an increase in the total number of individual

polyps, but only to the survival of polyps infrequently subjected to poor environmental conditions (Hubot et al. 2017). This free-drifting stage might facilitate their escape from unfavourable environmental conditions (unusual warmer temperatures) by either sinking or drifting to more appropriate (e.g. colder) depths or sites (Hubot et al. 2017).

Budding rates are positively correlated with temperature and food availability, both independently and interactively (Hernroth & Gröndahl 1985b; Keen & Gong 1989; Han & Uye 2010; Purcell et al. 2012; see Lucas & Dawson 2014; Ziegler & Gibbons 2018), though the actual temperature required for peak budding rates is recognised to be species- and site-specific. This must reflect eco-physiological tolerances and biogeographic distribution of populations (Lucas et al. 2012; Lucas & Dawson 2014; Hubot et al. 2017), which might indicate local adaptation. An inverse relationship between strobilation and polyp budding (both asexual reproduction modes) is clearly proven for the polyp populations of *Aurelia aurita* in the field off northern Adriatic Sea (Ancona, Italy) (Di Camillo et al. 2010). These two modes of asexual reproduction occurred at different periods of their annual cycle due to their opposite eco-physiological reliance on water temperatures. Laboratory investigations on *Aurelia* spp. indicated that individual polyps can yield 0.03–1.15 buds day^{-1} at temperatures ranging from 5–30 °C (see Purcell et al. 2012; Lucas & Dawson 2014). Budding rate records for other Discomedusa species are limited, however values are usually less than 0.25 (often <0.10) buds polyp^{-1} day^{-1} (see Purcell et al. 2012; Lucas & Dawson 2014). Han & Uye (2010) noted that the maximum budding rates of *Aurelia aurita* occurred (40.3 buds over a 35-day experiment) at the high feed ration and temperature (13.3 µg C polyp^{-1} day^{-1} and 26 °C) whereas the lowest budding rates (3.0 buds) occurred at the low feed ration and temperature (1.7 µg C polyp^{-1} day^{-1} and 18 °C), with numbers growing linearly over the duration of the experiment. Literature based maximum asexual budding rates relate towards the output of a single new polyp every 1–3 days, emphasising the ability of the polyp population (source) to develop rapidly (Lucas & Dawson 2014; Ziegler & Gibbons 2018). Thus far the limited published abundances of natural polyp populations show great variation, ranging 0.0005–88 cm^{-2} for *Aurelia* spp. (Miyake et al. 2002; Ishii & Katsukoshi 2010). Besides the influence of abiotic variables, the occurrence of conspecifics and other epibiota may influence budding rates and colony growth (Willcox et al. 2008), considering that dense aggregations of polyps have been found to impede budding (Chiba 1969). Experimental results indicated that population growth of *Aurelia*

*aur*ita s.l. within each polyp “colony” may be regulated around a carrying capacity by means of: (1) diminishing the polyp reproduction rates, (2) triggering the production of motile bud-like tissue particles and (3) causing the detachment of developed polyps (Schiariti et al. 2015). Hence, at very high densities polyps might shift their asexual reproductive mode to facilitate emigration. As such, the negative effects of intraspecific competition for space and food are reduced and new substrates can potentially be colonized, which would lead to the spatial expansion of polyp colonies (Schiariti et al. 2015).

The effect of different food rations (F1, F2, F3 = [9.3, 18.6, 27.9 respectively] µg C ind^{-1} $week^{-1}$) at different temperatures (14 °C, 21 °C) on the budding modes of both *Aurelia relicta* and *Aurelia coerulea*, indicated that the lowest food regime favoured direct budding over stolon budding (Hubot et al. 2017). Direct budding seems to be constantly supported at 14 °C whereas at 21 °C it is only supported at the lowest feed ration (F1). Stolon budding is supported at 21°C under high feed ration (F3). As well, the polyps of both *Aurelia relicta* and *Aurelia coerulea* allocated more energy towards stolon bud production at warm temperatures (21 °C) and intermediate food availability (two feeding sessions per week, 18.6 µg C ind^{-1} $week^{-1}$) than direct bud production. The *Aurelia relicta* polyp group seemed to react stronger to the change in budding mode. This is in contrast with the findings of Han & Uye (2010) on *Aurelia* sp. polyps, from Japan, cultured at similar or higher feed rations (11.9, 23.1, 46.2, 70 and 93.1 µg C ind^{-1} $week^{-1}$) and temperature (18, 22, 26 and 28 °C). Their experiments revealed that direct bud production was the main mode of asexual reproduction in every treatment (94% of total buds), while stolon bud production accounted for only 5%. Both budding modes (stolon buds and direct buds) exhibited increased production rates of new polyp recruits with raising food rations and temperature.

1.5 Medusae and factors affecting medusa

The medusa form in jellyfish is generally responsible for sexual reproduction, creating genetic variability in the population that allows for evolutionary adaptation to the environment. It also allows for geographical range expansion of the benthic polyp, via planulae release (Giangrande et al. 1994; Arai 1997; Colin & Kremer 2002; Ramirez Llodra 2002; Dawson 2005; Dawson & Hamner 2009). Medusae are the short living pelagic phase that usually live for <1 year in the field (Lucas & Dawson 2014). They have remarkable growth rates (Lucas & Dawson 2014), high prey clearance rates (Acuña et al. 2011) and can

survive starvation by degrowth (Hamner & Jenssen 1974). Many medusae mature precociously and are highly fecund (Lucas & Dawson 2014).

A very large number of mechanisms (individually or multiple) may have an effect throughout the various life cycle stages of jellyfish and as such drives medusa abundance – these are listed in Table 1.1, with some supporting references. As noted previously, medusa populations are dynamic, with periods/areas of high abundance interspersed with periods/areas of low abundance or absence (Mills 1981; Purcell 2005; Boero et al. 2008; Henschke et al. 2018; Schnedler-Meyer et al. 2018). This makes estimation of population size difficult (Kremer 1976; Kingsford et al. 2000). Variations in the abundance of scyphomedusae can occur on a variety of spatial/temporal scales ranging from hundreds of km or decades, to m and time of day (Mills 1981; Pitt & Kingsford 2000; 2003; Doyle et al. 2007b; Albert 2009; Brotz et al. 2012; Flynn et al. 2012; Suchman et al. 2012; Lucas & Dawson 2014; Dawson et al. 2015). It is very difficult to establish sampling methodologies in order to comprehend such variability (Kingsford 1998; Aubert et al. 2018), and perhaps as a result of this, most literature refers to relative changes in abundance within a given area instead of measurements of total population abundance (Kingsford et al. 2000).

The body of a medusa consists largely of a mass of transparent jelly-like matter within the mesoglea, which provides structural support to the animal and which has elastic properties allowing it to function as a hydrostatic skeleton (Ruppert et al. 2004). The mesoglea is sandwiched between two epithelial cell layers (the ectoderm and endoderm tissue) lining the external (epidermis) and internal body (gastrodermis). It has a very low metabolic demand due to being acellular (hydrozoans) or containing only a few cells (scyphozoans) (Pitt et al. 2013). Medusae are characterised by a very high water (~96%) and low carbon content (~0.5%) (Arai 1997; Lucas et al. 2011). Pitt et al. (2013) showed that the respiration rates of medusae (cnidarian medusae and ctenophores) are 28 times lower than that of non-gelatinous epipelagic taxa of comparable ESD (measured as equivalent spherical diameter). Interestingly, when medusa ESD is adjusted for carbon content, the differences in respiration rates between gelatinous and no-gelatinous epipelagos are insignificant (Pitt et al. 2013). The excretion rates of medusae are 257 times lower than those of non-gelatinous epipelagic taxa of equivalent ESD, and 10 times lower when ESD is adjusted for carbon content (Pitt et al. 2013). As a result, medusae do not require considerable amounts

of energy and carbon for the construction and up-keep of their skeletons and metabolic functioning (Lucas & Dawson 2014). Since they use low-carbon structures that require congruently low-energy input, available carbon and energy resources can be routed mainly towards vital tissue layers responsible for muscle movement, prey capture and digestion, as well as reproduction (Lucas & Dawson 2014).

Medusae are 3.2 times bigger in ESD than non-gelatinous epipelagic taxa of equivalent carbon content, and 2.5 times larger than those of equivalent nitrogen content (Pitt et al. 2013). Specific growth rates (K, day^{-1}) of medusae (0.05–0.24 d^{-1}) and ctenophores (0.09–0.47 d^{-1}) are significantly higher (3.5 times) than those of non-gelatinous epipelagic taxa of comparable ESD, and 2.2 times higher when ESD is adjusted for carbon content (Pitt et al. 2013). A comparison of growth curves for populations of *Aurelia aurita* showed that sigmoid curves are typical when all size classes, including ephyrae, are taken into account (Arai 1997). Young scyphozoan medusae grow almost exponentially, while growth rates of large medusae typically slow down to reach an asymptote, and they can in some instances become negative (Arai 1997). A number of factors (such as water temperature, food quality/quantity) are known to affect the growth rates of jellyfish (see Chapter 3; Garcia 1990; Olesen et al. 1994; Hansson 1997b; Widmer 2005), and periods of positive growth have been ascribed to the seasonal influences of food availability and temperature (Malej & Malej 1992). During favourable periods of food and water temperature, the low-carbon mesoglea enables the medusa to grow very rapidly causing. This leads to an increase in the external bell area and hence the feeding capacity of the individual, which may enable the bell to reach an exceptional size (Arai 1997; Dawson & Hamner 2009; Acuña et al. 2011; Rosa et al. 2013; Lucas & Dawson 2014). At maturation, these enhanced “capabilities” would allow individuals to redirect energy towards gamete production, allowing high numbers of eggs (and more larvae) to be produced (Lucas 1996), potentially leading to elevated larval recruitment (Lucas & Lawes 1998; Lucas 2001; but see Gibbons et al. 2016). Simultaneously, high levels of food in the water column can also influence the quantity of food arriving at the benthos (Boero et al. 1996; Kahn et al. 2012; Perea-Blázquez et al. 2012), which in turn can stimulate an increase in polyp budding rates (Section 1.4) (Ma & Purcell 2005; Hoover & Purcell 2009; Han & Uye 2010; Webster & Lucas 2012). This, in turn, has the potential to lead to high numbers of ephyrae, compared to years linked with low zooplankton biomass.

In essence, a “potential bloom” depends on the production and survival of large number of recruits (Dawson & Hamner 2009; Lilley et al. 2014a), which may develop into a “true bloom” (Section 1.3) following the rapid growth of individual medusae (Lucas & Dawson 2014). Thus, food availability is essential for somatic growth in order for the population biomass to increase much faster than increasing small sized juveniles numerically (Alldredge 1984; Arai 1997).

Field studies have revealed a reduction in the growth of *Aurelia aurita* at the time of reproduction, possibly due to the allocation of energy towards sexual reproduction (Hansson 1997b; Lucas 1996; Goldstein & Riisgård 2016). Unfavourable food conditions in the field can affect medusa growth: starvation leading to degrowth, while the return of favourable conditions results in regrowth (Hamner & Jenssen 1974; Fu et al. 2014; Lilley et al. 2014b, Goldstein & Riisgård 2016). The gonads of *Aurelia aurita* may be resorbed during degrowth and the bell reduced in size (Arai 1997). *Pelagia noctiluca,* when starved in the laboratory, has been shown to shrink in body size but continue to release eggs quasi-daily over a 28-day period (Lilley et al. 2014b). In the case of *Pelagia noctiluca* too, larger individuals have been shown to invest more heavily in reproduction, but have equivalently lower metabolic rates than smaller medusae at the same temperature (Lilley et al. 2014b). A laboratory study has shown that *Aurelia aurita* (<90 mm bell diameter) increase in mass twice as fast at 20°C than at 5°C, whereas intermediate specific growth rates are obtained at 10°C (Hansson 1997b). Food limitation is associated with spatial differences in size and growth of the *Aurelia aurita* population in Kertinge Nor, Denmark (Olesen et al. 1994). The slow growth rates of the *Phyllorhiza punctata* in the Laguna Joyuda, Puerto Rico, are linked with the summer season, because of food limitation (Garcia 1990).

Information regarding the timing of reproduction (days to seasons), reproductive strategy, fecundity, age/size at maturity and temporal-spatial variation in the reproductive characteristics of medusae is crucial to understand and predict the recruitment patterns of benthic polyps. The majority of scyphomedusae are dioecious (Lucas & Dawson 2014). The exception to the latter being the protandric *Chrysaora hysoscella* (Berrill 1949). Fertilisation in medusae can take place within the female gonad, female gastrovascular cavity or outside the medusa in the open seawater (Aria 1997). Some female pelagic Cnidaria are brooders (such as species of *Aurelia*, *Chrysaora hysoscella*, *Rhopilema verrilli*, *Cotylorhiza tuberculata*), and they retain their embryos within specialised brooding structures, liberating

fully developed planulae. Others are non-brooding (such as *Lychnorhiza lucerna*), and planula development occurs within the water column (Berrill 1949; Kikinger 1992; Arai 1997; Schiariti et al. 2012). There are some detailed descriptions of the anatomy of the gonads and gametogenesis (mainly of oogenesis) of Schypozoa (see Chapter 4; Eckelbarger & Larson 1988, 1992; Rottini-Sandrini & Avian 1991; Kikinger 1992; Pitt & Kingsford 2000; Lucas & Reed 2010; Ikeda et al. 2011; Schiariti et al. 2012). Information from histological observations can allow the maturity status of each medusa to be categorized on the basis of its gametogenic composition (proportion of gametes at different stages of development) (see Chapter 4; Schiariti et al. 2012). Sexually mature medusae can be identified by the presence of fully developed gametes in their gonads or by the presence of spent spermatic follicles. Oocyte size is widely regarded as a good proxy for female maturity in medusae (Rottini-Sandrini & Avian 1991; Pitt & Kingsford 2000; Toyokawa et al. 2010). By plotting the oocyte size frequency distributions over time, the progressive development of successive oocyte crops can be determined, and the reproductive cycle elucidated (Milisenda et al. 2016).

Several vertebrate-type hormones have been identified in cnidarian tissues and links with sexual reproduction are suggested (Tarrant 2005). The findings of Tarrant et al. (2009) suggest that cnidarians, at least anthozoans, presently have the capability to metabolize and synthesize sex steroids. The chronological changes of a well-defined gametogenic cycle require coordination with other activities within the animal (Giese & Pearse 1974). It is crucial for marine invertebrates to reproduce at a time that would enhance the survival of their progeny, and therefore their reproduction needs to synchronize with those environmental conditions that will be most favorable to recruitment success. Controlling factors such as day-length, water temperature, aggregative behaviour of medusae and mechanical damage to medusae have all been linked with gonad maturity, spawning and fertilisation of medusae (Rottini Sandrini & Avian 1991; Hamner et al. 1994; Lucas & Lawes 1998; Ohtsu et al. 2007; Tiemann et al. 2009; Ikeda et al. 2011; Liu et al. 2015).

Comparatively little is known about the life-history trade-offs in gelatinous zooplankton due to the difficulty in measuring their generation time, the absence of age-determining structures, the poor correlation between body size and age and size at maturity, and the variability in individual growth responses to changes in the food environment (growth, degrowth and regrowth: Lucas & Dawson 2014).

Although, several gelatinous species are characterised as being semelparous: to reproduce at a population-specific upper size limit and die shortly thereafter (Lucas & Dawson 2014), exceptions to the rule exist. Hamner & Jenssen (1974) reported that populations of *Aurelia aurita* (which is also considered to be a semelparous, annual spawner) in Tomales Bay, California, did not all die off after reproduction during the summer of 1970, but continued to grow and reproduce for another full season in the field. Some laboratory studies have also indicated that tissue deterioration after spawning is not mandatory for *Aurelia aurita* during favorable food conditions (Hamner & Jenssen 1974; Goldstein & Riisgård 2016), while aquarium-reared specimens are reported to have lifespans of 2-4 years (Raskoff et al. 2003). Milisenda et al. (2016) reasoned that *Pelagia noctiluca* favours an iteroparous reproduction strategy on the basis that all female animals possessed oocytes at various maturation stages throughout the year. Similar observations have been made for *Periphylla periphylla* (Jarms et al. 1999), *Catostylus mosaicus* (Pitt & Kingford 2000) and *Lychnorhiza lucerna* (Schiariti et al. 2012). Several species of medusa can reach maturity over an exceptionally short period ~2–7 months, with generation times and life spans of <1 year (see Lucas & Dawson 2014). Kingsford et al. (2000) indicated that the gender of *Catostylus mosaicus* can be identified at 10–160 mm bell diameter, indicating that age at first maturity is ~2 months of age (the time lapse since strobilation), while largest adults are generally 210–250 mm in bell diameter.

Egg size is a life history characteristic that reflects maternal energy investment, and is essentially determined by a trade-off between quantity and quality of offspring (Olive 1985; Moran & McAlister 2009). Generally, life-history models predict that females with a finite amount of resources available for reproduction will yield numerous, small sized eggs during favourable environmental conditions and lesser numbers of larger sized eggs during unfavourable conditions (Lucas & Lawes 1998; Olive 1985; Roff 1992).

Egg production varies greatly between taxa, medusa size, food availability and temperature (Larson 1968; Arai 1997; Lucas & Lawes 1998; Milisenda et al. 2016). *Periphylla periphylla* from the Gulf of Mexico and Cape Hatteras presented <22 oocytes per gonad (Lucas & Reed 2010). *Rhopilema esculentum* medusae have a spawning period of three months and the number of eggs increases with size from ~220 x 10^4 eggs at 23-cm bell diameter to ~ 6700 x 10^4 at 53-cm bell diameter, off Hangzhou Wan Bay (Huang et al. 1985). In the Strait of Messina (South Thyrrenian Sea), female *Pelagia noctiluca*

produce a large number of mature small-sized eggs (diameter <200 mm) during periods of high food availability, but fewer, larger sized eggs (diameter >200 mm) during low prey availability (Milisenda et al. 2016). Severely food-limited *Aurelia aurita* in the Horsea Lake showed a 30-fold numerical reduction in planula larvae than medusae of comparable size in Southampton Water (Lucas & Lawes 1998). During a 28-day starvation experiment (Lilley et al. 2014b), *Pelagia noctiluca* kept on releasing eggs on a quasi-daily basis despite shrinking in size and losing up to 85% of its mass (6.6–7.1% loss day^{-1}). These starved medusae had egg production rates proportional to their sizes (mean 759 eggs day^{-1} at 6 cm bell diameter), with up to 19 526 eggs released in a single spawning, by this means reflected their huge capacity for population growth despite undergoing starvation (Lilley et al. 2014b).

1.6 Jellyfish within marine ecosystems and functioning

Marine ecosystems are maintained by the energy movement from primary producers through intermediate consumers to top predators (including humans) and pathogens, and then returned by way of microbial pathways (Doney et al. 2012). Consequently, marine communities are biological networks in which the “success” of a taxon is connected directly or indirectly by ways of several biological interactions (e.g. predator-prey relationships, competition, symbionts and regulators) to the performance of other species in the community. The collective effect of these interactions signifies ecosystem functioning (such as nutrient cycling, primary - and secondary productivity) by which ocean and coastal ecosystems offer a wealth of free natural benefits on which the human society relies (Doney et al. 2012). Stable isotope analysis has emerged as one of the key tools for exploring feeding ecology and energy transfer in marine environments, and results feed into a variety of analytical models. These may be simple, qualitative inferences based on the isotopic niche, to Bayesian mixing models that can be utilised to portray food-web structure at multiple hierarchical levels (see Chapter 5; Fukuda & Naganuma 2001; Hedd & Montevecchi 2006; Hill et al. 2006; Purcell 2009).

Until recently, jellyfish were considered as trophic dead ends (Sommer et al. 2002; Heymans et al 2004; Bakun & Weeks 2006; Pauly et al. 2009; Hays et al. 2018), due to their low nutritional value (Doyle et al. 2007a). It is frequently assumed that they die, sink and decompose and energy transfer takes place at the level of detritus (Heymans et al. 2004). However, jellyfish are important predators in pelagic marine

systems and act as a food source (occasionally or predominately) for a wide range of marine predators such as fish, birds, turtles, sharks and several invertebrates such as octopus, sea cucumbers, crabs, barnacles and amphipods (Pauly et al. 2009; Hays et al. 2018). In addition, they provide extensive beneficial ecosystem services in their own right as outlined by Doyle et al. (2014). Pauly et al. (2009) identified 124 fish species and 34 species of other marine animals that are feeding on jellyfish. Of which, 11 fish species and the leatherback turtle *Dermochelys coriacea* are jellyfish specialists (Houghton et al. 2006; Pauly et al. 2009). However, as technologies advance many more species are uncovered that routinely consume jellyfish (Hays et al. 2018).

The stomach content analysis of fishes from the southwest Atlantic Ocean (33°–55°S) revealed that a total of 39 species consumed gelatinous zooplankton; 23 of which were recognised as "jellivores" for the first time (Diaz-Briz et al. 2017). The study classified fish by the frequency with which they included jellyfish in their diet, as very frequent consumers (10 fish taxa, six of which were exclusive), frequent consumers (five fish taxa) and occasional consumers (26 fish taxa). More recently, through the use of both DNA barcoding and stable isotope analysis, studies have discovered that the ocean sunfish (*Mola mola*) has a far more cosmopolitan diet than previously believed (Syväranta et al. 2011; Harrod et al. 2013; Sousa et al. 2016), revealing an apparent diet switch in larger animals toward a more gelatinous nature (Nakamura & Sato 2014).

Laboratory experiments have proven that *Aurelia aurita* are a potential food source for the thread-sail filefish *Stephanolepis cirrhifer* when other prey was scarce (Miyajima et al. 2011). On the Patagonian Shelf, stomach content analysis (Arkhipkin & Laptikhovsky 2013) confirmed that *Patagonotothen ramsayi* can feed on a variety of gelatinous plankton scyphozoans (particularly *Chrysaora* sp. and *Desmonema* sp.). In the Strait of Messina, *Boops boops* forage throughout the year on *Pelagia noctiluca* while feeding almost twice as much during the summer than in winter on them (Milisenda et al. 2014). These fish illustrated selective predation towards medusa gender – female gonads have higher energy content than male gonads – and body part – gonads have overall six times higher energy content than the somatic tissues (Milisenda et al. 2014). Energy wise, medusa gonads are a highly nutritious food source that are mainly available to *B. boops* throughout spring and summer (Milisenda et al. 2014). During the rest of the year, when gonads are scarce, fish predation shifts towards a less selective foraging mode of consuming

the somatic jellyfish biomass. Hence, evidence is accumulating that jellyfish can serve as an important food source for commercial fish species (Cardona et al. 2012; Milisenda et al. 2014; Lamb et al. 2017).

An adult marine turtle *Dermochelys coriacea* is capable of gorging on ~261 jellyfish day^{-1} (or 330 kg jellyfish wet mass day^{-1}), which is the equivalent of 73% of its body mass day^{-1} (Heaslip et al. 2012). DNA metabarcoding of scat samples revealed that scyphozoans are a common part of the Adélie penguin's (*Pygoscelis adeliae*) diet in the East Antarctica (Jarman et al. 2013). McInnes et al. (2017) confirmed the presence of cnidarian DNA in black-browed (*Thalassarche melanophris*) and Campbell albatross (*Thalassarche impavida*) scats off the Falkland Islands, Macquarie Island (Australia), Campbell Island (New Zealand), Bird Island (South Georgia), Kerguelen Island, Albatross Islet (Chile) and Diego Ramírez (Chile). The overall scat samples showed a 42% sample frequency of scyphozoan prey, with some sites having up to 80% in their samples (McInnes et al. 2017). In the North Atlantic, *in situ* observations and stomach content analysis have proved that the giant deep sea octopus *Haliphron atlanticus* can prey on *Phacellophora* and other gelatinous organisms (Hoving & Haddock 2017). Since *H. atlanticus* is an important food item for sperm whales (*Physeter macrocephalus*), swordfish (*Xiphias gladius*) and blue sharks (*Prionace glauca*) (Clarke et al. 1996; Santos et al. 2002; Hernández-Aguilar et al. 2015), it is suggested that *H. atlanticus* may serve as a trophic link between gelatinous zooplankton and top predators (Hoving & Haddock 2017). In the York River, barnacles (*Balanus eburneus*) catch and consume newly strobilated *Chrysaora quinquecirrha* ephyrae (Cones & Haven 1969). Through experimentation, Wakabayashi et al. (2012) concluded that phyllosomata (at all developmental stages) of the slipper lobster *Ibacus novemdentatus* could exploit any species, any body part and any size (ephyra to adult medusa) of jellyfish as food. Recently, Ates (2017) reviewed (and provided an extensive list: p. 72) instances of predation and scavenging on jellyfish (pelagic Scyphozoa, Hydrozoa and Ctenophora) by benthic invertebrates, mostly of sea anemones, corals, decapod crabs and echinoderms.

Intra-guild predation (Polis et al. 1989) can severely impact jellyfish dynamics and plays an important role in the structuring of pelagic communities (Feigenbaum & Kelly 1984; Bologna et al. 2017), with more than a hundred recognised predatory interactions among jellyfish taxa (Purcell 1991a, 1991b; Arai 2005; Titelman et al. 2007; Hosia & Titelman 2010; Tilves et al. 2013; Bayha et al. 2012). Most jellyfish display broad diets which include gelatinous zooplankton as prey (reviews in Purcell 1991a,

1991b; Purcell & Arai 2001); though some are specialised. *Drymonema larsoni* is one of the most effective medusivores by its associated characteristics of a large size, extensive tentacle lengths and quantities, and vast size of the oral arm bulk (Bayha et al. 2012). As such *D. larsoni* can exert significant predation pressure on *Aurelia* sp populations, especially when their prey is aggregated, due to its extremely high contact rates with *Aurelia* sp., fast digestion rates, vast water volume searching capabilities, high prey capacity and high prey clearance rates (Bayha et al. 2012). It is suggested that *D. larsoni* predation could severely reduce large blooms of *Aurelia* sp. and relieve the predation pressure that *Aurelia* sp places on zooplankton populations in the northern Gulf of Mexico (Bayha et al. 2012). The culturing of the medusae of *Chrysaora*, *Cyanea* and *Phacellophora* (Morandini et al. 2004; Widmer 2006, 2008b) in aquariums have highlighted the need for them to feed on other jellyfish in order for their successful growth and development (Widmer 2008b). An experimental growth study showed that ephyrae of *Cyanea capillata* developed and flourished on a diet of ctenophore *Bolinopsis infundibulum*, but not on a predominantly crustacean diet (Båmstedt et al. 1997). This demonstrates that gelatinous prey may be vital for the development and functioning of other jellyfish taxa (Båmstedt et al. 1997).

In Saanich Inlet off British Columbia, *Phacellophora camtschatica* preys heavily on *Aurelia* sp. and exhibits both preying strategies of ambush and cruising to enhance their prey encountering chances (Strand & Hamner 1988). *Cyanea capillata* is known to prey on *Aurelia aurita,* and *Aequorea victoria* can prey on up to 10 different jellyfish taxa (Purcell 1991b). During summer in the Chesapeake Bay ecosystem, *Chrysaora quinquecirrha* wields a top-down control on populations of *Mnemiopsis leidyi,* by this means permit copepod populations to increase with a concomitant reduction in phytoplankton biomass (Feigenbaum & Kelly 1984). Javidpour et al. (2009) reported that 57–72% of prey items in the guts of *Mnemiopsis leidyi*, during late summer, consisted of *Aurelia aurita* planula larvae which can be consumed at rates of 621 individuals per ctenophore day^{-1} in the Kiel Fjord. In late summer, newly settled *Aurelia aurita* polyps feed on planulae larvae of *Cyanea capillata* (Gröndahl 1988a) in the Gullmar Fjord. This predation interaction could be of importance in regulating the abundance of *Cyanea capillata* polyps in the Gullmar Fjord (Grondahl 1988b).

Jellyfish are themselves predators of fish eggs and crustacean zooplankton, and are argued to maintain high levels of diversity by freeing resources for outcompeted species (Boero et al. 2008; Baxter

et al. 2012). Jellyfish are carnivorous and prey on an assortment of mesozooplankton, ichthyoplankton, microplankton, emergent zooplankton, detritus and dissolved organic matter (Purcell 1997; Costello & Colin 2002; Colin et al. 2005; Purcell 2009; Skikne et al. 2009). As predators, jellyfish have the potential to consume and deplete resources that are crucial and accessible to commercial fish stocks (Brodeur et al. 2002; Lynam et al. 2005b; Hong et al. 2008). Some scyphozoans can increase their ingestion rates during excessive prey concentrations suggesting that they can efficiently exploit dense prey patches, restricted to short time periods (Titelman & Hansson 2006). By removing a significant percentage of the standing stocks of key zooplankton, jellyfish may compete with fish taxa that feed preferentially on the same assemblages (Brodeur et al. 2008b, 2014; Suchman et al. 2008; Shoji et al. 2009). For example, *Chrysaora melanaster* in the Bering Sea and *Aurelia* sp. in Japan can consume up to 33% day^{-1} and 26% day^{-1}, respectively, of the zooplankton standing stock (Brodeur et al. 2002, Uye & Shimauchi 2005). Consequently, during blooms, jellyfish consumption rates can be so excessive that this predation pressure directly or indirectly influences the population size of other zooplankton as well as larval fish (Purcell 1989, 2003). As a result, jellyfish pose a serious threat to the recruitment success and spawning biomass of commercial fish stocks (Hansson et al. 2005; Robinson et al. 2014 and references within; Ruzicka et al. 2016; Zeman et al. 2016). The commercially valuable juvenile coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon have less food in their stomachs at locations with a high biomass of *Chrysaora fuscescens*, and jellyfish biomass is negatively correlated with the strength of adult coho and Chinook salmon returns off the Pacific Northwest coast (Ruzicka et al. 2016). This suggests that jellyfish may have negative impacts on key fish species (Ruzicka et al. 2016).

Through the processes of messy-feeding, egestion, excretion and mucus production; jellyfish make organic and inorganic (carbon, nitrogen and phosphorus) nutrients available to the ecosystem that in turn can fuel phyto- and bacterioplankton production (Pitt et al. 2009b; Condon et al. 2011). Excretion rates of inorganic nutrients are influenced by the feeding status of medusae, water temperature and prey availability (Pitt et al. 2009b). Jellyfish blooms in coastal waters can supply 8–11% of the phytoplankton nitrogen requirements via ammonium excretion (Pitt et al. 2009b). A mesocosm experiment in Smiths Lake, New South Wales (Australia), showed that the excretion of phosphorous by *Catostylus mosaicus* caused a 10-fold increase in biomass of the diatom *Chaetoceros* sp., and as such could promote primary

production (West et al. 2009a). Incubation experiments revealed that free-living bacterial communities from the York River estuary consumed a large proportion of the excretory and mucus products of *Mnemiopsis leidyi* and *Chrysaora quinquecirrha* within 6–8 hours (Condon et al. 2011). Heterotrophic bacteria used this organic matter in respiration rather than production (Condon et al. 2011), and as a result only a small fraction of it could be routed towards higher trophic levels by way of flagellates and other bacterial grazers. The scyphozoan *Chrysaora quinquecirrha* is one of the major recyclers of nitrogen and phosphorus in the York River estuary system (Chesapeake Bay, USA), especially during summer when the biomass of medusae is high (Condon et al. 2010). Interestingly, however, these recycled nutrients contribute little towards the daily primary production of the York River estuary but rather, may give a competitive advantage to bacteria over phytoplankton (Condon et al. 2010).

Dead jellyfish can play an important role in bentho-pelagic coupling and carbon sequestration (Yamamoto et al. 2008; Doyle et al. 2014; Sweetman et al. 2016). Besides decomposing rapidly in the water column (Titelman et al. 2006), they provide an injection of organic matter at the benthos when they settle out (Yamamoto et al. 2008; Sweetman et al. 2016). Jellyfish-falls appear to be swiftly scavenged by a diversity of demersal and benthic species (Yamamoto et al. 2008; Sweetman et al. 2014b), though they can also smother seafloor sediments and decrease oxygen diffusion into sediments (Billett et al. 2006; Lebrato & Jones 2009). They will obviously elevate microbial metabolism (Titelman et al. 2006; West et al. 2009b; Tinta et al. 2010; Sweetman et al. 2014a, 2016) and can collectively cause large changes to community composition. Their decomposition reduces energy flow to upper trophic levels and it lowers the level of carbon-storage in sediments (Titelman et al. 2006; West et al. 2009b; Tinta et al. 2010; Sweetman et al. 2014a, 2016). Despite the paucity of data, the decay of jellyfish blooms results in massive nutrient recycling, and the elevated oxygen requirements are suggested to set off hypoxia, anoxia, dystrophy and the decimation of some benthic communities (Pitt et al. 2009b; West et al. 2009b).

1.7 Impacts of jellyfish blooms

Provided that medusae remain inconspicuous, cause no direct economic losses or impinge on human welfare they are generally overlooked. Their abrupt development into a bloom is regarded as a temporary and anomalous perturbation, with negative connotations towards ecosystem processes,

human activities and economies (Condon et al. 2012). Primarily, jellyfish blooms affect the 'provisioning' and 'cultural' ecosystem services, which involve mostly fishing, aquaculture, power and desalination industries and tourism (Lucas et al. 2014). From the perspective of ecosystem functioning, although the impact of jellyfish is "still a matter of speculation" (CIESM 2001: p. 15), jellyfish "invaders" can have negative impacts on communities (Kideys 1994; Shiganova et al. 2001) and their decomposing carcasses may cause localised hypoxic or anoxic conditions (Pitt et al. 2009b; Tinta et al. 2010). Jellyfish blooms often appear near coastal recreation areas and some taxa have acquired a reputation as public health risks, and threats to tourism. They can cause severe injuries, revenue loss through beach closures and even the death of bathers (Gershwin & Dabinett 2009). Beach closures can cause a significant financial loss for coastal communities (e.g. Wiley et al. 2006; NRDC 2014) and even in situations of unclosed beaches, the presence of jellyfish causes unease and drives people away from such plagued areas (Galil 2008). It is estimated that worldwide about 150 million jellyfish stings occur annually (Boulware 2006). In the United States, annual statistics estimate 200 000–500 000 jellyfish stings in the waters of Chesapeake Bay and Florida alone (Burnett 1992). At Waikiki Beach in Hawaii, a *Carybdea* species bloom led to mass envenomations, with more than 800 reported sting incidents, and beach closures in July 1997 (Thomas et al. 2001). Nematocyst stings on the skin causes inflammation and nerve irritation which creates pain, swelling and itching (Cegolon et al. 2013 and references within). Medusae have also gained a reputation for affecting power- and desalination plants by clogging sea water intake screens, which causes power reductions and may force temporally shutdowns on a wide geographical scale. Such has been demonstrated at the Orot Rabin Electric Power Station (Hadera, Israel), Torness power station (south-east coast of Scotland), the Shimane plant in western Japan and the Madras Atomic Power Station (south-east India) (Purcell et al. 2007; Lucas et al. 2014).

Aquaculture is another economic sector that can be negatively impacted by jellyfish blooms. When medusae, either intact or broken up into tentacles and other body fragments, enter into fish pens through wave or current action (Mitchell et al. 2012), they can cause skin lesions and gill damage leading to local inflammatory response, cell toxicity and histopathology (Helmholz et al. 2010; Bosch-Belmar et al. 2016). Protracted nematocyst discharges in fish tissues might lead to secondary bacterial infections and associated systemic reactions, as well as respiratory and osmoregulatory distress, changes in behaviour

and death of fish (Bruno & Ellis 1985; Seaton 1989; Rodger et al. 2011b). *Pelagia noctiluca*, in 2007, caused major fish mortalities in Northern Ireland, with >250 000 salmon killed (Doyle et al. 2008). Trial studies have shown that *Pelagia noctiluca* can cause significant gill damage after only a few hours of contact with farmed gilthead sea bream *Sparus aurata* (Bosch-Belmar et al. 2016). The extent and severity of gill lesions depends on jellyfish density and incubation time, and the gills of fish were even affected long after the removal of jellyfish from tanks (Bosch-Belmar et al. 2016). Consequently, *Pelagia noctiluca* blooms may represent a high risk for Mediterranean finfish aquaculture farms (Bosch-Belmar et al. 2016). Evidence is accumulating that unidentified small jellyfish play a more significant role related to annual fish mortality rates in Ireland and Scotland, as a result of injuring fish and as a vector of secondary bacterial infection (Ferguson et al. 2010; Rodger et al. 2011a, 2011b).

Jellyfish blooms can severely affect the commercial fisheries industry by clogging and the breaking of nets; killing and spoiling fish due to nematocyst stings with associated degraded product value; increasing labour in order to remove jellyfish from the nets; discarding entire hauls due to their overwhelming presence; closing fishing during the fishing season; increasing the risk of trawling vessels to capsize and stinging fishermen as they try to remove jellyfish (Kawahara et al. 2006; Purcell et al. 2007; Galil 2008; Uye 2008; Dong et al. 2010; Quiñones et al. 2013; Palmieri et al. 2014). In 2000, the shrimp industry suffered an estimated loss of US$ 10 million in the Gulf of Mexico due to the invasive *Phyllorhiza punctata* (Graham et al. 2003). The Japanese fishing industry suffered a financial loss of ~US$ 20 million, over a 5-month period, thanks to a bloom of *Nemopilema nomurai* (Kawahara et al. 2006). It was estimated that the Peruvian anchovy fishery lost in excess of U$ 200 000 over a 35-day fishing period as a result of *Chrysaora plocami* bycatch (Quiñones et al. 2013). An economic survey, conducted in 2011, estimated that in the Northern Adriatic Sea, Italian fisheries incurred annual losses of € 8.66 million, and nearly 90 000 man-hours were spent in repairing broken nets due to jellyfish bloom interference with fishing (Palmieri et al. 2014). Jellyfish blooms have also had an impact on the Slovenian economy. In 2004, the overall reduction in fish catches, value addition, gross income and employment was so great that the government and the EU granted financial assistance (~ € 150 000) to the fishermen affected (Nastav et al. 2013). The annual direct economic damage to fisheries by jellyfish in Korean

waters has been estimated at between US$ 68–205 million, with declines in catches of 6.5–33.7% and product value of 6.8–25.3% (Kim et al. 2012).

All this said, the main negative economic concerns of jellyfish blooms are related to the indirect effects that medusae can have on commercially important finfish and shellfish stocks through their position within the marine food web. By feeding on zooplankton, ichthyoplankton and juvenile fish, jellyfish act as both a potential competitor with, and predator on, fish (Purcell et al.1994; Arai 1997; Purcell & Arai 2001; Purcell & Sturdevant 2001; Sabatés et al. 2010; Purcell et al. 2014). They can alter trophic food webs in overfished ecosystems (Lynam et al. 2005b; Graham & Bayha 2007; Brodeur et al. 2008a; Richardson et al. 2009) and they can influence fish recruitment (Möller 1984; Lynam et al. 2006; Shoji et al. 2009). They further serve as intermediate hosts for fish parasites (Purcell & Arai 2001) and some taxa occupy similar trophic levels to that of small pelagic fishes (Brodeur et al. 2008b). When medusae overlap in space, time and diet with planktivorous forage fish in coastal ecosystems, they therefore have the potential to compete for the same zooplankton resources (Purcell & Sturdevant 2001; Hiromi et al. 2005; Brodeur et al. 2008b, 2014; Engelhard et al. 2013). As a result, when jellyfish blooms spatially coincide with jellyfish-fish overlap, jellyfish predation on icthyoplankton and zooplankton is anticipated to have an impact on larval fish mortality and the reduction of shared prey resources supporting planktivorous fishes (see Section 1.8; Robinson et al. 2014).

The literature contains a number of case studies that illustrate the effects of jellyfish on marine systems: *Periphylla periphylla* in fjords of western Norway (Sørnes et al. 2007; Dupont et al. 2009), and *Rhopilema* nomadica (reviewed in González-Duarte et al. 2016*)* and *Pelagia noctiluca* in the Mediterranean Sea (reviewed by Mariottini et al. 2008; Canepa et al. 2014). For example, *Rhopilema nomadica* was first recorded during the early 1970s in the Mediterranean, and since the early 1980s populations have bloomed during summer along the Levant coast (Galil et al. 1990; Kideys & Gücü 1995). These blooms cause envenomation (Silfen et al. 2003; Yoffe & Baruchin 2004; Sendovski et al. 2005; Öztürk & Işinibilir 2010), and have been documented to have affected tourism negatively by 3–10.5%, in terms of the number seaside visits, with an annual financial loss of € 1.8–6.2 million (Ghermandi et al. 2015). Their annual blooms disrupt coastal trawling and purse-seine fishing operations (net-clogging, yield) and block the water intake pipes of both desalination and coastal power plants. In the

summer of 2011, Israel Electric had to remove tons of jellyfish from its seawater inlet pipes at its largest power plants (www.bbc.co.uk/news/world-middle-east-14038729).

1.8 Factors that could be causing or contributing to an increase in numbers of jellyfish

Some jellyfish taxa are regarded as synanthropes since they benefit from human activities such as human-mediated dispersal, climate change, eutrophication, coastal and benthic habitat modification, aquaculture and fish stock overexploitation (Mills 2001; Purcell et al. 2007; Brotz et al. 2012; Purcell 2012; Boero 2013). These human-induced factors, possibly acting in synergy, are proposed as external factors that could be promoting local jellyfish blooms (Mills 2001; Richardson et al. 2009; Brotz et al. 2012; Purcell 2012). That said, most ecosystems are lacking long-time data series (>20 years) on jellyfish abundance/biomass and the perceived widespread or global increase in jellyfish is questioned (Condon et al. 2012; Sanz-Martín et al. 2016). The synergistic effects of these anthropogenic activities are showing intense and rising deterioration in global marine ecosystems, especially for coastal systems in water quality (Lotze et al. 2006), accelerated species invasions (Lotze et al. 2006), and where 50% of salt marshes, 25–35% of mangroves (Wilkinson & Salvat 2012), 60% of coral reefs (Wilkinson & Salvat 2012), and >65% of seagrass and wetland habitat (Lotze et al. 2006) are by now either lost or degraded (Wilkinson & Salvat 2012).

Due to increased globalisation, geographical barriers are frequently crossed and the number of marine biological invasions is climbing (Carlton & Gellar 1993; Molnar et al. 2008). Although assessing invasion success is an intricate process, invasive species are generally set apart by their tolerance of a wide-ranging set of environmental and anthropogenic stressors (Crooks et al. 2011; Lenz et al. 2011). In marine environments, the main introductory pathways that contributed to the dispersion, establishment and invasion of jellyfish taxa are man-made structures (inshore and offshore), international shipping (ballast water transport and hull fouling), aquaculture, global warming and inter-oceanic canals (reviewed in González-Duarte et al. 2016; Vodopivec et al. 2017).

The success of an invader is determined by its life history traits, the recipient ecosystem and the resident/native species community (Ehrlich 1989; Facon et al. 2006; Catford et al. 2012). The life history traits of jellyfish taxa (Costello et al. 2012; Bayha & Graham 2014) may enable their rapid population

growth on introduction to a novel environment (Purcell et al. 2001; Bayha & Graham 2014). These traits make invaders highly competitive, particular in situations where natural predators are uncommon or the ecological niche of the invader is free ensuring high resource availability (Sax & Brown 2000; Facon et al. 2006; Sorte et al. 2010). In addition, global climatic change seems to allow jellyfish with a tropical affinity to spread their range into the temperate zones. *Cassiopea andromeda, Phyllorhiza punctate*, and *Rhopilema nomadica* are some of jellyfish taxa identified as successful biological invaders (reviewed in González-Duarte et al. 2016).

Climate change, induced by anthropogenic pressures, is associated with rising atmospheric CO_2 levels which in turn lead to a rise in atmosphere and ocean temperatures (Doney et al. 2012). Climate change affects many facets of the ocean such as sea level (Mimura et al. 2013), subsurface oxygen concentration (Resplandy 2018), biogeochemical properties (Denman et al. 2007), stratification and ocean circulation (Behrenfeld et al. 2006), nutrient dynamics (Moore et al. 2018), precipitation (Trenberth 2011), runoff (Sinha et al. 2017), wind patterns (Moore et al. 2018), sea-ice extent (Walsh & Chapman 2001; Hoegh-Guldberg & Bruno. 2010) and pH levels (Walther et al. 2002). The effects of increasing CO_2 levels act in synergy with other regional human-induced activities, with consequently multiple stressors acting simultaneously and affecting the structure, functioning and biodiversity of the marine ecosystems (reviewed in Doney et al. 2012). As a consequence of climate change, marine species are showing population-level shifts (reviewed in Doney et al. 2012) as a result of physiological intolerance to the "changed" environments (Gardner et al. 2003; Wootton et al. 2008), alteration in dispersal patterns (Hare et al. 2010; Hoegh-Guldberg & Bruno 2010), and changes in species interactions (Hoegh-Guldberg & Bruno 2010). In conjunction with local climate-driven invasion and extinction, these processes ensure changes in community structure and diversity, including possible establishment of novel ecosystems (Ruiz et al. 2000; Hoegh-Guldberg & Bruno 2010).

Temperature is an important driver for jellyfish blooms as reflected in the various field and experimental studies that have investigated the effects of temperature (Purcell 2012). The reaction of the organism towards global warming is species-specific which might be uncovered when the exact timing of warming coincides with critical life cycle stages or life history events (Richardson 2008). Rising temperatures can favour or hinder marine taxa (depending on their thermal inclination) with regard to their

metabolic and physiological performances (Purcell 2005), to shift their distributions and to change their behaviour (Richardson 2008; Boero et al. 2016). The majority of jellyfish taxa reviewed by Purcell (2005, 2012), exhibit higher medusa abundances during warm, high-salinity conditions and polyps show an increase in asexual reproduction under higher temperatures. A rise in temperature may increase the population sizes of many jellyfish taxa and alter the onset and duration of their seasonal presence as well as their distributions (Purcell 2005, 2012; Dong 2019).

Jellyfish have a suite of physiological traits (Richardson et al. 2009) that enable them to take advantage of changing environmental conditions (with expected alterations outlined in Doney et al. 2012); which have been summarized in part previously, but include their ability to endure low oxygen concentrations (Condon et al. 2001; Decker et al. 2004; Rutherford & Thuesen 2005) and to shrink or encyst during periods of starvation or low food availability (Hamner & Jenssen 1974; Anninsky et al. 2005; Arai 2009a; Thein et al. 2012). In addition, rising temperatures may accelerate the growth of jellyfish or the rates of both asexual and sexual reproduction (Purcell 2005; Purcell et al. 2007, 2012; Richardson et al. 2009; Holst 2012a) and promote the range expansion of invasive alien taxa (Daly Yahia et al. 2013). Global warming also advances stratification causing water temperature elevation, leading flagellates to displace diatoms in the nutrient-poor surface waters (Cushing 1989; Sommer & Lengfellner 2008). Jellyfish have broad diets and some can prey on flagellates (Colin et al. 2005; Sullivan & Gifford 2004; Morais et al. 2015), which are a poor food source for fish (Cushing 1989) and under such circumstances jellyfish may outcompete fish (Parsons & Lalli 2002; Richardson et al. 2009).

Coastal eutrophication is a major pollution concern, leading as it does to widespread hypoxia and anoxia (Selman et al. 2008; Rabalais et al. 2009), habitat degradation (Lotze et al. 2006; Rabalais et al. 2009), shifts in food-web structure (Riegman 1995; Rabalais et al. 2009; Davis et al. 2010), biodiversity loss (Waycott et al. 2009; Rabalais et al. 2009) and an increase in the frequency, spatial range and timing of harmful algal blooms (Paerl 1997; Heisler et al. 2008; Rabalais et al. 2009). Much of this eutrophication is associated with increased nutrient input (mostly nitrogen and phosphorus) from agriculture fertilisers, human sewage, urban runoff, industrial effluent and fossil fuel combustion, which alters nutrient ratios (Howarth 2008; Purcell 2012). The overall effect of increased nutrients is an increase in the biomass at all trophic levels and complex shifts in the food web (Purcell 2012). Hence, eutrophication can lead to more

food for polyps and medusae with accelerated rates in growth, asexual reproduction and sexual reproduction (Purcell 2012). Cumulative evidence suggests that high N:P ratios causes an alteration of the phytoplankton assemblage, from a diatom to a flagellate-based food web (Egge & Aksnes 1992) within which jellyfish can be favoured over fish (Cushing 1989) as portrayed by the conceptial model of Parson & Lalli (2002). A reduction in the size of the zooplankton community is also linked with eutrophication, thus benefiting non-visual predators such as jellyfish (consume both small and large sized zooplankton) while handicapping fish (visual predators that select larger sized zooplankton) (reviewed in Purcell 2012). The degradation of an algal bloom can reduce oxygen concentrations rapidly leading to hypoxic or anoxic levels, which both medusae and polyps are better able to tolerate than fish (Condon et al. 2001). This high tolerance of reduced oxygen levels has been shown to permit the recruitment and growth of the benthic stage of *Aurelia aurita* in hypoxic bottom waters of Tokyo Bay: an area that cannot be tolerated by other species (Ishii et al. 2008; Ishii & Katsukoshi 2010).

The amount of artificial hard submarine substrata is expanding at rates of 3.7–28.3% per year in the coastal oceans of the world (Duarte et al. 2013), and is associated with shipping, aquaculture activities, marine litter and other coastal industries, as well as the number and size of shoreline stabilizing structures. Such marine habitat alterations are theorised to provide new settling surface areas to the benthic stages of medusae, and as such they act as nurseries by facilitating the propagation of jellyfish and fostering new jellyfish invaders (Purcell et al. 2007; Richardson et al. 2009; Purcell 2012; Duarte et al. 2013). This theory applies only to jellyfish taxa with benthic stages, and is supported by field and experimental evidence (Duarte et al. 2013). Although not all surfaces are equally suitable for the settlement of planulae (Purcell 2012), those of some scyphozoans appear to prefer artificial above natural surfaces (e.g. Holst & Jarms 2007; Purcell et al. 2007, 2009; Hoover & Purcell 2009; Duarte et al. 2013). Many polyps preferentially attach to the undersides of submerged objects (Lo et al. 2008; Duarte et al. 2013), especially, when artificial substrates suitable for polyps are likely to be crucial in benthic regions with predominantly soft sediments.

Apart from providing substrata for benthic polyps, ports and aquaculture lagoons offer calm, eutrophic water conditions that can retain jellyfish (Lo et al. 2008). Waters within ports are usually turbid, have a nutrient overload and support hypoxic bottom waters and pollutants (Duarte et al. 2013). These

anthropogenic conditions can potentially enhance the food availability for polyps and preclude their predators and competitors (reviewed in Purcell 2012), all of which facilitate polyp survival and asexual reproduction (Ishii et al. 2008; Ishii & Katsukoshi 2010; reviewed in Purcell 2012).

International shipping (ballast water transport and hull fouling) as well as the relocation of oil platforms at sea act as mechanisms for the translocation of invasive jellyfish from one part of the world to another, whereas docks and harbour walls act as new dispersal centers for these invaders (Purcell & Arai 2001; Graham & Bayha 2007). The spatial placement of artificial offshore constructions may be exploited by providing shortened distances between suitable larvae settlement sites; thereby facilitating the range expansions and invasive processes, consequently increasing the spatial extent of blooms (Duarte et al. 2013; Vodopivec et al. 2017). The global practice of live shellfish trade also support jellyfish populations through the introduction of invasive invertebrate species that piggy-back on their host (Wasson et al. 2001; Ruesink et al. 2005).

Aquaculture activities may integrate the anthropogenic effects of fishing, eutrophication, habitat modification and human-mediated dispersal (Purcell 2012), and thereby directly and indirectly aid the development of jellyfish blooms. The global aquaculture production of shellfish, marine fish and macroalgae has increased dramatically in recent decades (FAO 2012). Sea cages enclose 3.4 million tons of marine fish, whilst 13.9 million tons of shellfish and 19 million tons of macroalgae hang from floating ropes or grow on racks or in trays (FAO 2012). In addition, about 60 thousand tons of medusae are directly cultured by farms (FAO 2012). Thus, a substantial amount of “new” artificial substrata are created for the benthic stages to proliferate on (Chaplygina 1993; Duarte et al. 2013).

Aquacultural activities that focus on carnivorous finfish and shrimps are highly dependent upon wild capture fisheries for sourcing the key dietary ingredients –fishmeal, fish oil and low value trash fish – required for formulated aquatic feeds (Tacon et al. 2006). In order for the aquaculture sector to produce 30 million tons of fish and crustaceans, 20 to 25 million tons of fishmeal were estimated to be consumed as fish feed during 2003 (Tacon et al. 2006). Not only can these feeds contribute to eutrophication when administered, but they act as drivers for overfishing and the removal of potential jellyfish predators and competitors (Purcell 2012). Mariculture structures are now ubiquitous to many coastlines of the world,

including Namibia, and as expansion of this sector continues, an increase in jellyfish blooms and the incidence of interactions between jellyfish and aquaculture can be expected (Purcell 2012).

Overfishing serves to severely reduce fish population sizes and impacts trophic level interactions and flows through the removal of predators and the competitors of jellyfish (Pauly & Palomares 2005; Purcell et al. 2007; Purcell 2012). As a result, overfishing gradually facilitate a regime shift, from a fish- to a jellyfish-driven ocean (Pauly et al. 1998, 2002; CIESM 2001; Daskalov et al. 2007). Avian & Rottini-Sandrini (1988) and Harbison (1993) are among the initial researchers who suggested that a large group of pelagic predators might feed opportunistically on jellyfish and proposed that overfishing has the potential to liberate jellyfish from tight predator control. The explosion of jellyfish blooms in several heavily fished regions supports such a theory, though existing evidence shows that competitive release, and not the relaxation of top-down control, is the most probable mechanism (Brodeur et al. 1999; Daskalov 2002; Lilley et al. 2011; Chiaverano et al. 2018). Consequently, whilst overfishing of jellyfish consumers is portrayed in recent reviews as a plausible theory, there is little direct supportive proof (Richardson et al. 2009; Purcell et al. 2007; Cardona et al. 2012; Purcell 2012).

Global catch statistics indicate that 77.4 million tons of fish are caught each year; that 3.23 million marine fishing vessels are operating annually, and that 60% and 30% of fish stocks are fully exploited and overexploited, respectively (FAO 2012). The ten species that contribute most to global capture fisheries are fully to overexploited (FAO 2012) The majority of these fish species are forage fishes and are described as relatively small planktivorous fishes that are typically obligate schoolers in productive coastal environments (Robinson et al. 2014), and that serve as a key conduit between primary and secondary production and higher trophic levels (Bakun et al. 2010). There is evidence pointing towards some competitiveness between pelagic fishes and jellyfish, based on dietary, spatial and temporal overlap between each other (Purcell 1990; Purcell & Sturdevant 2001; Brodeur et al. 2008b; Engelhard et al. 2013). It has been hypothesized that the commercial fishing of these forage fish can lead to a competitive release for jellyfish, as a result indirectly boost jellyfish proliferation (Lynam et al. 2006; Purcell 2012; Roux et al. 2013; Angel et al. 2014). Hence, jellyfish may potentially move into the “space” that overfishing created and prevent the re-establishment of fish stocks over time which might lead to an ecological phase shift (Knowlton 2004).

A negative knock on effect may be applicable in ecosystems that have suffered from the overfishing of small pelagic species: small fish populations lead to low fish recruitment, leading to an increase in jellyfish and an increase in the number of ephyrae that are able to attain full size (Richardson et al. 2009). The latter replacing planktivorous fish in the marine food webs while imposing a constant larval predator pit on the fish larvae and eggs (Bakun 2006). Schnedler-Meyer et al. (2016) presented a general mechanistic food web model, which predicted the dominance of forage fish at low primary production whereas increasing productivity, turbidity and fishing showed a shift towards jellyfish dominance. This model also predicted that areas such as the California -, Humboldt -, Benguela current systems, East Bering -, Baltic - , eastern US continental shelf seas and the Gulf of Oman are quick to respond to environmental perturbations affecting the fish-jellyfish competitive interaction (Schnedler-Meyer et al. 2016).

1.9 Northern Benguela upwelling system and Namibia

The Benguela Current system is one of the four main eastern boundary upwelling marine ecosystems in the world and is located in the South East Atlantic Ocean off the southern coast of Angola, the entire coast of Namibia and the west coast of South Africa (Boyer et al. 2000; Hutchings et al. 2009). It is characterised by a primarily cool equatorward flowing current, high levels of Ekman-driven coastal upwelling with resultant highly productivity (Boyer & Hampton 2001; Shannon & O'Toole 2003; Fréon et al. 2009). It is subject to extensive oxygen depletion and intermittent hydrogen-sulphide eruptions, arising from both local and remote forcing (Bakun & Weeks 2004; Monteiro et al. 2006). This system is confined between two warm water currents: to the south – the warm, temperate Agulhas Current – and to the north – the warm, subtropical Angola Current (Boyer et al. 2000; Hutchings et al. 2009). The Benguela ecosystem is separated into two sub-systems, a northern and a southern part by a permanent and the world's strongest (Bakun 1996) upwelling cell at Lüderitz (27°S–28°S) (Shannon & Nelson 1996; Hutchings et al. 2009). The prevailing winds drive frequent Ekman transport and the upwelling of cool, nutrient-rich water to the surface along the edge of the continental shelf. Hence, there is a plentiful supply of new nutrients from deep water to the euphotic zone, resulting in very high primary production of 12 g C m^{-2} d^{-1} during algal blooms (Mitchell-Innes et al. 2000). The key processes and characteristics of the

Benguela Current ecosystem can be found in Shannon et al. (1986, 2006); Boyer et al. (2000) and Hutchings et al. (2009).

The collapse of the small pelagic fish stocks due to overfishing in the late 1960s (Venter 1988; Roux et al. 2013), coupled with environmental anomalies (Gammelsrød et al. 1998; Rouault et al. 2007; Bartholomae & van der Plas 2007; Salvanes et al. 2015), created a niche for opportunistic species to enter the system off Namibia (Bakun & Weeks 2006). These opportunists included jellyfish, the bearded goby and other mesopelagic fish and they have come to dominate the pelagic biomass off Namibia (Boyer & Hampton 2001; Roux et al. 2013). The inability of the pelagic fish stocks to recover off Namibia is thought to be due to the high jellyfish biomass (Lynam et al. 2006; Roux et al. 2013), their spatial and temporal overlap with fish (Kreiner et al. 2011; Flynn et al. 2012), and the negative effects of competition and predation between jellyfish and fish (Roux et al. 2013).

In Namibia, fisheries research has focused mainly on those species of direct commercial value (see Boyer & Hampton 2001), and the single-species management approach usually ignores the interactions and interdependencies between species sharing the whole ecosystem: it tends to forget those species without commercial value. Our understanding of jellyfish in the region is largely based on observations of medusa conducted offshore derived over restricted study periods (Pagès et al. 1992; Brierley et al. 2001, 2005; Buecher et al. 2001; Lynam et al. 2006; Flynn & Gibbons 2007; van der Bank et al. 2011). There is no information regarding the benthic life-history phase of jellyfish around Namibia, and only limited information concerning the ephyrae. The most common species of medusae reported off Namibia are *Chrysaora fulgida*, which has an inshore distribution, and *Aequorea forskalea*, which has an offshore distribution (Venter 1988; Brierley et al. 2001; Buecher et al. 2001; Sparks et al. 2001; Fearon et al. 1992; Pagès 1992). Both species of medusae are found perennially (Venter 1988; Fearon et al. 1992; Flynn et al. 2012) along the entire length of the Namibian coastline. Both species are found throughout the water column, although they are more abundant in the central Namibia area (20–24°S), at depths less than 200 m and in near-surface waters, though there is some evidence to suggest that regional jellyfish show possible winter and early spring peaks in abundance (Flynn et al. 2012).

This study was conducted in the Coastal Area off Walvis Bay. Walvis Bay (22.9390°S, 14.5247°E) is a port town on the coast of Namibia. This Coastal Area constitutes of the Walvis Bay

Lagoon, Bay and Harbour (DANIDA 2003). The Bay is enclosed by the Pelican Point Peninsula sand spit which shelters the town and Harbour (DANIDA 2003). The Walvis Bay Lagoon serves as a significant habitat for shorebirds and seabirds which was declared in 1995 as a Ramsar wetland site (DANIDA 2003). The Harbour is visited by many fishing boats, cargo vessels and an increasing number of passenger cruise liners. Other users of the Coastal Area include the processing of sea salt and the farming of shellfish (oysters and mussels).

1.10 Key questions

Even though gelatinous zooplankton appears to be of fundamental importance to the ecology of the northern Benguela upwelling system (Pauly et al. 2009; van der Bank et al. 2011; Roux et al. 2013), the number of published studies on their abundance, seasonality, life history and ecological roles off Namibia is strictly limited (Pagès & Gili 1991; Fearon et al. 1992; Pagès 1992; Flynn & Gibbons 2007; Koppelmann et al. 2014). Among jellyfish taxa in the Benguela Current, *Chrysaora fulgida* is one of the most common and prevalent medusa, and it is reported that (together with *Aequorea forskalea*) their biomass exceeds those of the commercially important fish stock off Namibia (Lynam et al. 2006).

For almost a century, there has been confusion regarding the identity of the species of *Chrysaora* found off Namibia. The first specimens to be actually collected and described were from Walvis Bay and they were regarded by Stiasny (1934) as *C. fulgida,* which had first been described in 1830 by Reynaud from off the Cape of Good Hope. That said, Stiasny (1939) considered the specimens to be the dactylometra stage of *C. fulgida,* owing to the fact that they had 40 tentacles and not 24. And this despite the fact that a 40 tentacle species of *Chrysaora* had been described in 1902 by Vanhöffen: *Chrysaora africana*. Kramp (1961), in his comprehensive review of world medusa, concurred with Stiasny (1939), and lumped *C. africana* with *C. fulgida.* Pagès et al. (1992) identified the Namibian species of *Chrysaora* as *Chrysaora hysoscella*, a decision supported subsequently by Mianzan & Cornelius (1999) but not by Morandini & Marques (2010). The latter authors considered all the *Chrysaora* off Namibia to be *Chrysaora fulgida*. Recent work by Neethling (2009) and Ras (2016), however, have demonstrated (using a suite of molecular, morphological and meristic tools) that there are two species of *Chrysaora* found off Namibia: *C. fulgida* and *C. africana*, with the former being more widespread than the latter.

Chrysaora fulgida medusae is also much more abundant than *C. africana,* and is one of the few species that has flourished in the region, following the decline of the pilchard fishery at the end of the 1960s (Roux et al. 2013). By comparison, *C. africana* medusae is rare, being recorded only in very nearshore waters, generally north of Walvis Bay. This poses two interesting questions: 1) why might one species bloom, and the other not? and 2) how do these two species co-exist?

Whilst some of the different stages of the life cycle of *Chrysaora fulgida* have been recorded in the field, the complete life cycle of this species has only been described in the laboratory. Polyps of *C. fulgida* population, in the northern Benguela, ecosystem, have not been discovered and the source area for their mass occurrence of ephyrae remains a mystery. Where possible, some attention will be given to examining the dynamic interactions between life history phases and the environment. This research aims to contribute towards improving our knowledge of the biology and ecology of *Chrysaora fulgida* off Namibia, with a view to understanding the reasons behind its success in the region by exploring the following key questions:

(1) Is there any seasonal changes in the abundance of ephyrae of each *Chrysaora* species off Walvis Bay?

(2) Can different morphological features be decerned between the ephyrae of each *Chrysaora* species and what are their growth rates?

(3) Is there any seasonal patterns with regard to the sexual reproduction of each *Chrysaora* species?

(4) What are the inshore trophic relationships of each *Chrysaora* species?

To address abovementioned questions, Chapter 2 provides first a field investigation focusing on the seasonal changes of the jellyfish community in the vicinity of Walvis Bay. This is followed by (Chapter 3) a description of the morphological differences between the pelagic developmental stages of the two *Chrysaora* species collected *in situ* during the study period. Chapter 4 describes and assess, through the histological examination of gonads, gonad development and maturation of each *Chrysaora* species. In Chapter 5, data from stable isotopes analysis were gathered to investigate trophic ecology relationships of each *Chrysaora* species with regard to presence of variability in medusae size, tissue type, seasonality, spatial and between species. Within each chapter the figures and tables follow the text while

annexures and references cited are combined for all chapters at the end of the thesis. A concluding chapter (Chapter 6) provides a synthesis of the main findings of the thesis, and makes recommendations on ways that the research can be carried forward.

TABLES

Table 1.1. Various mechanisms that may drive the medusa abundance throughout its various life cycle stages

Life cycle stage	Factors	Reference
polyps	water temperature	Rippingale & Kelly 1995; Purcell et al. 1999b; Purcell 2007; Han & Uye 2010; Prieto et al. 2010; see Lucas et al. 2012; Purcell et al. 2012; Hubot et al. 2017; Ziegler & Gibbons 2018
	nutrional status	Purcell et al. 1999b; Han & Uye 2010; see Lucas et al. 2012; Hubot et al. 2017; Ziegler & Gibbons 2018
	light intensity	Purcell 2007; Liu et al. 2009; Lucas et al. 2012
	day length	Rippingale & Kelly 1995; Miyake et al. 2002; Purcell 2007; Lucas et al. 2012
	salinity	Rippingale & Kelly 1995; Purcell et al. 1999b; Ma & Purcell 2005; Purcell 2007
	rainfall	Willcox et al. 2008
	presence of zooxanthellae	Kikinger 1992
	mortality	Cargo & Schultz 1967; see Lucas et al. 2012
	mode of asexual reproduction	Schiariti et al. 2014, 2015
	substrate availability	Hočevar et al. 2018
	competitor abundance	Kakinuma 1975; Colin & Kremer 2002; Willcox et al. 2008
planulae	settlement preferences	Brewer 1976; Keen 1987; Gröndahl 1989; Fleck et al. 1999; Holst & Jarms 2007; Astorga et al. 2012; Lucas et al. 2012; Webster & Lucas 2012; Duarte et al. 2013
	mortality	Brewer 1976; Gröndahl 1988a; Ishii et al. 2008; Javidpour et al. 2009; Lucas et al. 2012
	temperature	Fitt & Costley 1998; Prieto et al. 2010; Riascos et al. 2013; Webster & Lucas 2012; Gambill et al. 2016
	salinity	Holst & Jarms 2010; Conley & Uye 2015
	competitor abundance	Lucas et al. 2012
	substrate availability	Duarte et al. 2013
	advection	Lucas et al. 2012
ephyrae	mortality	Ishii et al. 2004; Fu et al. 2014
	advection	Suchman & Brodeur 2005; Lynam et al. 2004, 2010
	prey availability	Båmstedt et al. 1997; Fu et al. 2014
	temperature	Båmstedt et al. 1999, 2001; Astorga et al. 2012
	competitor abundance	Riisgård et al. 2010; Roux et al. 2013; Schnedler-Meyer et al. 2018
medusae	mortality	Gatz et al. 1973; reviewed in Pitt et al. 2014; Keesing et al. 2015
	advection	Graham et al. 2001; Suchman & Brodeur 2005; Lynam et al. 2004, 2010; Keesing et al. 2015; Goldstein et al. 2018; Schnedler-Meyer et al. 2018
	prey availability	Alldredge 1984; Arai 1997; Lynam et al. 2011; Roux et al. 2013; Lucas & Dawson 2014; Tiselius & Møller 2017
	competitor abundance	Lynam et al. 2011; Roux et al. 2013; Robinson et al. 2014; Schnedler-Meyer et al. 2016
	overwintering	Miyake et al. 1997; Costello et al. 2006; Javidpour et al. 2009; Ceh et al. 2015
	metagenic/holoplanktonic life cycle	Schnedler-Meyer et al. 2018
	phylogenetic lineages	Dawson & Hamner 2009
	zooxanthellae	Astorga et al. 2012

Oyster lines near Pelican Point Lighthouse.

PICTURE

CHAPTER 2

SEASONAL CHANGES IN THE JELLYFISH COMMUNITY IN THE VICINITY OF WALVIS BAY, NAMIBIA

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SEASONAL CHANGES IN THE JELLYFISH COMMUNITY IN THE VICINITY OF WALVIS BAY, NAMIBIA

INTRODUCTION

Different jellyfish taxa respond at different times to certain environmental conditions: this could result in seasonal medusae blooms in coastal waters (Mills 1981; Thibault-Botha et al. 2004; Boero et al. 2008; Bravo et al. 2011; Petrova et al. 2011; van Walraven et al. 2017). The large number of taxa inhabiting the relatively homogeneous pelagos may evade competition by having a sporadic and alternate presence in the plankton (Giangrande et al. 1994; Buecher & Gibbons 2000), which is facilitated in the case of most neritic medusae by exhibiting a bipartite life cycle. Not all medusozoans produce medusae (Hamner & Dawson 2009), but those that do tend to have an asexual, sessile polyp phase in the life cycle, which alternates with a dispersive, sexually reproducing pelagic medusa (Russel 1953; Arai 1997; Bouillon et al. 2004): a small number of scyphomedusae and hydromedusae, and most siphonophores lack an obviously distinct “polyp” stage. The polyp is the benthic, solitary or colonial, cylindrical shaped form that is crowned by a ring of tentacles around the mouth opening. The medusa form is the movable, bell-shaped organism that actively swims by means of rhythmic subumbrellar muscle contractions (Arai 1997; Richardson et al. 2009).

An ephyra in Scyphozoa originates via asexual reproduction of the polyp (a process known as strobilation) and is released into the water column as the most basic pelagic and immature stage of the medusa (Arai 1997). Strobilation may result in the release of a single ephyra (monodisc) or multiple ephyrae (polydisc) per polyp (Lucas et al. 2012). After the release of the last ephyra, the strobila reverts to a polyp (Aria 1997). The timing and frequency of natural strobilation cycles of polyps varies between species, locations and years, and this variability is attributed to small-scale differences in abiotic (temperature, salinity, light) and biotic (such as polyp, size, age, nutritional status, polyp density, inter-specific competition within and around the polyp colony) elements that singular polyps encountered (Lucas et al. 2012). The globally studied scyphozoan *Aurelia aurita* demonstrated site-specific strobilation

patterns which might be a reflection of ecological adaption of its life cycle strategies to local conditions across its geographical range and/or species crypsis (Lucas et al. 2012 and references therein).

Siphonophores are holoplanktonic and seasonal changes in their abundance might directly reflect temperature and/or seasonal changes in currents of prey supply (Arai 2009b). Their biology is influenced by a number of physical elements such as temperature, salinity, oxygen concentrations, pollution levels, pressure and light intensity (Arai 2009b). Medusoid taxa without benthic stages can be sharply seasonal to such an extent that doubts are generated about their holoplanktonic way of life (Bouillon et al. 2004).

Seasonal changes are typical in the abundance of hydromedusae in the field (Allwein 1967, 1968; Ballard & Myers 1996; Nicholas & Frid 1999; Hosia & Båmstedt 2007; Miglietta et al. 2008) but population peaks have seldom been distinct enough to pinpoint the controlling factor/s (Arai 1992a) since it/they can be governed by a combination of synergistic environmental factors, frequently disguised by time-lags. The lifespan of individual hydromedusae is equal to, or less than, their residence time observed in the plankton, and ranges between a few hours to one month (Mills 1981; Arai 1992a; Bouillon et al. 2004). Taxa that exist for short periods in the plankton are evidently short-lived whereas those existing over longer periods may represent multiple generations of holoplanktonic forms, or multiple pulses of released meroplanktonic taxa (Arai 1992a).

Seasonal activity patterns of hydroids and hydromedusae have been shown to be linked to annual cycles in water temperature off the SE coast of the USA, with communities being divided into warm water, cold-water and all year active groups (Calder 1990). In addition, the seasonal timing of gonophore production in these taxa was even more limited (Calder 1990). At the start of unfavourable conditions, some hydroids declined in density and vigour, undertook hydranth regression and displayed evidence of resorption of tissues into the stems; exhibiting seasonal dormancy (Calder 1990). During the return of favourable conditions, renewed growth and hydranth development occurred from the coenosarc of old stems, stolons or both (Calder 1990). In the Mediterranean, the distinct seasonality that coastal benthic communities display is believed to facilitate the spatial cohabitation of taxa by creating niche differentiation in time by permitting the presence of taxa with temperate and tropical affinities in the same basin (Coma et al. 2000). Broadly similar results have been observed for the benthic hydroid communities

in the Mediterranean Sea whilst gonophores were present during the winter, the warm season, and between winter and summer (Boero & Fresi 1986).

Lucas et al. (2012) attributed the long-term survival of some jellyfish populations during unfavourable conditions and 'sparse' years (resulting from conditions perpetrated by climate variability, anthropogenic stressors, predation and competition for space and resources) to the survival tactics of the benthic stage. These "tactics" *viz.* a perennial lifespan, broad physiological tolerance levels, the formation of chitin-covered podocysts and the ability to asexually proliferate via a variety of modes (Adler & Jarms 2009; Lucas et al. 2012) ensure the presence and continuance of a large foundation of thousands of parental polyps. In addition, asexual reproduction by the benthic stage is believed to be a key driver in the development of medusae outbursts in coastal areas whilst the expansion of artificial structures may aid as nurseries in so doing enables the spread of jellyfish blooms in adjacent waters (inshore ↔ offshore) and enhance connectivity between subpopulations (Duarte et al. 2013; Vodopivec et al. 2017).

Variability in medusa populations in the water column could be caused by factors influencing either or both metagenic phases (Boero et al. 2008; Lucas et al. 2012; Lucas & Dawson 2014). Thus, the identification of links between their abundances (and each other) with environmental or ecosystem variables will permit researchers to postulate theories and serves as a starting point for the testing of potential mechanisms responsible for variability in populations (Goldstein & Steiner 2017). An understanding of these mechanisms will enable researchers to differentiate between true (demographic) blooms as a consequence of seasonal life cycles (Boero et al. 2008) or apparent blooms (non-demographic) caused by temporary increases in local population densities associated with re-distribution or re-dispersion of densities by physical, chemical or animal behavioural phenomena (Graham et al. 2001).

Wind-induced coastal upwelling is the major oceanographic process along the Namibian coast (Shannon 1985; Boyd 1987; Boyd et al. 1987) that reaches maxima during winter and early spring and cause a broad expansion of homogenous, cold, nutrient-rich and low-saline water along the coastal edge of the continental shelf (O'Toole 1980 and references within; Boyer et al. 2000). This process involves the rise of cool nutrient-rich water from the subsurface waters to the surface zone that promotes high primary production, in the euphotic zone, which is propagated up the food chain (Bakun 1996; Boyer et al. 2000).

Although increased upwelling intensifies the supply of nutrients to the surface and hence primary production, protracted events can lead to the loss of production (primary and secondary) by means of mixing or turbulence and offshore advection (Bakun 1996; Boyer et al. 2000). During periods of reduced upwelling (relaxed southerly winds), sea surface temperatures rise, which contributes to thermal stratification (Bakun 1996; Boyer et al. 2000). The stratified surface layer benefits both primary and secondary production through enhanced vertical retention (Bakun 1996; Boyer et al. 2000). However, nutrients are quickly depleted by the phytoplankton communities due to the development of a strong thermocline (Louw et al. 2016). The existing phytoplankton communities are maintained (without significant bloom development) by the process of sporadic mixing (the effect of strong wind events and/or short upwelling pulses) that provides the necessary nutrients. Seasonal variation in upwelling is the greatest off northern and central Namibia due to latitudinal variation in the forcing processes of the Benguela Current system (Boyer et al. 2000 and references therein). North of 24°S off Namibia, a clear seasonal distinction is evident between vigorous upwelling activity, during winter (July) to spring (October), and more sluggish conditions, during summer (December) to autumn (April) (Boyer et al. 2000; Cole & Villacastin 2000; Louw et al. 2016). Walvis Bay (22.9390°S, 14.5247°E) is situated in the central Namibian region (19–24°S) that is characterised by moderate upwelling favourable winds and has a wide shallow Swakop shelf (Boyer et al. 2000).

This study aims to redress the gap in knowledge with regard to the gelatinous zooplankton community in the inshore area off Walvis Bay, by characterising their temporal distribution patterns in terms of diversity and density, and in relation to a number of measured environmental parameters (contemporary and preceding) such as bottom water temperature, wind speed, moon illumination and day length. In addition, the effect of upwelling on their population dynamics is examined. This study will provide a baseline against future studies whereby the potential increase in gelatinous zooplankton in the Walvis Bay area can be measured.

MATERIALS AND METHODS

Study site

Individual plankton samples were collected, between 9 am and 11 am, at approximately biweekly intervals from five stations (Fig. 2.1) off Walvis Bay over the period 29 February 2012 to 22 December 2013. Walvis Bay, is situated at a wide tidal lagoon, is a port town on the coast of Namibia, and is sheltered by the Pelican Point sand spit. Walvis Bay is an important logistical deep-sea port for the southern African region, providing port facilities for the import and export of cargo on national, regional and international basis. The fishing enterprise accounts for a major part of Walvis Bay's economy and other coastal area users include industries such as salt mining, tourism and mariculture.

Two distinct hydrographically periods have been identified (Hansen et al. 2005) at the Walvis Bay transect (stretching from 10 to 90 nautical miles from the coast) — a stratified water column across the entire 23° transect between February and April, and an active coastal upwelling period between May and December (especially during September). Large scale wind fields in the Walvis Bay region are dominated by southerly winds while the local wind measurements are subjected to a more westerly component (caused by geographical features of the bay and the temperature gradient between land and sea) and the presence of a significant percentage of northwesterly winds (DANIDA 2003; Delta Marine Consultants & CSIR 2009; Vogt 2016).

The Bay area has a pre-dominant counter-clockwise circulation pattern with a mean water residency period of half to one week that is highly dependent on the western wind component as a driving force (DANIDA 2003). The Bay area has stronger current velocities (>10 cm/s) that are typically directed northwards (coming from 180°) that are part of a clockwise eddy (Delta Marine Consultants & CSIR 2009). Modelled flowcharts indicated that the current patterns inside Walvis Bay are largely driven by the wind (Delta Marine Consultants & CSIR 2009). Upon strong southerly winds, the water seems to enter into the deeper middle part of Bay (the approach channel), where bed friction is lowest, and then split into two directions: a large clockwise eddy, that is formed in the southern part of the Bay, while that water is blown out of the Bay along the shallow areas (at Pelican Point) and a counter-clockwise circulation movement, in the northern part of the Bay, while being blown out of the Bay along the mainland shoreline (Delta Marine Consultants & CSIR 2009).

The water levels at the entrance of Walvis Bay are chiefly influenced by the astronomical tide while the largest tidal component along Namibia’s coast is affected by moon gravitation (Delta Marine

Consultants & CSIR 2009). The tidal range of the Bay over a typical neap-spring cycle varies between 0.6 m and 2.0 m with a 90 min unexplained water level oscillation (DANIDA 2003).The bathymetry inside the Bay of Walvis Bay varies from 16.5 m (at Pelican Point) to 2.5 m (at the Lagoon mouth) whilst outside the Bay it deepens quickly to >50 m (Delta Marine Consultants & CSIR 2009). The edge of the continental shelf (150 m depth) is situated 50 km offshore off Walvis Bay (Delta Marine Consultants & CSIR 2009). The vertical profile in the Bay indicated minimum water temperatures at the western, deep waters at Pelican Point, and maximum water temperatures at the shallow east coast and the mouth of the Lagoon (DANIDA 2003). Solar radiation and the circulation pattern in the Bay contribute towards this rise in water temperature (DANIDA 2003). Vertical gradient profiles also indicate maximum water temperatures at the surface while decreasing towards the bottom due to wind induced mixing, with a uniform vertical diffusion process in the Bay area (DANIDA 2003). Salinity stratification is absent in the deeper waters of the Bay. Current speeds (10 cm/s) are constant with depth in the Bay (DANIDA 2003).

A clear gradient in dissolved oxygen content is present due to respiration and oxygen consumption in the water column and the sea bed (DANIDA 2003). It is pertinent to note that the community of macrobenthos species (such as *Diopatra neopolitana*, Anthozoa sp., *Mytilus galloprovincialis*), molluscan shells, rocks, aquaculture - and port infrastructure in the Lagoon and Bay area provide suitable artificial and natural substrates for scypho- and hydroid polyps to settle on.

Field sampling

Samples were collected from a ski-boat using a weighted plankton-net of 50 cm mouth diameter (180 µm mesh size), fitted with a 1 L plastic cod-end jar, which was manually hauled vertically from just above the seabed to the water surface. The volume of water filtered by the net was calculated with the knowledge of the length of “wire-out”. The bottom depth varied between 8.5–11.5 m, and was determined using a Furuno GP-1640F echo sounder. On retrieval, the net was carefully rinsed to concentrate all zooplankton inside the cod-end, after which the sample was poured into a 2 L bucket and kept in the shade. The buckets were transported to the laboratory after which each sample was concentrated on a 100µ sieve and then fixed in 4% borax-buffered seawater formalin (Steedman 1976).

The following environmental data were obtained: sea bottom temperature (°C), day length (in minutes), moon illumination and wind speed ($m.s^{-1}$) (Fig. 2.2). The daily sea temperature (°C) was recorded hourly at the Swakopmund Jetty (30 km north of Walvis Bay) using a Starmon mini compact microprocessor-controlled temperature recorder at 7 m depth (bottom). Day length was calculated in minutes from sunrise till sunset times (for Walvis Bay) obtained from http://www.sunrise-and-sunset.com. The AANDERAA anemometer at the Pelican Point lighthouse (Fig. 2.1) was used to measure wind speed and direction at 10 min intervals: focal plane at 35 m, measurement height extended to 39 m. Implausible data were removed and an error in wind direction was corrected as described by Vogt (2016). Moon illumination, or the fraction of the moon's surface illuminated by the sun was used as a measure of the lunar cycle, and data were downloaded from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php; Fraction of the Moon Illuminated, at Midnight, Zone: 11h East of Greenwich). For practical purposes, phases of the moon and the fraction of the moon illuminated are independent of the location on the Earth from where the moon is observed: that is, all the phases occur at the same time regardless of the observer's position.

Sample processing

Medusae were identified, to the lowest taxonomic level, and counted from each sample using an Olympus SZ61 stereo microscope, following staining with Rose Bengal (final concentration ~50 mg L^{-1}). Counts were standardized to the number of individuals per 100 m^{-3} per sampling station with the knowledge of the volume of water filtered by the net. Scyphozoans were sorted morphologically into transitional stages of metamorphosis (see Chapter 3): Stage 0, Stage 1, Stage 2 and Stages 3–5 (combined). When the abundance of ephyrae in a sample appeared visually very high (>300 individuals), six subsamples were taken using a Hensen Stempel pipette, and all the individuals in each subsample were counted. In cases where the individual sample filled more than one 250 ml plastic jar and the visual presence of ephyrae was very high, all the jars were poured together and split into two equal parts by a Folsom Plankton Splitter before being subsampled as described above. Individual specimens that were too large to be pipetted were handpicked.

Data analysis

Environmental data: Missing wind speed values were estimated using the expected maximization (EM) algorithm function in Primer 6 (Clarke & Warwick 2001), since ≤5% of data were absent (Clarke & Gorley 2006). Measured environmental data were log(x + 1) transformed and normalized to remove the influence of differing scales of measurement. A similarity matrix between the data from each sampling date was generated based on Euclidean distance in order to explore structure in the multivariate environment, using PRIMER 6 (Clarke & Warwick 2001). Patterns were visualised using Principal Coordinates Analysis (PCO).

PERMANOVA (PERMANOVA+ for PRIMER 6) tested the multivariate hypothesis of no differences in the environmental "composition" of the samples by the fixed factors: (spring: September–November, summer: December–February, autumn: March–May, winter: June–August), and year (2012, 2013). The PERMANOVA routine, tests the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) experimental design, on the basis of Euclidian distance, using permutation methods (Anderson et al. 2008). Following the main overall test, pair-wise PERMANOVA tests were done when significant ($p < 0.05$) differences in the community structure were detected for the factors and their combinations. Significance level for the PERMANOVA routine is $p < 0.05$.

For preceding environmental data: In order to explore the response of the jellyfish community with the preceding environment, the best fit between these variables was identified by the coefficient of determination (R^2) of linear regressions. R^2 was calculated (1) between measured contemporary environmental parameters with each other, and (2) between mean abundances of main medusa species with measured contemporary and preceding environmental parameters (1–14 day lags), respectively.

Biotic data: Of the 181 samples collected, 166 contained pelagic cnidarians and ctenophores and were subjected to further analysis. Specimens that could not be identified to family or sub-class level were excluded from the analysis (0.8 % of the overall individuals). Before looking at temporal and spatial patterns in the multivariate dataset, all data were fourth-root transformed, to take into account the rarer species, and a Bray-Curtis resemblance matrix between each sample was computed using PRIMER 6 & PERMANOVA+ software. The similarity matrix was visualized using non-metric multi-dimensional scaling

(nMMDS), with station, year and season being considered as *a priori* factors (Anderson et al. 2008). A Canonical Analysis of Principal Coordinates (CAP) routine was performed and a vector overlay of Pearson's correlation of individual taxa (correlation >0.2) was superimposed with the resulting CAP axes in order to visualise which taxa characterise the differences among seasons since significant differences between seasons were established by PERMANOVA (see Results below). The PERMANOVA routine was applied to test for statistically significant differences in species abundances, among (*a priori* defined) groups of factors (stations, seasons and years considered as fixed), through the use of unrestricted permutation of raw data. Pair-wise PERMANOVA tests was done when significant ($p < 0.05$) differences in the community structure were detected for the factors and their combinations.

As season and year were identified as key drivers of community structure (see Results below), a Similarity Percentage (SIMPER) analysis was employed to the transformed abundance data to determine the contribution of each species to the average (dis)similarity between and within seasons, as well as for year. The SIMPER routine decomposes average Bray-Curtis similarities between all pairs of samples within seasons or years, respectively, into percentage contributions from each species while listing the species in decreasing order of such contributions (see Clarke & Gorley 2006 for details). This technique seeks to identify taxa that are principally responsible for differences detected in community structure between seasons or years.

In order to determine which measured contemporary and preceding environmental predictors (sea bottom temperature, moon illumination, day length and wind speed) were responsible for driving any observed pattern in the biological resemblance matrix, data were analysed by a Distance Based Linear Model (DistLM). The model is visualized by using distance-based redundancy analysis (dbRDA), which is an ordination of the fitted values from the multivariate regression model (Anderson et al. 2008). Since >5% of wind speed data were missing when data lags were applied, this parameter was excluded from the preceding environmental predictors in the DistLM analysis.

The non-parametric Kendall's tau correlation coefficient was computed (with a bias and corrected accelerated confidence interval (BCa), estimated from 1000 bootstrap samples) to assess the likelihood of a temporal trend between the abundance of hydromedusae and scyphozoans. Kendall's tau measures

the strength of the monotonic relationship and is based on ranks, is resistant to effects of outliers and is well suited for identifying trends when extreme values and skewness are present (Helsel & Hirsch 1992).

Upwelling phase data: Sea bottom temperature and wind speed data were grouped into three phases of upwelling as described by O'Toole (1980), Boyer et al. (2000), Cole & Villacastin (2000) and Louw et al. (2016), as following: active upwelling (during July to October), inactive upwelling (during December to April), and an intermediate period for the rest of the remaining months (November, May and June). All of the 181 biological samples collected were subjected to analysis. To test for differences in the phases of upwelling, by sea bottom temperature and wind speed, the Kruskal-Wallis tests were used since the data was not normally distributed. This test was also used to test for significant differences in the abundance of medusae (hydromedusae and scyphomedusae (only Stages 0–1)) collected across the three phases of upwelling. When significant differences were detected Dunn's post-hoc tests were carried out on each pair of groups. For these multiple pair tests, SPSS makes a Bonferroni adjustment to the *p*-value: by multiplying each Dunn's *p*-value by the total number of tests being carried out. The non-parametric Kendall's tau correlation coefficient was calculated (with a bias and corrected accelerated confidence interval (BCa), estimated from 1000 bootstrap samples) between medusa abundance (hydromedusae and scyphozoans) and sea bottom temperature and wind speed. Correlations were calculated across the year and between upwelling phases. All statistical tests were conducted using IBM SPSS v23 Statistics software (SPSS Inc., Chicago, USA).

RESULTS

Environmental data

The mean monthly sea bottom temperatures repeatedly oscillated between 12.9 °C in spring (September) and 18.3 °C in summer (December) (Fig. 2.2). Day length was longest (812 minutes) between 14–27 December and shortest (643 minutes) between 15–26 June. There was an apparent visual lag between day length and sea temperature of 50 days and 90 days among each other's peaks and troughs, respectively. There was no seasonal change in the length of synodic months or the pattern of moon illumination. Monthly average wind speed values varied between 4.4 and 6.4 $m.s^{-1}$. Generally,

wind speed values were highest during late winter (August) to mid spring (October) while lowest values were observed during summer (November–January).

The two axes of the PCO (Fig. 2.3) explained 68.1% of the variability in the multivariate data set. It is clear from this that environmentvaried were separated by season and those parameters that vary in a seasonal way (temperature, day length and wind) (Fig. 2.3A), but not on an annual (Fig. 2.3B), basis. Note that lunar illumination fails to separate samples on the basis of seasonality, as expected. These observations are supported by the results of the PERMANOVA, which confirm that no significant differences (*p*(perm) = 0.433) in environmental variables existed between the years (Table 2.1), but that significant differences (Tables 2.1 and 2.2) were detectable by season (*p*(perm) = 0.001). That said, there was a significant interaction between season and year (*p*(perm) = 0.001).

Seasonal abundance and occurrence of taxa

In total, 12 taxa were found from two phyla: Cnidara and Ctenophora. Eight genera could be identified (*Chrysaora*, *Muggiaea*, *Obelia*, *Proboscidactyla*, *Bougainvillia, Clytia, Pleurobrachia* and *Mitrocomella*) from seven families (Pelagiidae, Diphydiae, Campanulariidae, Proboscidactylidae, Bougainvillidae, Pleurobrachiidae and Mitrocomidae). Only three taxa were identifiable to species level: *Chrysaora fulgida, Chrysaora africana* and *Muggiaea atlantica*. Three taxa could only be determined to subclass (Anthomedusae and Leptomedusae) or order (Calycophorae) levels. The rest of the taxa were either too damaged to identify or were juveniles, and so were not identifiable using adult-based keys (Kramp 1959; Pagès et al. 1992; Bouillon et al. 2006).

The monthly mean abundance of assemblaged members varied greatly between seasons and years (Fig. 2.4; Fig. 2.5). The highest number of *Chrysaora fulgida* (all stages combined) was recorded (Fig. 2.4.A) in October 2012 (170 219 ind. 100 m^{-3}), whilst a much lower peak was present during August 2013 (23 499 ind. 100 m^{-3}). *Obelia* sp. peaked in abundance (Fig. 2.4.B) in March 2012 (1 089 ind. 100 m^{-3}) and in February 2013 (947 ind. 100 m^{-3}) and was absent, in both years, during September. *Bougainvillia* sp. was present almost all year around (Fig. 2.4.C), illustrating peaks in abundance during September 2012 (84 ind. 100 m^{-3}), February 2013 (155 ind. 100 m^{-3}), August 2013 (351 ind. 100 m^{-3}) and November 2013 (144 ind. 100 m^{-3}); and was absent in May 2012, July 2012 and March 2013. *Muggiaea*

atlantica illustrated two peaks (Fig. 2.4.D) in abundance during August 2012 (1 198 ind. 100 m^{-3}) and December 2013 (475 ind. 100 m^{-3}). Unidentified Leptomedusae (Fig. 2.4.E), Anthomedusae (Fig. 2.4.F) and *Proboscidactyla* sp. (Fig. 2.4.G) peaked in December 2012 (161 ind. 100 m^{-3}) and January 2013 (1 296 ind. 100 m^{-3}); in August 2012 (94 ind. 100 m^{-3}) and January 2013 (161 ind. 100 m^{-3}); and in October 2012 (84 ind. 100 m^{-3}) and August 2013 (473 ind. 100 m^{-3}), respectively.

The less common taxa (Fig. 2.4. H-J) included *Clytia* sp., *Mitrocomella* sp., *Pleurobrachia* sp. and ephyrae of *Chrysaora africana* (Fig. 2.5). *Clytia* sp. showed two peaks during the months of August 2012 (29 ind. 100 m^{-3}) and January 2013 (17 ind. 100 m^{-3}). Both *Mitrocomella* sp. and *Pleurobrachia* sp. were present in only one specific year (Fig. 2.4.I-J). *Chrysaora africana* Stage 0 (Fig. 2.5.A) was only recorded during July 2012 (4 ind. 100 m^{-3}) whereas Stage 1 (Fig. 2.5.B) was present, although in very low abundance, during July 2012 (20 ind. 100 m^{-3}), August 2012 (4 ind. 100 m^{-3}), June 2013 (1 ind. 100 m^{-3}), August 2013 (20 ind. 100 m^{-3}) and October 2013 (4 ind. 100 m^{-3}). Combined, both *C. africana* Stages 0 and 1 were absent in all zooplankton samples, in both years, during the period November till May (Fig. 2.5.C).

No rudimentary ephyrae (Stage 0) of *Chrysaora fulgida* were recorded in the zooplankton samples during the months of December to June, however they made a first appearance in the water column (Fig. 2.5.D) in July 2012 (225 ind. 100 m^{-3}) and in August 2013 (771 ind. 100 m^{-3}), and peaked in abundance in September 2012 (11 158 ind. 100 m^{-3}) and in August 2013 (771 ind. 100 m^{-3}). *Chrysaora fulgida* Stage 1 (Fig. 2.5.E) was absent during the period January to June, and peaked in October 2012 (160 643 ind. 100 m^{-3}) and in August 2013 (22 618 ind. 100 m^{-3}). Combined, both *C. fulgida* Stages 0 and 1 were absent in all zooplankton samples, in both years, during the period January to June (Fig. 2.5.F) whilst dominating assemblages each month over the period July to November. This stage (0 & 1) showed peaks in October 2012 (168 933 ind. 100 m^{-3}) and in August 2013 (23 389 ind. 100 m^{-3}). *Chrysaora fulgida* Stage 2 peaked in October 2012 (107 ind. 100 m^{-3}) and in September 2013 (190 ind. 100 m^{-3}), and was absent during the period January to June (Fig. 2.5.G). Stages 3–5 of *C. fulgida* peaked (Fig. 2.5.H) in May 2012 (107 ind. 100 m^{-3}), October 2012 (213 ind. 100 m^{-3}), December 2012 (282 ind. 100 m^{-3}), May 2013 (189 ind. 100 m^{-3}) and in December 2013 (80 ind. 100 m^{-3}).

Assemblages

It is clear from the way that the samples are distributed in the nMMDS plots (Fig. 2.6–2.8) that communities collected from the five stations within Walvis Bay were similar (Fig. 2.6), but that there was a separation by season (Fig. 2.8). These observations are supported by the PERMANOVA results, which confirm that no significant differences (*p*(perm) = 0.492) in community structure existed between the stations (Table 2.3), but that significant differences (Tables 2.3 and 2.4) were detectable by season (*p*(perm) = 0.001), year (*p*(perm) = 0.001) and the interaction between season and year (*p*(perm) = 0.001). This interaction indicates that the seasonal patterns differed between years.

The CAP analysis illustrated a clear separation of the four seasons (Fig. 2.8B) and calculated two test statistics which were both highly significant for seasonality. In a leave-one-out cross validation as an integral part of CAP 67.47% of the samples were classified correctly into their respective seasonal groupings. The vector overlay on the CAP axes separated the following taxa groups in high abundance during a particular season: *Chrysaora fulgida* Stages 0, 1 and 2 during some winter periods and predominantly in spring; *Chrysaora fulgida* Stages 3–5 during summer; *Proboscidactyla* sp. during some spring periods and predominantly in winter.

The total abundance of scyphozoans was significantly, although negative, correlated with the abundance of hydromedusae: T = -0.144 [-0.244, -0.039], n = 166, *p* = 0.009.

Environment-biotic relations

With contemporary environment: The results of the marginal DistLM test on the biological data indicated that three of the four predictor variables had a significant impact on the structure of the communities (sea bottom temperature, day length and wind speed in order of importance), whereas moon illumination was not significant (Table 2.5). Even though the overall model included all four predictor variables, it could simply explain 28.16% of the pattern (Table 2.5). This is illustrated in the dbRDA ordination plot (Fig. 2.9; Fig. 2.10), the first two (of four) axes captured 92.28% of the fitted variation and 25.99% of the total variation, separating samples by sea temperature (dbRDA1) and day length (dbRDA2). Four clear seasonal groupings could be discerned (Fig. 2.9), but not for years (Fig. 2.10).

In an effort to understand the relatively low proportion of the variability in structure of the biological communities that could be ascribed to the measured environmental variables, reference is made to the results of the SIMPER analyses. These data are shown in Fig. 2.11, Fig. 2.12, Table 2.6 and Table 2.7, from which it is clear that changes in communities through time (season or year) reflect not so much the presence or absence of taxa but of changes in the relative abundance of the community.

With preceding environment (see Annexure 1): The coefficients of determination (R^2) were very low between measured environmental parameters of each other (Table S1) and between the main medusae and preceding environmental parameters (Table S2). A 14-day lag for all environmental parameters was applied to the DistLM analysis. The results of the marginal DistLM test on the biological data indicated that all three predictor variables had a significant impact on the structure of the communities (sea bottom temperature, day length and moon illumination in order of importance) (Table S3). Even though the overall model included all three predictor variables, it could simply explain 22.28% of the pattern (Table S3). This is illustrated in the dbRDA ordination plot (Fig. S1; Fig. S2), the first two (of three) axes captured 96.3% of the fitted variation and 21.46% of the total variation, separating samples by sea bottom temperature (dbRDA1) and day length (dbRDA2). Four clear seasonal groupings could be discerned (Fig. S1), but not for years (Fig. S2).

Upwelling phases

Strong evidence of a difference between the mean ranks of at least two pairs of groups was detected between the upwelling phases by sea bottom temperature ($H(2) = 33.03$, $p < 0.001$) and wind speed ($H(2) = 12.169$, $p = 0.002$), respectively. Sea bottom temperature was significantly cooler ($p < 0.001$) during the active upwelling phase (Median *(Mdn*) = 12.99) than during the inactive phase (*Mdn* = 17.54), while it was significantly warmer ($p = 0.010$) during the inactive phase than the intermediate phase (*Mdn* = 14.00). Wind speed was significantly higher ($p = 0.006$) during the active upwelling phase (*Mdn* = 4.96) than during the inactive phase (*Mdn* = 3.51), while it was significantly higher during the active phase ($p = 0.020$) than the intermediate phase (*Mdn* = 3.67). Wind speed and sea bottom temperature were significantly, although negative, correlated across the year (T = -0.238 [-0.400, -0.079], n = 42, $p = 0.026$); with no significant relationship within each upwelling phase. These results are consistent in characterising

the phases of upwelling as described by O'Toole (1980), Boyer et al. (2000), Cole & Villacastin (2000) and Louw et al. (2016).

There were no significant differences ($H(2) = 2.371$; $p = 0.306$) between the abundance of hydromedusae of the different phases of upwelling. However, difference between the mean ranks of at least two pairs of groups was detected between the abundance of scyphomedusae (Stages 0–1) of the different phases of upwelling ($H(2) = 26.451$, $p < 0.001$). The abundance of scyphomedusae (Stages 0–1) was significantly higher ($p < 0.001$) during the active upwelling phase (*Mdn* = 4211.25) than during the inactive phase (*Mdn* = 0), whilst it was also significantly higher ($p = 0.001$) during the active phase than the intermediate phase (*Mdn* = 0). No significant correlations were found between the abundance of hydromedusae and sea bottom temperature (Fig. 2.13A) and wind speed (Fig. 2.13B), respectively, for across the year or within the upwelling phases. Scyphomedusae (Stages 0–1) abundance (Fig. 2.14) correlated significantly, although negative, with sea bottom temperature (T = -0.551 [-0.656, -0.428], n = 45, $p < 0.001$) and positive with wind speed (T = 0.259 [0.006, 0.473], n = 42, $p = 0.022$) for each across the year, whilst no further relationships were evident within the upwelling phases.

DISCUSSION

From this 23-month time series, all of the taxa recovered were characteristically neritic, and include meroplanktonic Hydrozoa and Scyphozoa (Kramp 1959; Pagès & Gili 1991), as well as cydippid ctenophores and shallow water siphonophores. In general the same assemblage of jellyfish taxa (*Bougainvillia*, *Obelia*, *Clytia*, *Chrysaora fulgida* and *Muggiaea atlantica*) was present across seasons and years. However, the community composition and densities varied seasonally and inter annually. Studies have reported significant inter annual variability in the abundance of jellyfish populations (Lucas et al. 1995; Nicholas & Frid 1999; Ballard & Myers 2000). Several species of jellyfish are capable of rapid growth, high fecundity short generation times and high ingestion rates; and their populations may thus respond quickly to favorable environmental conditions (Alldredge 1984). No clear seasonal succession of species was observed, in this study, except for the l developing stages of ephyrae.

All taxa mentioned here have been previously reported from the wider Benguela upwelling ecosystem (Pagès & Gili 1991; Fearon et al. 1992; Gibbons et al. 1992; Pagès 1992; Pagès et al. 1992;

Jung 2010). Whilst ephyrae of *Chrysaora fulgida* (Stages 0 and 1) were dominant overall, and peaked in abundance during mid-spring (Year 2012: 168 933 ind. 100 m^{-3}) and late winter (Year 2013: 23 389 ind. 100 m^{-3}), they were not present all year round, being replaced (in part) by *Obelia* in summer and autumn, *Bougainvillia* in spring and summer, and *Muggiaea atlantica* in summer. Seasonal changes in the composition and structure of the community were driven primarily by bottom water temperature and day length (explaining 24% of the variability in community structure), with wind speed and moon illumination playing a secondary role. There are no comprehensive long-term data on the abundance and distribution of jellyfish in the northern Benguela system for comparative purposes, and even seasonal studies sampled frequently throughout the whole year are lacking. Most studies that have been conducted in the northern Benguela have tended to focus on short window periods of sporadic sampling and they have often implemented different sampling methods and equipment (Pagès & Gili 1991; Fearon et al. 1992; Gibbons et al. 1992; Pagès 1992; Jung 2010). Some differences with the study of Pagès et al. (1992) were noted regarding *Obelia* sp. and *Aglauropsis edwardsii*.

The environmental trigger for the release of medusae by the benthic life-history stage of cnidarians may involve synergistic interactions of multiple factors in a correct sequence at critical periods (Berrill, 1949). This in turn is likely to be influenced by microscale variations in hydrography, topographic complexity and the location of polyps (Pitt and Kingsford 2003), and of course will vary with individual species (Elmhirts 1925; Thiel 1962; Boero 1984; Gröndahl & Hernroth 1987; Carré & Carré 1990; Brewer & Feingold 1991; Arai 1992a; Byrne 1995; Purcell et al. 1999b; Ballard & Myers 2000; Lucas 2001; Colin & Kremer 2002; Willcox et al. 2008; Lucas et al. 2012; Baumsteiger et al. 2017; Sukhoputova & Kraus 2017). The generally small amount of variation in the biological data collected here that could be explained by the measured environment is testament to this complexity, though a fuller suite of variables could have been measured.

That said, the abundance of scyphomedusae (Stages 0–1) was negatively correlated with sea bottom temperature and positively correlated with wind speed: the onset of upwelling clearly impacts ephyra release but it had no effect on hydromedusa abundance. In the Bay of Panama (Tropical East Pacific), a two-fold increase in hydromedusa abundance was linked with active upwelling (reduced water temperature and increased primary and secondary production), despite that the number of taxa remained

constant throughout the year (Miglietta et al. 2008). Reasons for the different responses of the two medusae groups, sharing the same upwelling environment, are unclear in this study. Whether this is due to a lack in capturing the (unmeasured) environmental variables in this study, or that the changes in hydromedusae abundance are effected through more subtle and continued changes in the environment that favour the gradual recruitment and differential survival of the assemblage members (Gibbons & Buecher 2000) is unknown, it represents an interesting topic for future investigations. Despite considerable variation that exist due to regional and local fluctuations in environmental parameters off Namibia, seasonality due to the influence of upwelling has been reported for water temperature, salinity, primary production and secondary production (O'Toole 1980 and references therein; Cole & Villacastin 2000; Hansen et al. 2005; Louw et al. 2016).

Strobilation by polyps of *Chrysaora fulgida,* in this study, thus seems to be initiated by the same types of environmental stimuli (temperature and possibly day-length) observed for other schyphozoans, elsewhere in the world, and is summerised as following: Ephyrae production (in the laboratory) and medusae abundance (*in situ*) of *Chrysaora quinquecirrha* in Chesapeake Bay (USA) were regulated by water temperature, salinity and prey abundance whilst no apparent relationship between rainfall and the timing of recruitment of *Catostylus mosaicus* in Botany Bay (Australia) were evident (Pitt & Kingsford 2003). Purcell et al. (2009) suggested that strobilation in *Aurelia labiata* may be cued *in situ* by increasing temperature, rainfall (causing nutrient runoff) and light intensity in Cornet Bay, Washington, USA. These environmental factors stimulate plankton production (primary and secondary), which would ensure high food abundances for the polyps and newly strobilated ephyrae (Purcell et al. 2009). The latter authors also showed that elevated levels of light, temperature, and zooplankton coincided with an above average year of increased and accelerated strobilation. Almost all year-round strobilation of *Aurelia* sp. 5 was exhibited in the Veliko Jezero lake (Croatia) whilst the parental polyps were found at depths below the thermocline (>20 m) where the temperature was relatively stable throughout the year (Kogovšek et al. 2012). The bathymetry of this lake may be a pivotal factor in allowing the continuous recruitment of ephyrae and might also be linked to other factors than temperature such as light and/or food availability (Kogovšek et al. 2012).

Absolute temperature and magnitude of temperature change are important factors (Lucas & Dawson 2014) that initiate the strobilation process of polyps by influencing the timing and rate of ephyra production (e.g. Kawahara et al. 2006; Prieto et al. 2010); determine the development duration, the number of ephyrae produced per polyp, the frequency of strobilation events and the proportion of polyps to strobilate (e.g. Purcell 2007; Holst 2012a); and can be species-specific. Water temperature has the greatest support in the timing of strobilation, as illustrated by the seasonal appearance of ephyrae in the majority of taxa residing in the temperate areas of northern hemisphere (see Lucas et al. 2012). Temperate Semaeostomeae populations broadly exhibited their main strobilation periods *in situ* during late winter–early spring for *Aurelia aurita* and *Aurelia labiata*, and mid spring–late spring for *Chrysaora quinquecirrha (*Lucas et al. 2012). Elevated temperatures generally stimulate temperate species to produce more ephyrae although polyps of some tropical species may be intolerant towards greatly elevated temperatures such as *Mastigias* (Lucas et al. 2012).

Studies associated with the onset of strobilation with a drop in water temperature are also reported. The release of *Aurelia aurita* ephyrae in the Suez Canal seemed to be induced by a drop in ambient temperature to <16 °C, with a peak release that occurred in winter (El-Serehy & Al-Rasheid 2011). In Gullmar Fjord, Sweden, the ephyrae of *Aurelia aurita* were the most abundant during autumn when the temperature at 20 m depth dropped from 15 °C to 12 °C to 9 °C (Hernroth & Gröndahl 1983, 1985a) and coincided with the highest peak in zooplankton. These high numbers of polydisc polyps were equated towards high food availability and a second strobilation peak was shown during winter-spring period (Hernroth & Gröndahl 1983, 1985a). *Aurelia aurita* polyps in the northern Adriatic Sea strobilated during the winter (November–December) when temperature was <15 °C *in situ* and this was also confirmed by polyp culturing (Di Camillo et al. 2010). In Tapong Bay (Taiwan, China), the strobilation of *Aurelia aurita* occurred during autumn–winter, when the water temperature reached minima (~17 °C vs. ~30 °C in summer) (Lo & Chen 2008). Laboratory experiments showed that strobilation of *Rhizostoma octopus* could be induced by both a drop (15 to 10 °C), with the most abundant ephyrae released, and rise (5 to 10 °C; 10 to 15 °C) in temperature (Holst et al. 2007). It is therefore suggested that this species may strobilate twice a year, in autumn after a temperature drop and again in spring after a temperature increase (Holst et al. 2007) similarly as to *Aurelia aurita* in the Gullmar Fjord (Hernroth & Gröndahl 1983,

1985a). However, the magnitude of temperature change might be more crucial than absolute temperature for inducing individual polyps of most species to strobilate (Liu et al. 2009; Lucas et al. 2012).

The most common Scyphozoa described in the Benguela system is *Chrysaora fulgida* and it is more abundant in the northern than the southern Benguela, and shows patchiness in waters shallower than 200 m (Gibbons et al. 1992). Even though medusae of *C. fulgida* were present throughout the year in this study, the various ephyral transitional stages corresponded to a seasonal sequence: the early stages only being present during the mid-winter to early summer periods since the individuals grew into older transitional stages. This is in contrast with *Catostylus mosaicus*, inhabiting the subtropical southern hemisphere (Australia, Botany Bay and Lake Illawarra), that displayed a sporadic annual recruitment pattern apart from during late winter and spring (Pitt & Kingsford 2003).

The highest observed abundance of *Chrysaora fulgida* ephyrae (168 933 ind. 100 m^{-3}) was almost 5.14 times higher than the maximum value reported in the literature for any scyphozoan *in situ* (Table 2.8). The abundance of ephyrae is typically higher in enclosed and semi-enclosed ecosystems than in open environments (Yasuda 1968; Möller 1980; Hernroth & Gröndahl 1983; Papathanassiou et al. 1987; Schneider 1989; Olesen et al. 1994; Ishii & Båmstedt 1998; Toyokawa et al. 2000; Marques et al. 2015). The Bay of Walvis Bay is an open oceanic embayment and has a circulation pattern with eddies that allows a water residency time duration of half to one week (DANIDA 2003; Delta Marine Consultants & CSIR 2009), which could allow accumulation of ephyrae.

The presence of Stage 0 ephyrae of both *Chrysaora* species confirm the presence of polyps in the vicinity of Walvis Bay and the absence of year round recruitment. This is in agreement with conclusions from Flynn et al. (2012) who suggested that polyp beds of *C. fulgida* likely exist along the Namibian coastline, despite its generally muddy and sandy geology (Rogers & Bremner 1991), and is in contrast to Fearon et al.'s (1992) hypothesis that a northern population of polyps sustains the *C. fulgida* population off Namibia. Evidence of a good temporal correlation between the onset of strobilation and the abundance of ephyrae is not a given in the field (Thiel 1962; Malej et al. 2012) although some studies did report positive correlations (Hernroth & Gröndahl 1983).

A contributing factor towards the high abundances might also be the readily availability of various suitable artificial and natural substrates for planulae to settle on in the Bay. Polyps of *Chrysaora pacifica*

(Toyokawa 2011) are found on bivalve shells and stones amongst shallow sediments in Sagami Bay, Japan, while *Chrysaora quinquecirrha* polyps are attached to oyster shells in Chesapeake Bay, USA (Cargo & Schultz 1967). Although not all surfaces are equally suitable for the settlement of planulae (Purcell 2012), the planulae of some scyphomedusae appear to prefer artificial above natural surfaces (e.g. Holst & Jarms 2007; Hoover & Purcell; Purcell et al. 2007, 2009; Duarte et al. 2013), and many polyps preferentially attach to the undersides of submerged objects (Lo et al. 2008; Di Camillo et al. 2010; Duarte et al. 2013). Particularly, in the Walvis Bay area where the substrates mainly consist of diatomaceous mud and sandy mud (Shannon 1985), as such artificial substrates for polyps are likely to be more crucial for settlement. It is noteworthy that, although the study of Unterüberbacher (1964) primarily dealt with Copepoda observed in the coastal - and routine area off Walvis Bay (while big Ctenophora and medusae were removed from the samples before measuring), the author never mentioned the presence of ephyrae despite noting jellyfish species — *Liriope tetraphyllum*, siphonophores (*Muggiaea atlantica*, *Abylopsis tetragona*, *Agalma* sp., *Lensia* spp., *Physophore hydrostatica*), *Beroë* and *Pleurobrachia* — in his samples. Hence, suggesting the possible absence of ephyrae of *Chrysaora* or that their numbers were limited and not deemed worthy enough to be mentioned during that time period (1959–1962) off Walvis Bay.

The very low abundance and infrequent appearance of *Chrysaora africana* suggest that it is a relatively rare species in Walvis Bay, which is in agreement with our understanding of its distribution along the central west coast of Africa (Kramp 1961). Patterns of ephyrae release appear to be different from those of *C. fulgida*, which is perhaps not surprising give their different centres of distribution, though data are too scant for detailed analysis. In this study, polyps of *C. africana* appeared to strobilate and release ephyrae at a slightly earlier date than those of *C. fulgida* in the winter, which is reflected by their larger size in July. Interspecific predation among jellyfish is broadly documented (Strand & Hammer 1988; Hansson 1997a; Purcell 1991a, 1991b; Arai 2005; Hosia & Titleman 2010; Bayha et al. 2012; Tilves et al. 2013), and personal observations indicate that ephyrae of *C. africana* eat ephyrae of *C. fulgida.* On the other hand, the temperature range by which strobilation occurs can be species-specific whereby the dissimilarities in the first appearance of the ephyrae might reflect the physiological temperature limits of the different species (Lucas et al. 2012).

There was considerable inter-annual variability in the timing and abundance of *Obelia* medusae with the greatest abundance during summer and early autumnin Walvis Bay. Medusae of *Obelia* may be present in plankton samples throughout the year (Russel 1953), whereas their greatest abundances in temperate waters are generally observed between spring and autumn (Russel 1953; Nicholas & Frid 1999). Contrary to the present study, Pagès & Gili (1991) did not report its presence while Pagès (1992) reported this taxon as absent in his samples from December to February, with a very low density during March (0.03 ind. 1000 m^{-3}). Pagès et al. (1992) described this taxon as a coastal species off Namibia albeit characterizing it as "quite scarce in the samples examined" which could only be found inshore off Cape Cross, in Namibia waters. Jung (2010) reported the inner shelf presence of *Obelia* sp. (195 ind. 1000 m^{-3}) during December 2009, in the northern Benguela current region. Many nominal species of *Obelia* hydroids are commonly found worldwide but as yet no characteristics are available to reliably identify the medusae specimens of this genus down to species level (Russel 1953; Bouillon 1999).

Aglauropsis edwardsii, described by Pagès et al. (1992) as a common species throughout the northern Benguela, was noticeably absent in the samples collected for this study and of Jung (2010). Pagès & Gili (1991) reported, during a strong intrusion of Angolan water and the abatement of upwelling, the highest densities (10.4 ind. 1000 m^{-3}) of this species in the central area (20° to 23°S), followed by lower densities (3.4 ind. 1000 m^{-3}) in the southern area (23° to 26°30'S) whilst being absent in the northern area (17°15' to 20°S) off Namibia. According to Pagès et al. (1992) this taxon forms inshore and offshore aggregations – with higher densities noted during upwelling periods – in the northern Benguela and is noted as absent in the southern Benguela. The highest densities reported by Pagès (1992) were observed during February (5.1 ind. 1000 m^{-3}) while it was present throughout the 4-month study period (December to March). All hydroids can become dormant while regressing to resting hydrorhizae, and substantially long periods of diapause have been reported for some species (Bouillon et al. 2004). This alternated pattern of presence makes it possible for the animals to be active during favourable conditions, but might also be a tactic for a species to disappear for decades and to reappear suddenly again (Bouillon et al. 2004). In addition, the ability of gelatinous plankton (and of its benthic stage) to be present in mass occurrence and to be absent even for decades afterwards forms integral part of their ecology

(Bouillon et al. 2004). On the other hand, the absence of some species might be a warning sign for the imminent loss of a particular habitat type (Boero & Bonsdorff 2007).

In this study, the Siphonophorae *Muggiaea atlantica* showed considerable inter-annual variability in the timing and abundance with the greatest abundance during summer and early autumn in Walvis Bay. Compared to this study, Pagès (1992) found a similar continuous inshore presence of *M. atlantica* from early summer to early autumn off Namibia which was reported as the most abundant Hydrozoa species (up to 1 283.18 ind. 1000 m^{-3}) during that time period. Pagès (1992) characterised *M. atlantica* as a strict neritic species that can be found along the Namibian coast, with the highest abundance inshore that progressively decline towards the offshore direction (Pagès 1992; Pagès & Gili 1992). However, Unterüberbacher (1964), primarily studying copepods in the coastal – and routine area off Walvis bay, noted (during the period 1959–1962) that "the most abundant Siphonophore is *Muggiaea atlantica*, which is more common beyond the continental shelf, but is also found near the coast". Pagès & Gili (1991) indicated that their population abundances did not vary significantly between periods of high and low upwelling activities in the Benguela current while the highest densities (2 125.4 ind. 1000 m^{-3}) were sampled in the central area (20° to 23°S) off Namibia. *Muggiaea atlantica* is a low- to mid-latitudinal (55°N–37°S; Pugh 1999) neritic species that has progressively expanded geographically towards new habitats such as the North Sea (Greve 1994) and Adriatic Sea (Kršinic & Njire 2001; Miloš & Malej 2005; Batistić et al. 2007), South Pacific Ocean (Palma et al. 2011, 2014) and northeast Atlantic Ocean (Blackett et al. 2017); and has establish itself as a resident in the Western English Channel (body of water that links the southern part of the North Sea to the Atlantic Ocean) (Blackett et al. 2014). Its abundance is documented as seasonal, and in parts of the northern hemisphere it has population peaks in spring (May to June) and again in autumn (September to November) (Arai 2009b). Temperature and food availability are considered as the main environmental factors linked to the successful reproduction of *Muggiaea* sp. (Purcell 1982; Carré & Carré 1991; Batistić et al. 2013). The invasion of *M. atlantica* into the German Bight during July 1989 demonstrated that this species can reach maxima of 500 siphonophore colonies m^{-3} in inshore waters that lead to the depletion of copepods with concomitant cascading ecosystem effects (Greve 1994). A bloom of *M. atlantica* caused mass mortalities of caged salmon (>100 000 fish) in

Norway during 2007 at densities of 2 000 colonies m^{-3} (Fosså et al. 2003) and is believed to be the culprit that caused the death of >1 000 000 cultured salmon in Ireland during 2003 (Cronin et al. 2004).

The calycophoran siphonophore *Muggiaea atlantica* is a holoplanktonic species with a metagenic life cycle comprising an alternation of generations between an asexual polygastric colony stage (nectophore with trailing siphosome that bears zooids), and the sexual eudoxid colony stage (monogastric) that becomes detached from the nectophore (Blackett 2016). Note that eudoxids and polygastric nectophores are not differentiated in this study. Blackett et al. (2015) indicated a significant linear relationship for *M. atlantica* between the abundance of the eudoxid - and the polygastric stage: the eudoxid stage is created straight from the polygastric stage, and that the eudoxid production rates are therefore linearly related to the size of the polygastric colony. A rapid growth in abundance of the population of *Muggiaea atlantica* was associated with the fast release of eudoxids and maturation of gonophores (Batistić et al. 2013). Greve (1994) reported the invasion of *M. atlantica* siphonophore colonies in the German Bight were accompanied by eudoxids, whilst the highest densities of siphonophore colonies (500 m^{-3}) were associated with the presence of eudoxids (53 m^{-3}). This implies a total reproduction period of two months for *M. atlantica* in Walvis Bay during mid-summer and in late winter. Or alternatively that the abundances of *M. atlantica* might be a reflection of 'apparent' blooms or aggregations, bearing in mind that it is holoplantonic and found in the upper 100 m of temperate and subtropical inshore waters (Arai 2009b): making it more inclined to be transported by the ocean surface currents (Mackie et al. 1987).

Bougainvillia sp. was present during every season, and recorded the highest densities during late winter to summer in Walvis Bay. Compared to this study, Pagès (1992) found a similar uninterrupted inshore presence albeit in very low densities of *Bougainvillia macloviana* over the period December 1981 to March 1982. Pagès et al. (1992) described the presence of two species of *Bougainvilla viz. Bougainvillia macloviana* and *Bougainvillia platygaster* in the Benguela Current. The most likely species present in Walvis Bay would be *Bougainvillia macloviana* since it is characterised as a common coastal water species in the northern Benguela, mainly present during active upwelling that can reach densities of 38 ind. 1000 m^{-3} and is less common in the southern Benguela (Pagès et al. 1992).

Clytia sp. was sporadically present in small quantities in Walvis Bay. A *Clytia* sp. recorded as the second highest abundant coastal Hydroidomedusa species in Pages' (1992) study, during December 1981 and January 1982, in the northern Benguela system. Pagès et al. (1992) described the presence of two species of *Clytia viz*. *Clytia hemisphaerica* and *Clytia simplex* in the Benguela current. *Clytia hemisphaerica* is characterised as a species present in the upper 100 m, mainly in the surface water and was only found at three inshore stations between Walvis Bay and Cape Frio in the northern Benguela (Pagès et al. 1992). On the other hand, *Clytia simplex* is characterised as an occasional present species to be found in the surface layer off the Cunene river, inshore off Cape Frio and near Lüderitz, in the northern Benguela (Pagès et al. 1992).

In this study, *Proboscidactyla sp.* was sporadically present during mid-summer to early winter whereas it showed a more common occurance and higher abundance during the period mid-winter to early summer in Walvis Bay. *Proboscidactyla menoni* was present from December 1981 to March 1982 as the highest abundant coastal Hydroidomedusa species in Pagès (1992) off Namibia. The presence of the two species of *Proboscidactyla viz*. *Proboscidactyla menoni* and *Proboscidactyla stellata* in the Benguela current is described by Pagès et al. (1992). *Proboscidactyla menoni* is distributed along the northern coast of Namibia between 0–60 m depths whereas *Proboscidactyla stellata*is rare in the northern Benguela that dwells in the surface layers inshore near Cape Cross and Möwe Bay off Namibia (Pagès et al. 1992). Jung (2010) found *Proboscidactyla menoni* at one shelf station (7.49 ind. 1000 m^{-3}) during December 2009, this taxon was also reported as the highest (154.26 ind. 1000m^{-3}) coastal abundant Hydroidomedusae during March 2008 off Namibia.

Unidentified Leptomedusae and Anthomedusae showed considerable inter-annual variability in the timing and abundance, both being more common during the year 2013 in Walvis Bay. Pagès et al. (1992) described the presence of two species of *Mitrocomella viz*. *Mitrocomella grandis* and *Mitrocomella millardae sp. n.* in the Benguela current. *Mitrocomella millardae sp. n.* was distributed only in the southern Benguela forming high inshore densities throughout the water column whereas *Mitrocomella grandis* was sampled exclusively in Namibian waters (Pagès et al. 1992). Pagès (1992) classified *Mitrocomella grandis* as a Benguela shelf species, however the coastal presence of *Mitrocomella* sp. in this study may support the hypothesis of the aforesaid author that their hydropolyp stage resides inshore and would be

carried by Ekman transport from inshore out to the oceanic front. Gibbons et al. (1992) noted that two neritic species of ctenophore *viz. Pleurobrachia pileus* and *Beroe cucumis* were common in the Southeastern Atlantic and the Benguela Current system. Nonetheless, both *Mitrocomella* sp. and *Pleurobrachia* sp. were present in just one of the two years in Walvis Bay, respectively. The lack of ctenophore dense aggregations in the Benguela, according to Gibbons et al. (1992), may be a reflection of data deficiency and poor sampling techniques, or may be due to the scarcity of enclosed bays, vigorous physical processes and the short-pulsed nature of prey supply. The distance that a neritic medusa may be transported by a current from its place of origin depends on the speed and direction of the currents and the lifespan of the medusa (Kramp 1959). The distribution of a medusa may be restricted by unfavourable conditions in the area that it was transported to, or the conditions within a certain area may be highly variable between years; thereby giving rise to isolated occurrences of taxa due to exceptional conditions (Kramp 1959). These taxa might be designated as stray visitors in such remote areas which on the other hand are not applicable for data poor areas (Kramp 1959). As well, the geographical distribution of a medusa does not necessarily overlap with its native habitat, since it may be transported to an area where it could continue to be active in its swimming and feeding abilities, however is unable to proliferate (Kramp 1959).

Although changes in the abundance of a group of species are mainly responsible for the detection of high levels of dissimilarity between seasons in Walvis Bay, one cannot always assume that the variation in abundances and diversity are a true reflection of seasonal change. It is likely that the presence and/or abundance of medusae in off Walvis Bay can be associated with the movement pattern of the currents which is also influenced by wind. Attempting to describe a seasonal trend in zooplankton abundance has many pitfalls since the acquired samples represent only a snapshot of the ecosystem as a whole taken at that moment. Despite that life history, aggregating behaviour (Graham et al. 2001) and population dynamics control the abundance of jellyfish; their abundance and spatial distribution can also be regulated by hydrographic changes. The latter involve thermoclines, haloclines, stratification, upwelling fronts (Graham et al. 2001), areas of flow discontinuity (Purcell et al. 2000), Langmuir circulation cells (Larson 1992), as well as eddies, currents and tides (Arai 1992a; Graham et al. 2001), the direction and speed of prevailing winds and surface currents that condense these animals along the shoreline (Shenker

1984; Larson 1990) and even light (Arai 1992a) whereas season can often encompass several of these factors. It is a common practice to note the seasonal appearance of taxa in classification and geographic distribution literature (Russel 1953, 1970; Bouillon et al. 2004) to assist in the process of their identification. Yet, not all studies could demonstrate a seasonal effect on cnidarian abundances. The review of Mackie et al. (1987) showed the absence of seasonality in species communities of siphonophores can be valid, and that changes in their inshore communities can represent the population dynamics of the individual species or localised winds, currents and changing hydrographic conditions that could be falsely interpreted as seasonality (Mackie et al. 1987 and references therein).

In addition, the accuracy of zooplankton sampling is often affected by the patchiness in their distribution (Tranter 1968; de Wolf 1989; Mills 1995; Regula et al. 2009; Colin et al. 2010), which is especially relevant for jellyfish, thus complicating the discrimination between population growth and its redistribution due to advection (Mills 1981; Arai 1992a; Graham et al. 2001). It is possible that the sampling interval and the "missed sampling opportunities" might have overlooked changes in the abundance and diversity or the presence of a species entirely since most small medusae have a short presence in the pelagic column due to their short life spans of a few weeks to months (Aria 1992; Mills 1993). Mills (1981) found that "medusae may be abundant at one time, yet within an hour become rare or altogether missing; they may reappear in abundance an hour or a day later, or not at all". This becomes especially likely when grouping the different types of taxa together, as the grouped community is even more likely to miss changes of species composition within the season. Although, the succession of different species of jellyfish may also be the effect from the predation of one of them on the other (e.g. Falkenhaug 1996). In this study, predation pressure on hydromedusae between the period July and November should be considered as highly likely since personal observations indicated that ephyral stages of *Chrysaora* species are capable of consuming the hydromedusae taxa caught in the samples and the occurrence of a negative relationship between their abundances. On the other hand, the general presence of high densities of larger sized *Chrysaora* medusae observed in the Walvis Bay area (Chapter 4) may through predation pressure be the dominant factor influencing the hydromedusae species composition and abundance towards an underestimate (Mackie et al. 1987; Strand & Hamner 1988; Purcell 1991b) in this study. Intraguild predation is not uncommon among taxa of hydromedusae,

scyphomedusae and ctenophores (summarized in Purcell 1991a; Arai 2005). For example, *Rathkea octopunctata* and *Obelia* sp. can comprise of >80% of the prey diet of *Aurelia aurita* during the spring months (Purcell 1991a). Thus, the interpretation of the data results from this study, although abundances of taxa seem to be equally distributed among the four sampling stations off Walvis Bay, needs to be regarded with caution when abovementioned factors are considered since an overestimate or underestimate of population density and diversity may be a possible result.

FIGURES

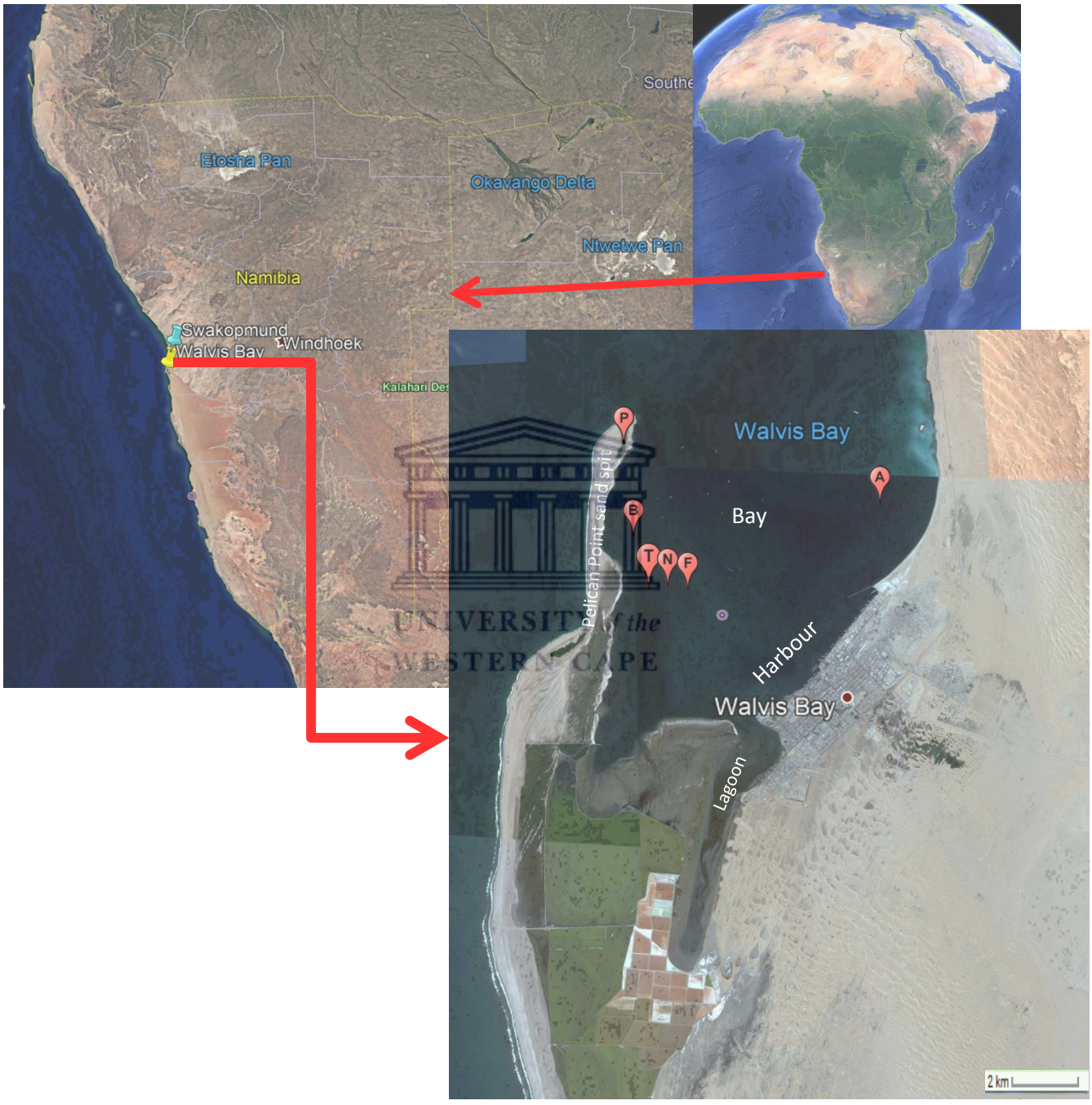


Figure 2.1. Map illustrating the stations sampled in Walvis Bay: A = AP, B = Beira, F = FD, N = NAMA and T = TET. P = Pelican Point lighthouse (origin of wind data).

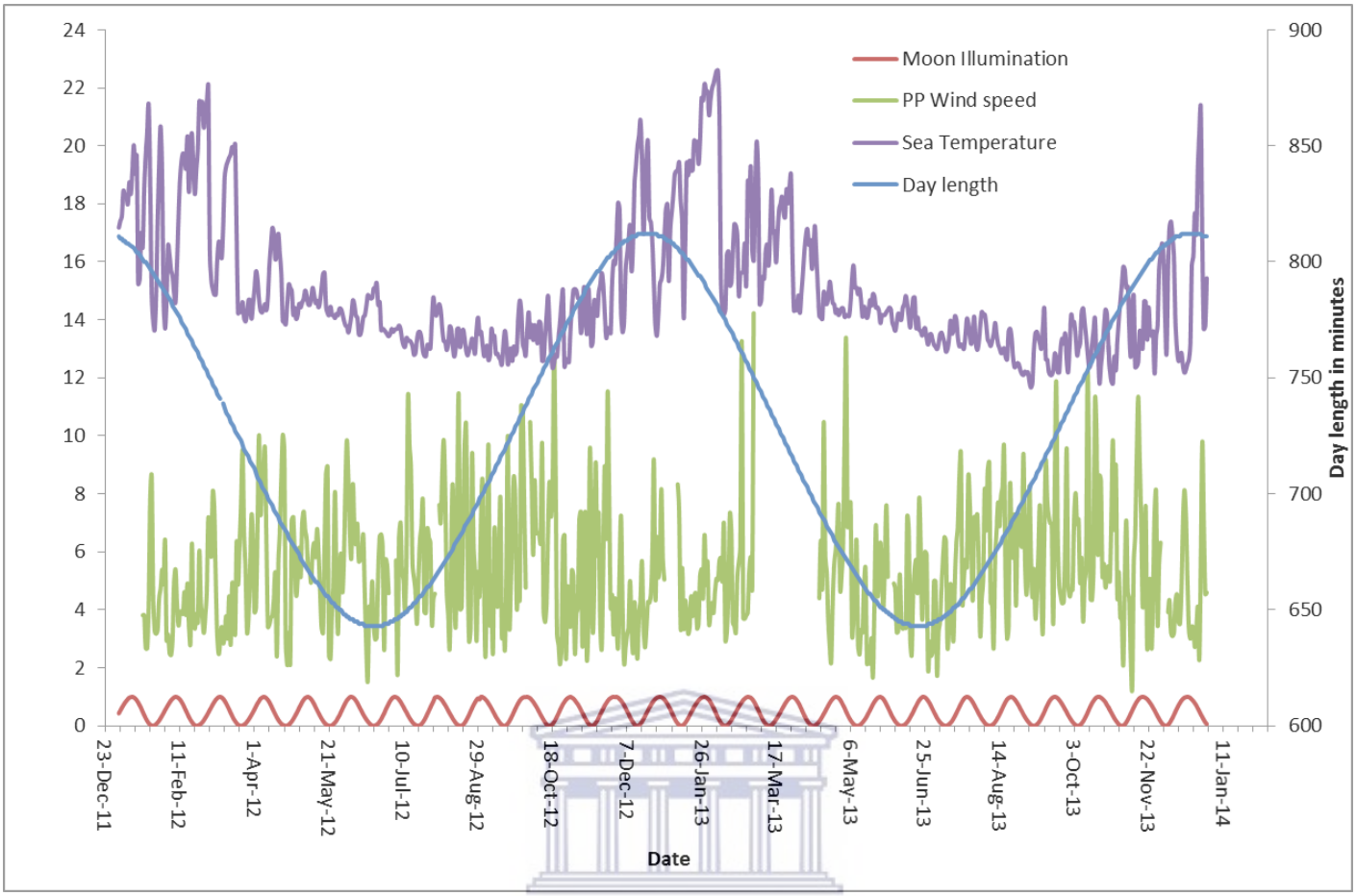


Figure 2.2. Intra-annual variability in moon illumination (fraction), wind speed ($m.s^{-1}$), sea temperature (°C) on the primary axis and and day length (minutes) on the secondary axis.

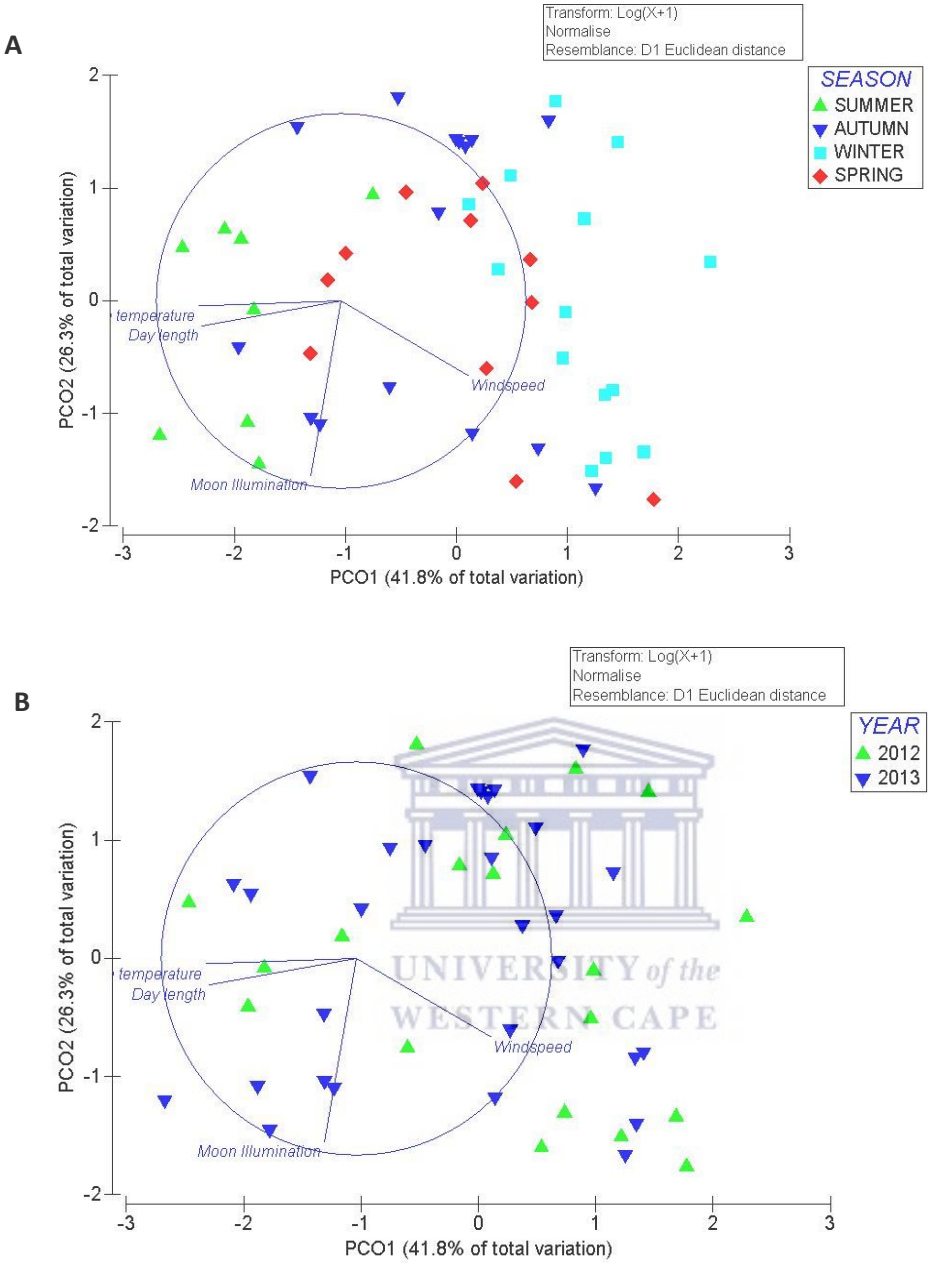


Figure 2.3. Two dimensional visualisations of environmental variables. PCO plot, on the basis of a Euclidian distance matrix, showing the distribution of the samples collected during the (A) seasons and (B) years. Pearson correlation vectors, with values greater than 0.70, overlaid.

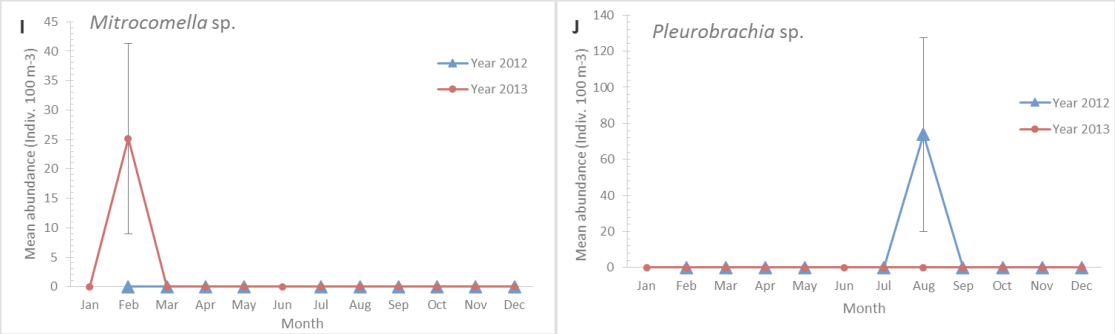


Figure 2.4. Average monthly abundance with standard errors (ind. 100 m^{-3}) of gelatinous taxa. Secondary axis represents Year 2013, where applicable.

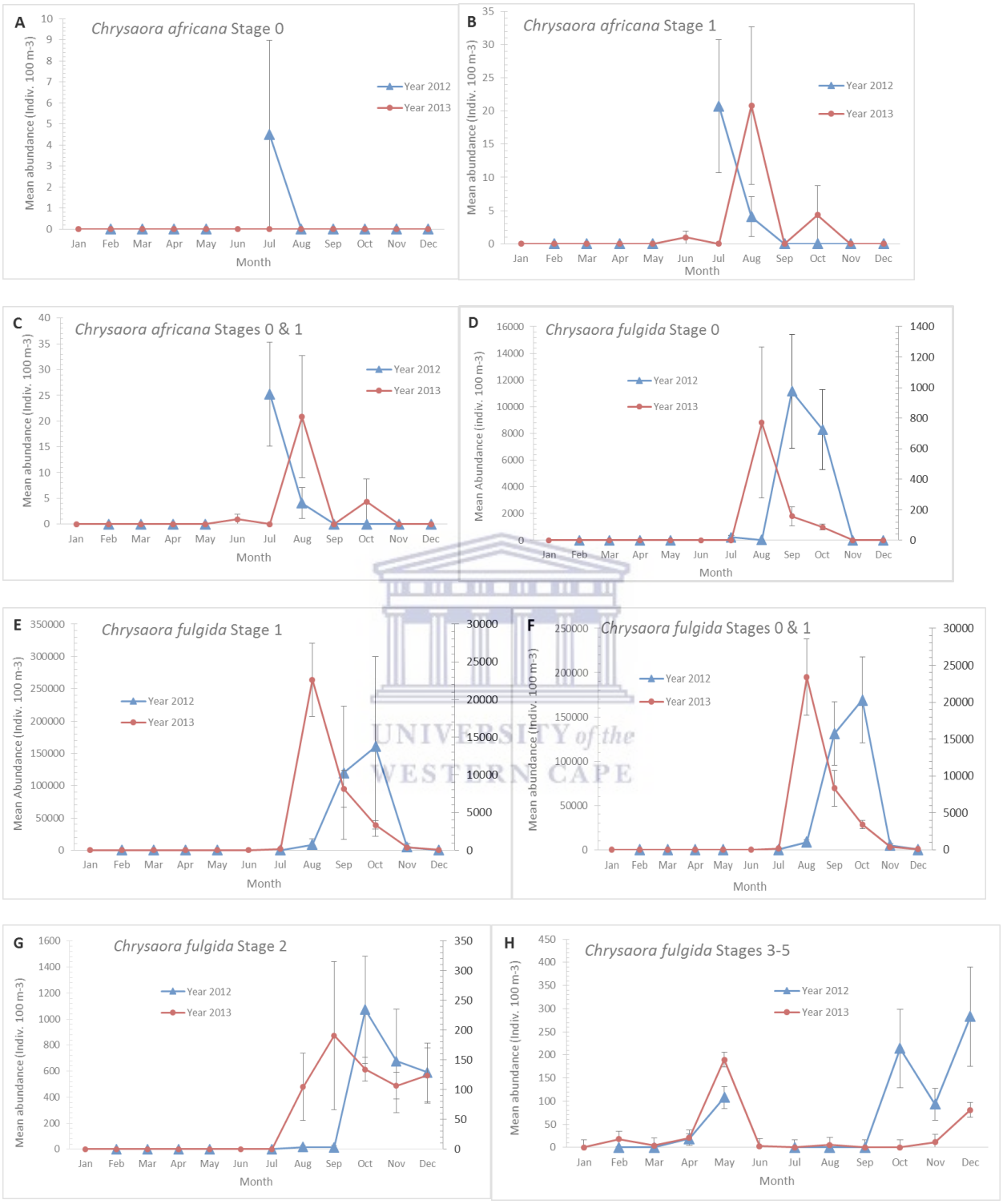


Figure 2.5. Average monthly abundance with standard errors (ind. 100 m^{-3}) of each *Chrysaora* species at different stages. Secondary axis represents Year 2013, where applicable.

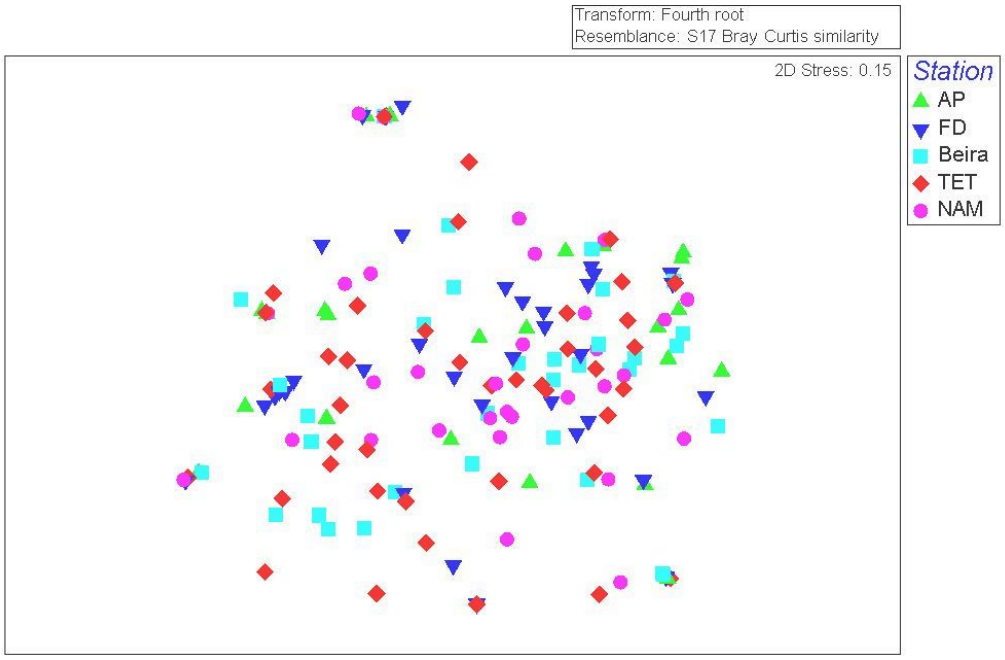


Figure 2.6. Two-dimensional visualisations of gelatinous communities. nMMDS plot of the similarity in the gelatinous species composition of samples collected at different stations in Walvis Bay.

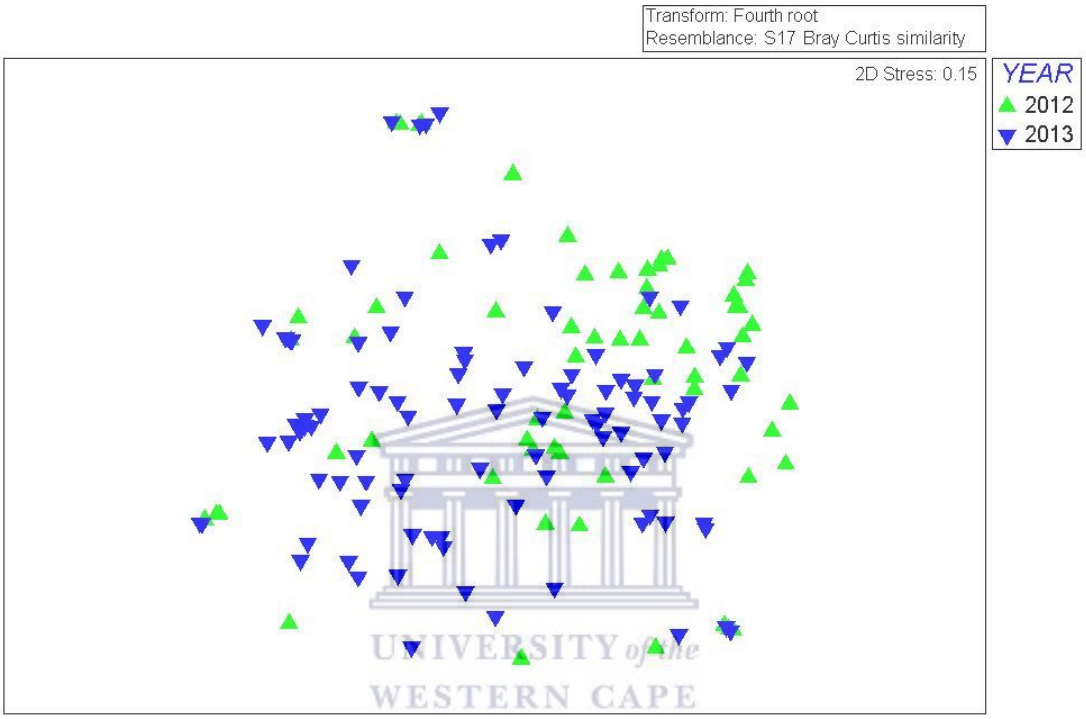


Figure 2.7. Two-dimensional visualisations of gelatinous communities. nMMDS plot of the similarity in the gelatinous species composition of samples collected during different years in Walvis Bay.

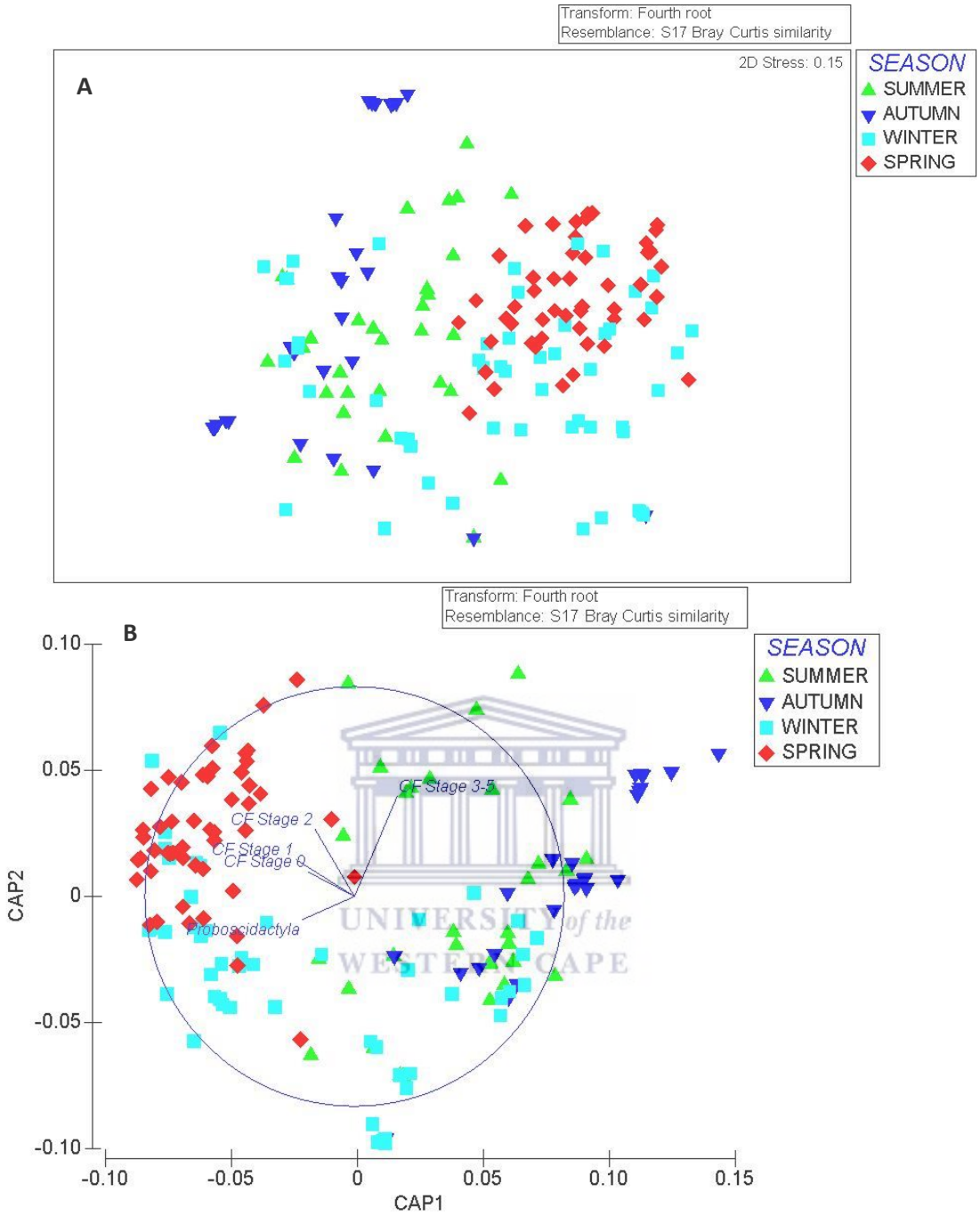


Figure 2.8. Two-dimensional visualisations of gelatinous communities. (A) nMMDS plot of the similarity in the gelatinous species composition of samples collected at different seasons in Walvis Bay. (B) CAP visualisation of taxa group assemblages during the different seasons. Only taxa are represented with correlations to the CAP-axes above 0.2. CF = *Chrysaora fulgida*; 166 samples; m = 6; leave-one-out cross validation total correct = 67.47%; test statistic1 and test statistic2: $p < 0.001$; 999 permutations.

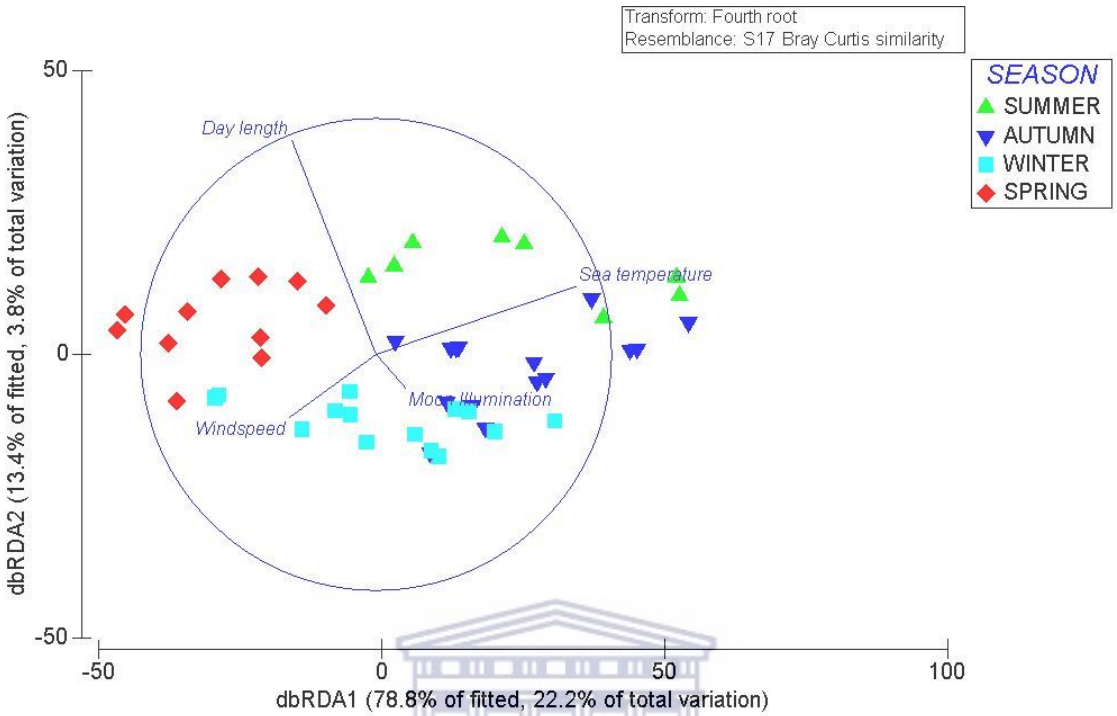


Figure 2.9. Two-dimensional visualization of the multivariate multiple regression dbRDA performed on the gelatinous community and environmental predictors: vectors show the direction and strength of the environmental gradients. The seasonal presence of the samples is indicated in symbols.

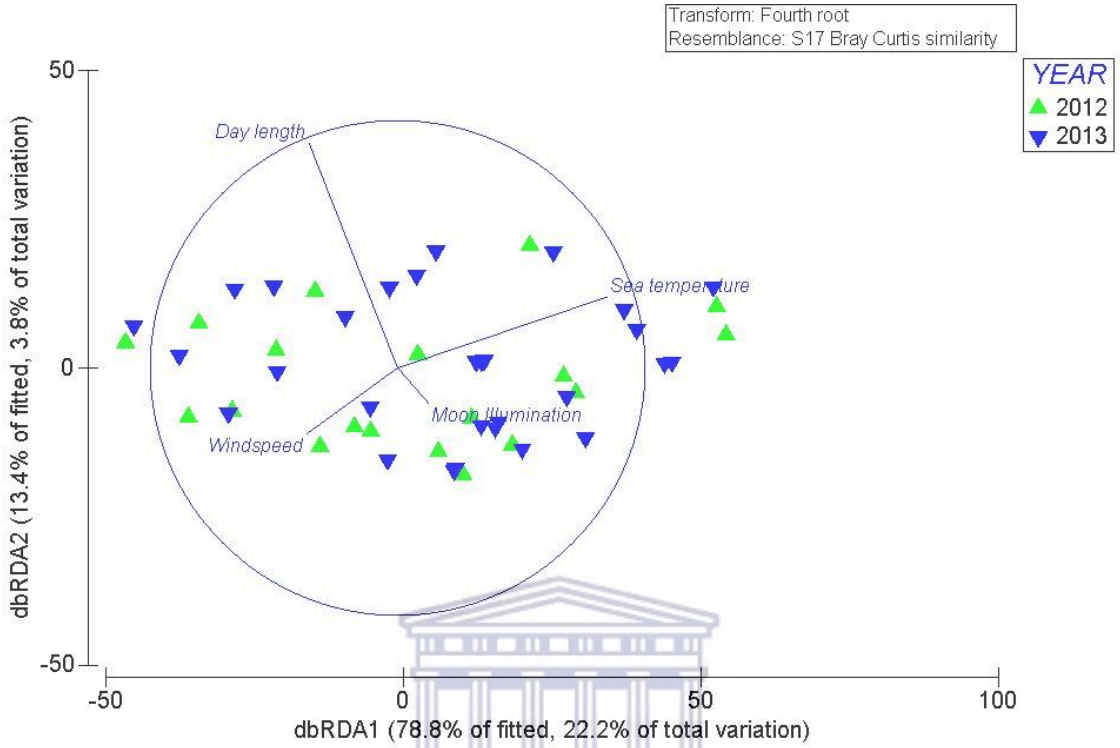


Figure 2.10. Two-dimensional visualisation of the multivariate multiple regression dbRDA performed on the gelatinous community and environmental predictors: vectors show the direction and strength of the environmental gradients. The annual presence of the samples is indicated in symbols.

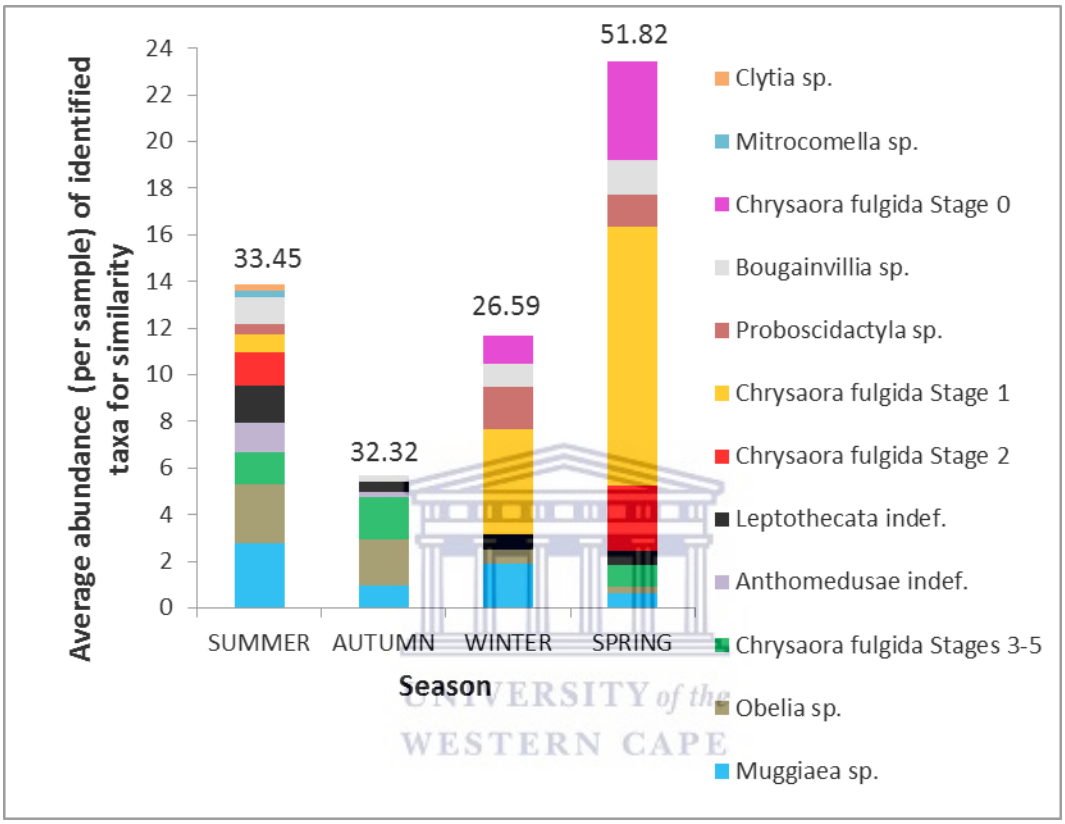


Figure 2.11. Average abundance of those taxa characteristic of each season. Histogram illustrating the average (fourth root) abundance per season, of the identified gelatinous taxa by the SIMPER routine in PRIMER 6 as being responsible for 100% of the identity of each of the seasons sampled within Walvis Bay area. The numbers on top of each bar indicate the average similarity (%) of samples within each season.

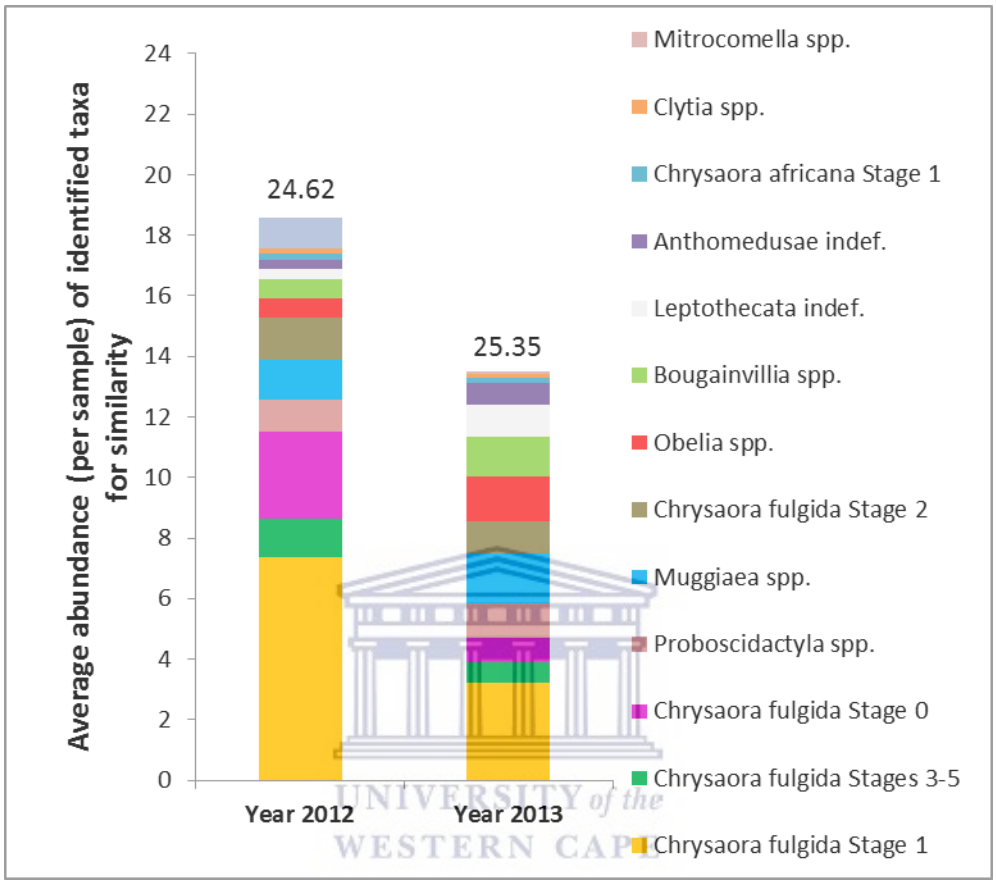


Figure 2.12. Average abundance of those taxa characteristic of each year. Histogram illustrating the average (fourth root) abundance per year, of the identified gelatinous taxa by the SIMPER routine in PRIMER 6 as being responsible for 100% of the identity of each of the year sampled within Walvis Bay area. The numbers on top of each bar indicate the average similarity (%) of samples within each year.

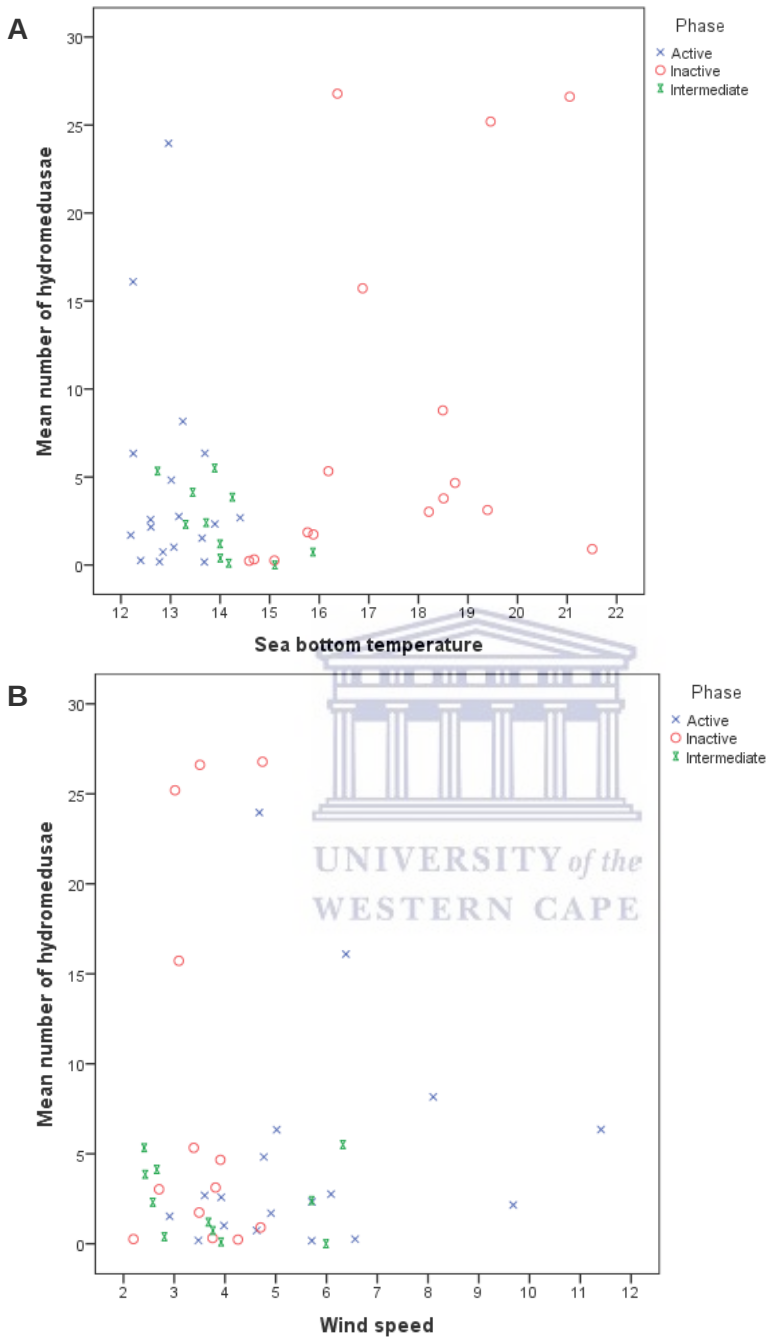


Figure 2.13. The mean number of hydromedusae (m^{-3}) per sample with (A) sea bottom temperature (°C) and (B) wind speed (m^{-s}) according to the upwelling phases.

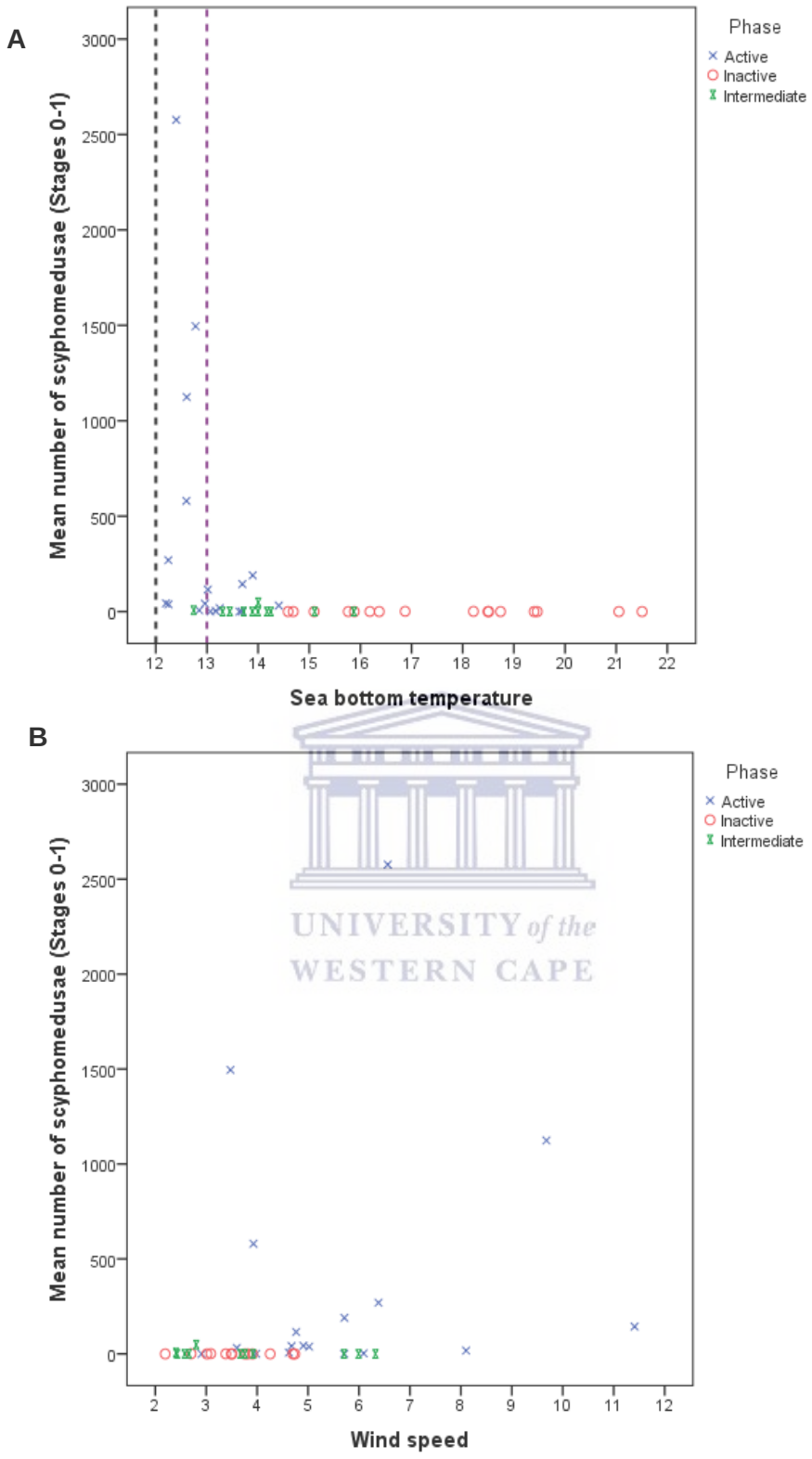


Figure 2.14. The mean number of scyphomedusae (m^{-3}) per sample with (A) sea bottom temperature (°C) and (B) wind speed (m^{-S}) according to the upwelling phases. Dotted reference lines denote the maxima abundance of medusae (Stages 0–1) detected between 12 and 13 °C.

TABLES

Table 2.1. PERMANOVA results for the environmental structure between season (SE) and year (YE)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
SE	3	250.1	83.368	37.339	0.001	999
YE	1	2.1	2.0778	0.93063	0.433	999
SExYE	3	21.644	7.2145	3.2313	0.001	998
Res	158	352.77	2.2327			
Total	165	660				

Table 2.2. PERMANOVA pair-wise results for the environmental structure between seasons and between year x season

Groups	t	P(perm)	Unique perms
SUMMER, AUTUMN	5.0828	0.001	999
SUMMER, WINTER	8.8718	0.001	998
SUMMER, SPRING	6.9557	0.001	998
AUTUMN, WINTER	4.0364	0.001	998
AUTUMN, SPRING	5.2717	0.001	999
WINTER, SPRING	5.8473	0.001	998
2012, 2013 for SUMMER	1.5066	0.099	579
2012, 2013 for AUTUMN	1.264	0.21	993
2012, 2013 for WINTER	2.304	0.008	998
2012, 2013 for SPRING	1.8453	0.033	995

Table 2.3. PERMANOVA results for the community structure between station (St), season (SE) and year (YE)

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
St	4	8691.1	2172.8	0.9793	0.492	998
SE	3	132010	44002	19.832	0.001	999
YE	1	14438	14438	6.5076	0.001	999
StxSE	12	32694	2724.5	1.228	0.121	997
StxYE	4	7022.7	1755.7	0.79131	0.749	997
SExYE	3	19515	6505.1	2.932	0.001	997
StxSExYE	12	20658	1721.5	0.7759	0.902	997
Res	126	279560	2218.7			
Total	165	531730				

Table 2.4. PERMANOVA pair-wise results for the community structure between seasons and between year x season

Groups	t	P(perm)	Unique perms
SUMMER, AUTUMN	2.4788	0.001	999
SUMMER, WINTER	3.0213	0.001	999
SUMMER, SPRING	5.1545	0.001	999
AUTUMN, WINTER	4.5268	0.001	999
AUTUMN, SPRING	7.1279	0.001	997
WINTER, SPRING	3.7544	0.001	998
2012, 2013 for SUMMER	2.249	0.002	999
2012, 2013 for AUTUMN	0.96732	0.392	998
2012, 2013 for WINTER	1.1754	0.248	999
2012, 2013 for SPRING	3.7238	0.001	998

Table 2.5. Results of the DistLM marginal and sequential tests for the abundance of gelatinous fauna collected at Walvis Bay during 2012-2013, with day length, moon illumination, wind speed and sea temperature as predictors.

Marginal Tests*							
Variable		**SS(trace)**	**Pseudo-F**	**p**	**Proportion**		
Day length		21130	6.7867	0.001	0.03974		
Moon illumination		6018.9	1.8776	0.086	0.01132		
Wind speed		30583	10.008	0.001	0.05752		
Sea temperature		85409	31.384	0.001	0.16063		
Sequential Tests							
Variable	**AICc**	**SS(trace)**	**Pseudo-F**	**p**	**Proportion**	**Cumulative**	**res.df**
+Sea temperature	1314.9	85409	31.384	0.001	0.1606	0.16063	164
+Day length	1300.8	41456	16.691	0.001	0.0780	0.23859	163
+Wind speed	1296.6	15202	6.3204	0.001	0.0286	0.26718	162
+Moon illumination	1295.4	7681.7	3.2378	0.008	0.0144	0.28163	161

Sequential tests were conducted using the 'step-wise' procedure and AICc criteria. All variables were log(x+1) transformed, prior to analysis.

* Residual DF = 164

Table 2.6. Results of the similarity percentage (SIMPER) analysis among the four seasons.

Groups SUMMER & AUTUMN						
Average dissimilarity = 77.55%						
Species	Average abundance		Av.Diss	Diss/SD	Contrib%	Cum.%
	SUMMER	AUTUMN				
Muggiaea atlantica	2.8	0.96	14.6	1.08	19.11	19.11
Obelia sp.	2.5	1.98	13.92	1.05	18.21	37.31
Chrysaora fulgida Stages 3-5	1.4	1.79	11.31	0.93	14.8	52.12
Leptotheca indef.	1.62	0.42	8.18	0.83	10.7	62.82
Chrysaora fulgida Stage 2	1.43	0	7.16	0.67	9.37	72.18
Bougainvillia sp.	1.14	0.31	6.31	0.66	8.26	80.44
Anthomedusae indef.	1.22	0.24	6.06	0.73	7.92	88.36
Proboscidactyla sp.	0.46	0.08	3.21	0.43	4.2	92.57
Chrysaora fulgida Stage 1	0.74	0	3.09	0.51	4.04	96.61
Clytia sp.	0.27	0.06	1.39	0.35	1.82	98.43
Mitrocomella sp.	0.28	0	1.2	0.32	1.57	100
Groups SUMMER & WINTER						
Average dissimilarity = 79.64%						
Species	Average abundance		Av.Diss	Diss/SD	Contrib%	Cum.%
	SUMMER	WINTER				
Chrysaora fulgida Stage 1	0.74	4.52	13.9	1	17.46	17.46
Muggiaea atlantica	2.8	1.89	10.41	1.08	13.07	30.53
Obelia sp.	2.5	0.62	9.6	0.92	12.05	42.57
Proboscidactyla sp.	0.46	1.79	7.04	0.87	8.83	51.41
Leptotheca indef.	1.62	0.63	6.59	0.82	8.28	59.69
Bougainvillia sp.	1.14	1.02	5.92	0.78	7.43	67.11
Chrysaora fulgida Stage 2	1.43	0.35	5.86	0.69	7.36	74.47
Chrysaora fulgida Stage 3-5	1.4	0.1	5.66	0.72	7.1	81.57
Anthomedusae indef.	1.22	0.7	5.35	0.77	6.72	88.3
Chrysaora fulgida Stage 0	0	1.22	3.72	0.54	4.67	92.96
Chrysaora africana Stage 1	0	0.48	1.91	0.42	2.4	95.37
Clytia sp.	0.27	0.27	1.73	0.42	2.17	97.54
Mitrocomella sp.	0.28	0	0.95	0.31	1.19	98.73
Pleurobrachia sp.	0	0.26	0.65	0.27	0.81	99.54
Chrysaora africana Stage 0	0	0.05	0.19	0.13	0.24	99.78
Calychophorae gonophores indef.	0	0.06	0.17	0.14	0.22	100
Groups AUTUMN & WINTER						
Average dissimilarity = 90.30%						
Species	Average abundance		Av.Diss	Diss/SD	Contrib%	Cum.%
	AUTUMN	WINTER				

Chrysaora fulgida Stage 1	0	4.52	17.98	0.95	19.91	19.91
Chrysaora fulgida Stage 3-5	1.79	0.1	12.39	0.83	13.73	33.64
Muggiaea atlantica	0.96	1.89	11.9	0.87	13.18	46.81
Obelia sp.	1.98	0.62	11.62	0.89	12.87	59.68
Proboscidactyla sp.	0.08	1.79	10.41	0.81	11.53	71.22
Bougainvillia sp.	0.31	1.02	5.83	0.63	6.45	77.67
Chrysaora fulgida Stage 0	0	1.22	4.91	0.53	5.44	83.11
Leptotheca indef.	0.42	0.63	4.56	0.57	5.05	88.16
Anthomedusae indef.	0.24	0.7	3.83	0.52	4.24	92.4
Chrysaora africana Stage 1	0	0.48	2.84	0.41	3.14	95.54
Clytia sp.	0.06	0.27	1.49	0.33	1.65	97.2
Chrysaora fulgida Stage 2	0	0.35	1.25	0.31	1.38	98.58
Pleurobrachia sp.	0	0.26	0.8	0.27	0.89	99.46
Chrysaora africana Stage 0	0	0.05	0.27	0.14	0.29	99.76
Calychophorae gonophores indef.	0	0.06	0.22	0.14	0.24	100
Groups SUMMER & SPRING						
Average dissimilarity = 82.45%						
Species	Average abundance		Av.Diss	Diss/SD	Contrib%	Cum.%
	SUMMER	SPRING				
Chrysaora fulgida Stage 1	0.74	11.09	27.28	2	33.09	33.09
Chrysaora fulgida Stage 0	0	4.22	10.04	1.15	12.18	45.26
Muggiaea atlantica	2.8	0.61	7.44	1.19	9.02	54.28
Chrysaora fulgida Stage 2	1.43	2.8	7.16	1.2	8.68	62.96
Obelia sp.	2.5	0.28	6.74	0.95	8.17	71.14
Bougainvillia sp.	1.14	1.47	5.06	0.94	6.13	77.27
Leptotheca indef.	1.62	0.61	4.87	0.83	5.91	83.18
Chrysaora fulgida Stage 3-5	1.4	0.93	4.58	0.88	5.55	88.73
Proboscidactyla sp.	0.46	1.42	4.28	0.83	5.19	93.92
Anthomedusae indef.	1.22	0.15	3.34	0.72	4.06	97.97
Clytia sp.	0.27	0.05	0.83	0.34	1	98.97
Mitrocomella sp.	0.28	0	0.7	0.32	0.85	99.83
Chrysaora africana Stage 1	0	0.05	0.14	0.14	0.17	100
Groups AUTUMN & SPRING						
Average dissimilarity = 93.56%						
Species	Average abundance		Av.Diss	Diss/SD	Contrib%	Cum.%
	AUTUMN	SPRING				
Chrysaora fulgida Stage 1	0	11.09	36.82	2.48	39.36	39.36
Chrysaora fulgida Stage 0	0	4.22	12.39	1.19	13.24	52.6
Chrysaora fulgida Stage 2	0	2.8	9.91	1.32	10.59	63.19
Chrysaora fulgida Stage 3-5	1.79	0.93	7.12	0.94	7.61	70.8
Obelia sp.	1.98	0.28	6.86	0.89	7.34	78.14

Bougainvillia sp.	0.31	1.47	5.68	0.83	6.07	84.21
Proboscidactyla sp.	0.08	1.42	5.13	0.77	5.48	89.69
Muggiaea atlantica	0.96	0.61	4.49	0.69	4.8	94.49
Leptotheca indef.	0.42	0.61	3.24	0.58	3.46	97.95
Anthomedusae indef.	0.24	0.15	1.35	0.38	1.44	99.39
Clytia sp.	0.06	0.05	0.39	0.21	0.42	99.81
Chrysaora africana Stage 1	0	0.05	0.18	0.14	0.19	100
Groups WINTER & SPRING						
Average dissimilarity = 71.07%						
Species	Average abundance		Av.Diss	Diss/SD	Contrib%	Cum.%
	WINTER	SPRING				
Chrysaora fulgida Stage 1	4.52	11.09	23.81	1.45	33.49	33.49
Chrysaora fulgida Stage 0	1.22	4.22	10.16	1.16	14.3	47.79
Chrysaora fulgida Stage 2	0.35	2.8	7.83	1.23	11.02	58.81
Muggiaea atlantica	1.89	0.61	5.59	0.91	7.87	66.68
Proboscidactyla sp.	1.79	1.42	5.58	0.99	7.85	74.53
Bougainvillia sp.	1.02	1.47	5.06	0.9	7.13	81.66
Leptotheca indef.	0.63	0.61	2.99	0.62	4.21	85.86
Chrysaora fulgida Stage 3-5	0.1	0.93	2.46	0.6	3.47	89.33
Obelia sp.	0.62	0.28	2.4	0.54	3.38	92.71
Anthomedusae indef.	0.7	0.15	2.04	0.51	2.87	95.59
Chrysaora africana Stage 1	0.48	0.05	1.47	0.46	2.07	97.66
Clytia sp.	0.27	0.05	0.85	0.33	1.2	98.86
Pleurobrachia sp.	0.26	0	0.53	0.27	0.74	99.6
Chrysaora africana Stage 0	0.05	0	0.14	0.13	0.2	99.8
Calychophorae gonophores indef.	0.06	0	0.14	0.14	0.2	100

Table 2.7. Results of the similarity percentage (SIMPER) analysis among the years.

Years 2012 & 2013						
Average dissimilarity = 78.60%						
Species	Average abundance		Av. Diss	Diss/SD	Contrib%	Cum.%
	YEAR 2012	YEAR 2013				
Chrysaora fulgida Stage 1	7.36	3.23	21	1.19	26.71	26.71
Muggiaea atlantica	1.32	1.62	8.18	0.81	10.41	37.13
Chrysaora fulgida Stage 0	2.87	0.82	8.03	0.85	10.21	47.34
Obelia sp.	0.62	1.48	7.18	0.69	9.14	56.47
Chrysaora fulgida Stage 3-5	1.29	0.66	6.48	0.65	8.24	64.71
Chrysaora fulgida Stage 2	1.43	1.07	5.83	0.8	7.42	72.13
Proboscidactyla sp.	1.03	1.15	5.77	0.72	7.34	79.47
Bougainvillia sp.	0.63	1.33	5.24	0.73	6.67	86.14
Leptotheca indef.	0.34	1.06	4.28	0.62	5.44	91.58
Anthomedusae indef.	0.28	0.72	3.05	0.52	3.88	95.46
Chrysaora africana Stage 1	0.22	0.13	1.41	0.33	1.8	97.26
Clytia sp.	0.18	0.16	1.07	0.32	1.36	98.62
Pleurobrachia sp.	0.2	0	0.51	0.23	0.65	99.27
Mitrocomella sp.	0	0.09	0.28	0.17	0.36	99.62
Chrysaora africana Stage 0	0.04	0	0.16	0.12	0.2	99.82
Calychophorae gonophores indef.	0.05	0	0.14	0.12	0.18	100

Table 2.8. Presence and maximum abundance of different species of ephyrae: *ephyrae present; **peaks in ephyrae production; ***highest peak in ephyrae observed; [S]strobilation of polyps observed; [na]not available; [p]presence of <50 mm bell diameter medusae.

Region	MONTH												Species	Max abundance ephyrae (Ind. per m^{-3})	References
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC			
NORTHERN HEMISPHERE															
Sweden, Gullmar Fjord	*	*	**	**	*					**	***	**	*Aurelia aurita*	14.96	Hernroth & Gröndahl 1983
Sweden, Gullmar Fjord	*	*	*	**	**					**	***	*	*Aurelia aurita*	0.134	Hernroth & Gröndahl 1985a
Sweden, Gullmar Fjord	*	**	**S	*S	***S	S	S						*Cyanea capillata*	~0.009	Gröndahl 1988a
Sweden, Gullmar Fjord	*	*S	*S	*S	*					**S	***S	**	*Aurelia aurita*	0.134	Gröndahl 1988a
Sweden, Gullmar Fjord			*	**	**	***							*Cyanea capillata*	0.065	Gröndahl & Hernroth 1987
Great Britain, Horsea Lake	*	***	**	*	*	**						*	*Aurelia aurita*	na	Lucas 1996
Great Britain, Southampton Water	*	*	***	*	**	*							*Aurelia aurita*	8.71	Lucas & Williams 1994
Denmark, Kertinge Nor and Kerteminde Fjord		*	**	***									*Aurelia aurita*	~300	Olesen et al. 1994
Denmark, Kertinge Nor		*	***										*Aurelia aurita*	~55	Riisgård et al. 2012
Germany, Kiel Bight	*	*	*	*	***	*	*	*			*	**	*Aurelia aurita*	0.073	Möller 1980
Croatia, Mljet Island, lake Veliko Jezero	*				***	*	*	*	*		*		*Aurelia* sp. 5	16	Kogovšek et al. 2012
Slovenia, Port of Koper	S	S									S***	S	*Aurelia sp. 8*	2-6	Malej et al. 2012
Slovenia, Gulf of Trieste						**	*	**	*	*		***	*Pelagia noctiluca*	na	Malej & Malej 1992
Greece, Elefsis Bay	*	***	**	*	**	*						*	*Aurelia aurita*	44	Papathanassiou et al. 1987
Greece, Ionian Island of Lefkada						***	*	*					*Cotylorhiza tuberculata*	0.08	Kikinger 1992
France, Thau lagoon, southwestern Mediterranean Sea	*	***	*	**							*	*	*Aurelia aurita*	0.2	Bonnet et al. 2012
France; Thau -, Berre- and Bages-Sigean lagoons; in the northwestern part of the Mediterranean Sea	*	***	**	*	*						*	*	*Aurelia aurita*	14.72	Marques et al. 2015

Italy, Ancona, northern Adriatic Sea											S	S	*Aurelia aurita*	na	Di Camillo et al. 2010
China, Jiaozhou Bay					***	*							*Aurelia aurita*	2.38 ± 0.56	Wang & Sun 2014
China, Taiwan, Tapong Bay	***	*	**	*					*	*	**	*	*Aurelia aurita*	328	Lo & Chen 2008
Japan, Tokyo Bay	*												*Aurelia aurita*	1	Kinoshita et al. 2006
Japan, Tokyo Bay		*	***										*Aurelia aurita*	2.8	Ishii et al. 2004
Japan, Tokyo Bay	*	**	***	*	*					*		*	*Aurelia aurita*	2.4	Toyokawa et al. 2000
Japan, Harima Nada, Inland Sea of Japan	*	***	**	*	*								*Aurelia aurita*	~6.5	Makabe et al. 2015
Japan, Urazoko Bay	*	*	**	***	*	**							*Aurelia aurita*	68	Yasuda 1968
USA, Washington, Cornet Bay	S	S	S	S									*Aurelia labiata*		Purcell et al. 2009
USA, Chesapeake Bay, St. John Creek						**S	**S	*S					*Chrysaora quinquecirrha*	na	Cargo & Rabenold 1980
USA, Chesapeake Bay, St. John Creek					**	***	**	*					*Chrysaora quinquecirrha*	na	Cargo & Schultz 1967
USA, Connecticut, Niantic River				***	*								*Cyanea* spp.	na	Colin & Kremer 2002
USA, California, Tomales Bay		S***	*										*Aurelia aurita*	na	Hamner & Jenssen 1974
SOUTHERN HEMISPHERE															
Australia, Tasmania, Derwent Estuary and D' Entrecusteaux Channel								S	S	S			*Aurelia* sp.	na	Willcox et al. 2008
Australia, Victoria, Port Phillip Bay	***	*		*	**	**	*	*		*			*Cyanea capillata*	0.204	Fancett 1986
Australia, Victoria, Port Phillip Bay				*	*	*				*			*Aurelia aurita*	<0.005	Fancett 1986
Australia, Victoria, Port Phillip Bay	*	*	*	*									*Pelagia noctiluca*	<0.005	Fancett 1986
Australia, Sydney, Botany Bay and Lake Illawarra		p	p	p	p	p	p					p	*Catostylus mosaicus*	na	Pitt & Kingsford 2003
Namibia, Walvis Bay							*	*	***	*	*		*Chrysaora fulgida*	1 689	This study
Namibia, Walvis Bay						*	***	*		**			*Chrysaora africana*	0.25	This study

"Research vessel" the Stingray.

PICTURE

CHAPTER 3

CHARACTERISATION AND OBSERVATIONS ON THE DEVELOPMENT OF WILD CAUGHT EPHYRAE OF *CHRYSAORA FULGIDA* AND *CHRYSAORA AFRICANA*

CHAPTER 3

CHARACTERISATION AND OBSERVATIONS ON THE DEVELOPMENT OF WILD CAUGHT EPHYRAE OF *CHRYSAORA FULGIDA* AND *CHRYSAORA AFRICANA*

INTRODUCTION

Most scyphozoans have a complex two-part life cycle that typically includes two types of reproduction, with sexual reproduction befalling on the dispersive medusa (pelagic) stage and asexual reproduction on the sessile polyp (generally benthic) stage (Arai 1997). Eggs and sperm are produced by medusae, which develop after fertilisation into motile planulae (on completion of embryogenesis) that characteristically settle on hard substrata to metamorphose into fully developed sessile polyps (Lucas et al. 2012 and references therein). These benthic polyps can reproduce through various modes of asexual reproduction (e.g. Schiariti et al. 2008; Adler & Jarms 2009; Arai 2009a; Han & Uye 2010; Fuentes et al. 2011). The transition from the sessile polyp benthic stage to the dispersive medusa pelagic stage transpires through the process of strobilation.

This specific asexual mode describes the entire developmental process of the polyp that gives rise to ephyrae (Arai 1997). Strobilation comprises of two key phases *viz*. segmentation of the discs and metamorphosis of polyp structures (Spangenberg 1965; Kroiher et al. 2000). A sequence of anatomical changes leads to transverse constrictions subdividing the polyp body from the oral to the aboral end into segmental discs. Each of these segments metamorphoses into a complete young medusa, called an ephyra – the most basic pelagic and immature stage of the medusa, which is sequentially released in the water column (from the parental polyp), grows in size, takes on the morphology of the adult medusa and initiates sexual reproduction. After the release of the last ephyra, the strobila reverts to a polyp which, under the appropriate conditions, can again propagate through various modes of asexual reproduction. Strobilation may result in the release of a single ephyra (monodisc) or multiple ephyrae (polydisc) per polyp (Arai 1997).

As an ephyra grows it proceeds through various developmental changes such as growth of the bell margin between the rhopalia; tentacle extension; expansion of the oral appendages and

gastrovascular cavity; development of the gastric system; alternations in flow dynamics, prey capture surfaces and nematocyst densities and distribution (Sugiura 1966; see Arai 1997; Higgins et al. 2008; Schiariti et al. 2008; Fuentes et al. 2011; Straehler-Pohl et al. 2011). During this ontogenic process, developmental differences between genera become more pronounced while progressing towards their adult morphological features (Russel 1970). The development of ephyrae to juvenile medusa have been described in the literature for a number of species such as *Cephea cephea* (Sugiura 1966), *Pelagia noctiluca* (Rottini Sandrini & Avia 1983), *Rhizostoma pulmo* (Fuentes et al. 2011), *Lychnorhiza lucerna* (Schiariti et al. 2008), *Sanderia malayensis*, *Chrysaora fuscescens*, *Chrysaora lactea*, *Cyanea lamarckii* and *Cyanea capillata*, *Aurelia aurita* and *Aurelia limbata* (Higgins et al. 2008; Straehler-Pohl et al. 2011).

The identification of an unknown specimen, the naming of it, is often driven by economical, legal or a conservational purpose which is also applicable in the case of jellyfish (see Duarte et al. 2014). To better understand the ecological effects and environmental drivers of jellyfish populations and possibly forecast their blooms, or detect invasions; it is essential to successfully identify the species before such studies can be undertaken. In particular, the early development phases of ephyrae can serve as an early warning system for potential blooms (Straehler-Pohl & Jarms 2010), if robust, diagnostic morphological descriptions for all ephyrae exist that allows their correct identification (alive or preserved state) in plankton samples (Holst 2012b). Regrettably, the accurate identification of jellyfish is hampered by a very limited number of species-specific studies that describe the young stages (Russel 1970; Widmer 2008a; Straehler-Pohl et al. 2011; Holst 2012b; Gambill & Jarms 2014) and by the fact that many species share similar morphological features (Calder 1977; Gershwin & Collins 2002).

Documenting the morphological characteristics and development of ephyrae to juvenile stages can aid in the clarification of the taxonomic status of their genera and/or species (Straehler-Pohl et al. 2011; Holst 2012b). This is typically done by the laboratory rearing of ephyrae from polyps (Russel 1970; Widmer 2008a; Straehler-Pohl & Jarms 2010; Straehler-Pohl et al. 2011; Holst 2012a, 2012b; Gambill & Jarms 2014). Studies are now revealing that to avoid species crypsis and synonymization, species identification of jellyfish should be an integration of different approaches that considers the complete life cycle stages (scyphistoma, ephyra and medusa) with regard to their individual morphological descriptions, genetic differentiation, geographical distribution, ecological interactions and life history

strategies (Brewer 1991; Dawson & Martin 2001; Lucas 2001; Schroth et al. 2002; Dawson 2005; Bayha et al. 2010; Morandini & Marques 2010; Gambill & Jarms 2014; Holst & Laakmann 2014; Dawson et al. 2015; Chiaverano et al. 2016; van Walraven et al. 2016).

The benthic phase of both *Chrysaora fulgida* and *Chrysaora africana* in the northern Benguela ecosystem have yet to be discovered and the source areas for the ephyrae have not been confirmed in the field. *Chrysaora fulgida* and *C. africana*, sampled off Nambia, have been confirmed as two distinct species through morphological descriptions, quantitative statistical analyses and molecular sequencing of their medusae, sized between 105–407 mm in bell diameter (Neethling 2012). Descriptions of the morphological features of cultured polyps and their newly liberated ephyrae are only available for *C. fulgida* (Ras 2016). The latter polyps originated from planulae that were a product from the gonads of *C. fulgida* medusae collected off Walvis Bay, Namibia (Ras 2016).

The aims of this study were to: (1) identify and describe the most basic ephyrae, (2) describe the morphological development and (3) estimate growth rate from ephyra to juvenile medusa of wild caught *Chrysaora fulgida* and *Chrysaora africana*, where applicable.

MATERIALS AND METHODS

The methods used to collect zooplankton samples have been described in Chapter 2. Specimen shrinkage following preservation was standardised by ensuring that a fixed amount of preservative (borax-buffered 4-percent formaldehyde filtered seawater solution) was added to each sample, and the ephyrae were measured after 24 months following fixation (Möller 1980). Ephyrae were stained with Rose Bengal (200 mg l^{-1}) prior to measurement, for a minimum of 24 h, thereafter a minimum of 50 individuals per sample were examined under an Olympus SZ61 microscope, with an Olympus SC100 camera attached. Image analysis software (Olympus Stream) was used to capture all images, which were measured to an accuracy of 0·01 mm. Data are reported where applicable as mean ± standard deviation (SD). Standard measurements were carried out according to the descriptions of Straehler-Pohl & Jarms (2010), with additional formulated measurements (see Fig. 3.1): Central disc diameter (CDD) = adradial diameter of the central disc; Lappet Stem Length (LStL) = length from lappet base (line between the bases of two marginal lappet clefts) to base of rhopalial niche (base of cleft between two rhopalial

lappets); Rhopalial Lappet Length (RLL) = length from rhopalial niche base to level of rhopalial lappet tips; Manubrium Length (ML) = length between base and rim of manubrium; Velar Canal Length (VCL) = length from lappet base (line between the bases of two marginal lappet clefts) to velar canal tips (line between the bases of two velar canal tips); Rhopalial Canal Length (RCL) = length from rhopalial niche base to rhopalial canal tips (line between the bases of two rhopalia canal tips).

The number of gastric filaments per ¼ disc, manubrium shape (Table 3.1), position of the velar canal tips, position of the rhopalial canal tips, primary tentacle phase, length of the primary tentacle, secondary tentacle phase and length of the secondary tentacles were also recorded. The longest intact tentacle was also measured. Gastric filaments were counted to a maximum of 20 per quadrant, hereafter they were recorded as ≥20. The position of the velar canal tips was referenced relative to the lappet base: minus (-) for below or plus (+) for extending beyond the lappet base. The position of the rhopalial canal tips was referenced relative to the rhopalial niche base: minus (-) for below or plus (+) for surpassing the rhopalial niche base. Tentacle length could not be recorded for all specimens. In addition, the following measuring points were calculated as defined by Straehler-Pohl & Jarms (2010), inclusive with the additional measurements: Total Marginal Lappet Length (TMLL) = LStL + RLL; Total Body Diameter (TBD): (2 x TMLL) + CDD; Total Lappet Stem Body Diameter (TLStBD) = (2 x LStL) + CDD.

Data were standardised to body width as following (Russell 1970; Straehler-Pohl & Jarms 2010): CDD/TBD x 100; TMLL/TBD x 100; LStL/TBD x 100; RLL/TBD x 100; VCL/TBD x 100; RCL/TBD x 100; CDD/TLStBD x 100; TMLL/TLStBD x 100; LStL/TLStBD x 100; RLL/TLStBD x 100; RCL/TLStBD x 100; VCL/TLStBD x 100; RLL/TMLL x 100; LStL/TMLL x 100; VCL/TMLL x 100; RCL/TMLL x 100; ML/CDD x 100; VCL/CDD x 100; RCL/CDD x 100; LStL/CDD x 100.

Stage duration (in days) for each developmental stage was estimated from the number of days elapsed between the first appearances of each stage in sequence. Overall growth rate (% d^{-1}) was calculated by using the formula of Båmstedt et al. (1997):

% growth $day^{-1} = \ln[(D_2/D_1)^3]/(t_2 - t_1) \times 100\%$,

where D_1 and D_2 are the overall mean total body diameter (mm) between t_1 (the day of first appearance of ephyrae) and t_2 (the day of the maximum D_2 recorded) measuring groups (in days), respectively.

RESULTS

Observations and measurements were based on a total of 791 specimens of *Chrysaora fulgida* ranging in size between 1.18–84.56 mm TBD, and 18 *C. africana* ranging in size between 26.66–28.65 mm TBD. In addition, two hand net caught *C. africana* specimens (54 and 43 mm) were included.

Identification of Stage 0 ephyrae

An ephyra is defined as the smallest, youngest and most rudimentary stage (least developed) of the medusa that results from the strobilation of a scyphistoma (Kingsford et al. 2000). For the purpose of this study, they are the least morphological developed ephyrae caught in the field. The body proportions (in %) are summarised in Fig. 3.2 & 3.3.

***Chrysaora fulgida* (Fig. 3.4A & 3.5A):** The most undeveloped ephyrae were allocated to Stage 0 and constituted 12.14% of the total number of specimens measured. Staged 0 ephyrae had a TBD of 20.67± 0.48 mm, a CDD of 0.96 ± 0.29 mm, a RLL of 0.30 ± 0.075 mm and a LStL of 0.025 ± 0.056 mm (Table 3.2; Fig. 3.6). The manubrium was 0.32 ± 0.16 mm long. Live specimens were peach to pale pink in colour (Fig. 3.7), while preserved specimens lost their colour. The majority (87.5%) had a total of eight elongated lappet stems (each possessing two rhopalial lappets), 16 rhopalial lappets and eight velar canals. Symmetrical and asymmetrical deviations, in the ratio of the lappet stem: velar canal: rhopalial lappet, were observed in some specimens – 6:6:12 (n = 1), 7:7:14 (n = 5), 9:9:18 (n = 5) and 8:7:16 (n = 1). The rhopalial lappets were slightly pointed terminally (see Fig.3.5A) and did not overlap. The rhopalial canals were forked with rounded tips and did not overtop the rhopalia. The rhopalial canal tips did not reach past the rhopalial niche base. Velar canals were slightly forked, with rounded tips, and reached to the lower third of the rhopalial canals. The majority (72.9%) of velar canal tips passed beyond the lappet base. Four gastric filament sockets were observed with gastric filaments that ranged per quadrant from 0 to 1, with some specimens having only 1, 2 or 3 gastric filaments in the overall of the four gastric filament sockets. The majority (47.9%) contained 0 gastric filaments per quadrant. The manubrium shape ranged from 1–3. No marginal tentacles or tentacle bulbs were observed. Nematocyst clustering features were inconspicuous and difficult to observe on most ephyrae. Some ephyrae possessed oval-shaped

nematocyst clusters at the base of the marginal lappets, along the rhopalial canals and on the central disc area of the exumbrella (Fig. 3.8).

***Chrysaora africana* (Fig. 3.4B & 3.9A):** Only one specimen was observed (5% of the overall number), with a TBD of 26.67 mm, a CDD of 1.13 mm, a RLL of 0.49 mm and a LStL of 0.28 mm (Table 3.2). The manubrium was 0.31 mm long with a manubrium shape of 3. When alive, the specimen was translucent with dark maroon-purple rhopalia, rhopalial canal tips and manubrium. The dark maroon-purple coloration on the rhopalium and rhopalial canal tips form a roundly pointed arrow shaped pattern at the top of each lappet stem. Faint rose tinges in the muscular system, velar canals, rhopalial canals and gastric filaments were also present (Fig. 3.10). After two years of preservation no coloration was visible on this specimen. This ephyra had a total of eight elongated lappet stems (each possessing two rhopalial lappets), 16 rhopalial lappets and eight velar canals. The rhopalial lappets were non-overlapping and terminated sharply (see Fig.3.9A). The rhopalial canals were forked with rounded tips and did not overtop the rhopalia. The rhopalial canal tips did not reach past the rhopalial niche base. Velar canals were flat and spade-like, and reached to half of the length of the rhopalial canals. The velar canal tips did not pass beyond the lappet base. Gastric filament sockets were inconspicuous. One gastric filament per quadrant was present. No marginal tentacles or tentacle bulbs were observed. Conspicuous oval shaped nematocyst clusters organised in a ring like pattern around the central stomach and as pairs clustered at the base of the marginal lappets on the upper half of the lappet stems on the exumbrella.

Morphological development of post-ephyrae

Since the specimens were wild caught and displayed different developmental stages within and/or between the sampling periods, the chronological order of the different post-ephyrae stages is given below without time periods. The following sequences are illustrated in Fig. 3.5 (B–F) for *Chrysaora fulgida* and in Fig. 3.9 (B–F) for *Chrysaora africana*.

Stage 1:

***Chrysaora fulgida* (Fig. 3.5B):** This stage represented 78.13% of the total number of specimens measured. The post-ephyra had a TBD of 4.45 ± 1.77 mm and a CDD of 2.85 ± 1.46 mm (Table 3.2). The

manubrium (ML) was 1.62 ± 1.13 mm long. The manubrium shape ranged from 1–5. The majority of specimens (96.3%) had a total of eight lappet stems, eight velar canals and 16 rhopalial lappets. Symmetrical and asymmetrical deviations, in the ratio of the lappet stem:velar canal:rhopalial lappet, were observed in the rest of the specimens – 6:6:12 (n = 3), 7:7:14 (n = 8), 9:9:18 (n = 6), 8:7:16 (n = 5) and 9:7:18 (n = 1). The velar canals grew in a centrifugal direction while following the outgrowing rim of the umbrella. The tips of the velar canals broadened, surpassed the adradial clefts (96.1%) and extending into the marginal stems parallel with the rhopalial canals. Single primary tentacle buds appeared between the midpoint of the tips of the velar canals at the subumbrella rim of the base of the marginal lappet clefts as elongations of the velar canals. The majority of the rhopalial canal tips (85.4%) did not extend into the rhopalial lappets. Both the rhopalial and velar canals expanded in size through growth. Primary tentacle length development ranged from a little stub (0.02–0.20 mm; total percentage = 38%) towards intermediate (0.20–0.90 mm; total percentage 48.6%), to well developed (0.90–10.16 mm; total percentage = 13.40%). The majority of this stage had eight primary tentacles (89.5%) however the number ranged from 1 to 9. The total number of primary tentacles appears to depend on the state of advancement of the specimen within this stage and is limited to the total number of velar canals. The gastric filaments developed on the periphery of the sockets and increased in numbers per quadrant (ranged between 0 and seven; the majority (65.2%) had but one). No secondary tentacle development was observed.

Chrysaora africana **(Fig. 3.9B):** A total of 12 animals (60% of the overall animals) were measured. All specimens had a total of eight lappet stems, eight velar canals and 16 rhopalial lappets. No irregular shaped animals were noted. Post-ephyrae had a TBD of 5.28 ± 2.28 mm and a CDD of 3.10 ± 1.72 mm (Table 3.2). The manubrium was 1.91 ± 1.33 mm long. The manubrium shape ranged from 2–4. Primary tentacle length development ranged from a little stub (0.08–0.20 mm; total percentage 18.2%) through intermediate (0.26–0.75 mm; total percentage 72.7%) to well developed (1.38 mm; total percentage 9.1%). All specimens had eight primary tentacles. The number of gastric filaments per quadrant ranged from 1–10. Stage 1 post-ephyrae were readily recognised by their dark maroon-purple coloration when alive. For the most part, the ontogenic pattern of development of *C. africana* was similar

to that of *Chrysaora fulgida.* A slight developmental dissimilarity observed was the development of terminal end tips on the velar canals.

Stage 2:

***Chrysaora fulgida* (Fig. 3.5C):** This stage constituted 6.07% of the total number of specimens measured. Individuals measured 14.24 ± 4.03 mm TBD, and 10.95 ± 3.44 mm CDD (Table 3.2). The manubrium (ML) was 5.16 ± 2.58 mm long and ranged in shape from 4–5. The majority (89.6%) were normal with eight rhopalial canals: eight velar canals. Symmetrical and asymmetrical deviations, in the ratio of the rhopalial canals: velar canals, were observed in the rest of the specimens – 6:6 (n = 1), 9:9 (n = 1), 7:8 (n = 1), 6:8 (n = 1) and 5:6 (n = 1). The marginal lappets became less pointed, more rounded and broader relative to individuals in Stage 1. The velar canals lengthened centrifugally. The terminal ends of the velar canals grew in a lateral direction, into the marginal lappets. Each side-edge of rhopalial canal appears to indent just below each rhopalial canal tip opposite of the lateral velar terminal ends; thereby initiating the division of the radial septa into distal, base and proximal portions. The forked rhopalial canal tips grew further into the marginal lappets and were equivalent to or surpassed the position of the rhopalial lappet clefts. Primary tentacles elongated from intermediate (0.37–0.56 mm; total percentage 9.7%) to well developed (0.94–11.19 mm; total percentage = 90.3%). The majority of individuals had eight primary tentacles (89.6%), a number that dictated by the total number of velar canals present in the specimen. The numbers of gastric filaments per quadrant increased (ranged between three and ≥20; the majority (14.6%) had six). No secondary tentacles were observed. Small embayments (blind endings) in the periphery of the velar - and rhopalial canal pair tips started to develop in the more advanced specimens.

***Chrysaora africana* (Fig. 3.9C):** Only one specimen (5% of the overall number) was collected of this stage, measuring 8.80 mm TBD and 6.24 mm CDD (Table 3.2). The manubrium was 5.38 mm long with a manubrium shape of 4. It was symmetrical in shape with eight rhopalial and velar canals. Eight well developed (length: 5.10 mm) primary tentacles were present. The number of gastric filaments per quadrant was seven. This specimen was easily distinguishable by the dark maroon-purple pattern when alive. Morphological dissimilarities observed, from the counterpart stage of *Chrysaora fulgida* included (1)

the shallower, less pronounced embayments on the periphery of velar canal pair tips, (2) the more slender shaped rhopalial canal tips and (3) the narrower pointed tips of the velar canal.

Stage 3:

***Chrysaora fulgida* (Fig. 3.5D):** This stage was represented by 2.02% of the total number of specimens measured. It had a TBD of 25.91 ± 6.84 mm and a CDD of 20.98 ± 6.05 mm (Table 3.2). The manubrium shape was 5. The majority (89.6%) of specimens had eight rhopalial and velar canals, though one was observed with seven rhopalial and velar canals. Branched canals (of the small embayments) started to grow from the periphery of the velar and rhopalial canal tips, in a centrifugal direction, into the base of the marginal lappets. Singular secondary tentacle buds appeared at each marginal corner of the velar canal tip. The division of the radial septa into distal, base and proximal portions was more distinct since the basal region of the radial septa broadened laterally – giving a convexed appearance. The terminal lateral velar canal tips extended more, in growth laterally, into the marginal lappets in the direction of rhopalial canal tips thereby inducing concavity in the shape of the radial septa, distally. The majority of specimens had eight primary tentacles (93.8%), a number that was tied to the total velar canal count. Primary tentacles elongated in length and were well developed (1.35–28.79 mm; total percentage = 100%). The length of the secondary tentacle ranged from a little stub (0.05–0.18 mm; total percentage = 68.8%) towards intermediate (0.25–0.47 mm; total percentage 31.2%). The number of secondary tentacles ranged from two to 16; the majority (50%) had 16. The numbers of gastric filaments per quadrant increased (ranged between 14 and ≥20; the majority (75%) had ≥20).

***Chrysaora africana* (Fig. 3.9D):** Two specimens (10% of the overall number) of this stage were collected. Due to structural damage to the bell only the least developed specimen could be measured (Fig. 3.9.D1). It had a TBD of 12.41 mm and a CDD of 9.30 mm (Table 3.2). The manubrium was 6.19 mm long with a manubrium shape of 5. The specimen had eight rhopalial and eight velar canals; it possessed eight primary tentacles that were well developed (length: 11.25 mm) and nine stub-like secondary tentacles (in the process of forming) were visible (length: 0.07 mm). The number of gastric filaments per quadrant was 15.

Both specimens are illustrated (Fig. 3.9.D1 & 3.9.D2) to document the morphological development of this stage. The terminal lateral velar canal tips extended, in growth laterally, into the marginal lappets in the direction of rhopalial canal tips thereby inducing concavity in the shape of the radial septa, distally. A pear-shaped appearance of the rhopalial canals began to manifest. Rhopalial canal tips were broad and the area between the primary and secondary tentacles of each velar canal tip developed broad "protrusions" in a centrifugal direction, into the base of the marginal lappets. They were readily distinguishable by the dark maroon-purple pigmentation when alive. Key morphological dissimilarities noticed from the counterpart stage of *Chrysaora fulgida*, were the absence of branched canals on the periphery of velar and rhopalial canal tips and the presence of broad "protrusions" between the primary and secondary tentacles in the periphery of velar canals.

Stage 4:

***Chrysaora fulgida* (Fig. 3.5E):** This stage constituted 1.26% of the total number of specimens measured, measuring 32.82 ± 6.83 mm TBD and 26.94 ± 6.03 mm CDD (Table 3.2). The manubrium shape was 5. All specimens had eight rhopalial, eight velar canals and eight primary tentacles. The aradial septa enlarged distally. The radial septa narrowed distally and widened gradually at the proximal end; exhibiting pear-shaped outline at the base. The outer 1/7 of the radial septa bended towards the rhopalia (~45°). The velar canal tips lengthened centrifugally and laterally. The peripheral branched canals of the velar canal pair tips developed centrifugally in number and depth. The lateral terminal velar tips changed direction of growth by ~45° towards the periphery of the marginal lappets. The rhopalial canals tips lengthened centrifugally while their terminal ends grew in a lateral direction into the marginal lappets. The tips of the velar canal pairs reached nearly the same level in length as the rhopalial canal tips. Splits appeared at the base of the marginal lappets opposite each secondary tentacle in order to initiate the parting of the marginal lappets to form the new tentacular lappets. This stage had eight well developed primary tentacles (length: 13.31 mm). Secondary tentacles ranged in size from a little stub (0.04–0.18 mm; total percentage = 40.0%) towards intermediate (0.22–0.48 mm; total percentage 60.0%). The number of secondary tentacles ranged from 14 to 16. The total number of secondary tentacles depended on the state of advancement of the specimen within this stage and was limited to the total velar

count. The numbers of gastric filaments per quadrant increased (between 11 and >20; the majority (90%) had >20).

***Chrysaora africana* (Fig. 3.9E):** Two specimens (10% of the overall number) of this stage were collected, measuring between 24.14 ± 6.38 mm TBD and 19.45 ± 6.64 mm CDD (Table 3.2) with a manubrium shape of 5. Both specimens had eight rhopalial and eight velar canals, and eight well developed primary tentacles (length: 4.77 ± 3.33 mm). The 16 secondary tentacles ranged in length from intermediate (0.71 mm) to well develop (2.26 mm), respectively. The number of gastric filaments per quadrant was >20. Splits (in the process/completed) were present at the base of the marginal lappets opposite the secondary tentacles. New tentacular lappets were shaped upon the completion of the splitting of the marginal lappets. The terminal rhopalial canal tips narrowed and extended, in growth laterally, into the marginal lappets. The "protrusion" of each velar canal tip lengthened centrifugally into the marginal lappet. The tentacular pouches enlarged at ~1/5–1/7 distal part. The division of the radial septa into distal, base and proximal portions was more distinct since the basal region of the radial septa broadened laterally – giving a convexed appearance. The radial septa widened gradually at the proximal end (rounded base), straight up to 1/2 of the margin, then made an "S" (first thinning next to the enlargement of the tentacular pouch, then enlarging it) to be terminated in the rhopalar lappet. Specimens can be identified by their dark maroon-purple coloration when alive. Key morphological dissimilarities noticed, from the counterpart stage of *Chrysaora fulgida*, include (1) the absence of branched canals on the periphery of velar and rhopalial canal tips, (2) the presence of broad "protrusions", between the primary and secondary tentacles, in the periphery of velar canals, (3) the tentacular clefts at the same depth, (4) the less "pear" shaped appearance of the rhopalial canals, (5) the rhopalial canal tips that are not in close proximity with the terminal tips of the velar canals and (6) the crescent shape thickening of the endoderm (Table 3.3G) at the base of the rhopalial stalk.

Stage 5:

***Chrysaora fulgida* (Fig. 3.5F):** This stage was represented by three specimens (0.31% of the overall number) measuring 63.41 ± 18.42 mm TBD and 54.30 ± 16.21 mm CDD (Table 3.2). The manubrium shape was 5. All individuals examined had eight rhopalial, eight velar canals and eight

primary tentacles. The number of gastric filaments per quadrant was >20. Marginal lappets were completely formed: the tips of both the velar canal and rhopalial canal pairs were of approximately equal length. The four marginal lappets per octant consisted of two rhopaliar and two tentacular gastrovascular pouches per octant. The tentacular clefts varied in depth. The rhopaliar lappets were non-overlapping ("open-rhopalia" condition). A total of 24 tentacles: three per octant, arranged as 2:1:2. Primary tentacle length was well developed (range length: 10.90–18.18 mm). The peripheral branched canals were present on both the velar – and rhopalial canal pair tips. The radial septa narrowed distally and widened gradually at the proximal end; exhibiting a pear-shaped outline at the base. The outer ~1/7 of the radial septa bended towards the rhopalia (~45°) to terminate near the tentacular base of the rhopalial lappets. The radial septa's distal ends were wider than their proximal ends. Tentacular gastrovascular pouches (aradial septa) enlarged at ~1/5 distal part and terminated, in close proximity, at the periphery of the rhopalial lappets.

Chrysaora africana **(Fig. 3.9F):** Two specimens (10% of the overall number) were collected, with a bell diameter of 54 and 43 mm (measured with a ruler; due to physical damage to the bells no other measurements were taken): both had eight rhopalial, eight velar canals, eight well developed primary tentacles and 16 well developed secondary tentacles. The number of gastric filaments per quadrant was >20 with a manubrium shape of 5. The tips of the rhopalial canals were slightly longer than the "protrusion" tips of each velar canal. Four marginal lappets per octant consisted of two rhopaliar and two tentacular gastrovascular pouches per octant. The tentacular clefts did not vary in depth. The rhopaliar lappets were non-overlapping. A total of 24 tentacles (three per octant), arranged in 2:1:2. The tentacular pouches enlarge at 1/5 distal part and terminated at the periphery of the rhopalial lappets. The radial septa widened gradually at the proximal end (rounded base), straight up to 1/2 of the margin, then made an "S" (first thinning next to the enlargement of the tentacular pouch, then enlarging it) to terminate midway of the rhopalial lappet. The terminal points of the radial and aradial pouches did not terminate in close proximity of each other. As in previous stages, specimens were readily distinguishable by their dark maroon-purple coloration when alive. Key morphological dissimilarities noticed, from the counterpart stage of *Chrysaora fulgida*, include (1) the absence of branched canals on the periphery of velar and rhopalial canal tips, (2) the presence of broad "protrusions", between the primary and secondary

tentacles, in the periphery of velar canals, (3) the tentacular clefts at the same depth, (4) the less “pear” shaped appearance of the rhopalial canals, (5) the rhopalial canal tips that are not in close proximity with the terminal tips of the velar canals, (6) the broader crescent-like appearance of the endoderm (Table 3.3H) where the base of the rhopalial stalk is attached to, and the (7) shape of the radial and aradial septa.

Presence and growth

***Chrysaora fulgida*:** During each year, younger stages (0–1) appeared for the first time in the population at earlier dates than later stages (2–5) (Table 3.4). The developmental period from Stage 0 (ephyra) to Stage 5 (juvenile) was ~164 days (Table 3.5). The minimum total body diameters (Table 3.6) corresponded with the presence of Stage 0 ephyra (Table 3.4) during the following weeks: Week 28 to 29 and Week 36 to 45 during 2012; and Week 32 to 43 during 2013, respectively. Maximum total body diameter (Table 3.6) related to Week 51 of each respective year. Overall growth rates (Table 3.7), estimated between the first and last sampling day, were 4.33 and 3.45% d^{-1} for 2012 and 2013, respectively.

***Chrysaora africana*:** All stages occurred during Week 27–41 (5 July 2012–12 October 2012) and Week 21–51 (26 May 2013–22 Dec 2013), respectively (Table 3.4). The limited sample size prevents an estimation of the development period or the growth rate.

DISCUSSION

In tracking jellyfish blooms, one of the most challenging problems is the identification of Stage 0 ephyrae in the field, due to their simple morphology and the lack of reliable descriptions (Russell 1970; see Tronolone et al. 2002). However, some diagnostic features can be used to distinguish between different species (Russell 1970). Ephyrae of *Chrysaora* can be recognised by (1) rounded rhopalial canal tips (Russel 1970) and (2) the presence of nematocyst batteries arranged in a prominent pattern of elongated patches flanking each rhopalium, with a matching circle of round nematocyst clusters on the exumbrellar surface (Gershwin & Collins 2002). The latter characteristic is supposed to occur in all species of *Chrysaora* for which the ephyra has been described (Russell 1970: figure 53; Gershwin &

Collins 2002: figure 6; Tronolone et al. 2002: figure 4A; Widmer 2008a: figure 6, figure 8; Straehler-Pohl et al. 2011: figure 5, plate 3), although Holst (2012b) reported their occasional absence in ephyrae of *Chrysaora hysoscella*. Nematocyst clustering has also been noted for the ephyrae of non-*Chrysaora* species: *Catostylus mosaicus* (Pitt 2000), *Pelagia noctiluca* (Russell 1970: figure 45), *Sandria malayensis* (Uchida & Sugiura 1975; Straehler-Pohl et al. 2011) and *Rhopilema esculentum* (Straehler-Pohl & Jarms 2010). In this study, the nematocyst battery pattern in Stage 0 ephyrae was inconspicuous for *Chrysaora fulgida,* but clear for *C. africana*. Since, at present, only two species of *Chrysaora* are recognised in the northern Benguela this character might assist in differentiating between them.

General characteristics shared by the ephyrae of *Chrysaora* species are the presence of eight marginal lobes, 16 marginal lappets and eight rhopalia. Other useful morphological characteristics of stage 0 ephyrae that might assist in the identification or description when attempting to determine species identity include (1) coloration, (2) rhopalial lappet shape, (3) velar canal shape, (4) rhopalial canal shape, (5) number of gastric filaments present, (6) position of the velar canal tips, (7) position of the rhopalial canal tips, (8) presence/absence of tentacle buds (5) body proportions and (6) the use of linear discriminant analysis on the ratios of their morphometric measurements (Russel 1970; Straehler-Pohl & Jarms 2010; Holst 2012b; Gambill & Jarms 2014). In this study, only three key characteristics could be discerned: features 1, 3 and 4. An additional potential feature might be the reach (level) of the velar canal in relation to that of the rhopalial canal (*C. fulgida*: 1/3; *C. africana*: 1/2). However, due to the limited sample size of *C. africana* specimens, the potential use of the remaining characters (2, 5 and 6) for identification purposes requires further investigation.

Common problems that have been encountered during the morphological examination of gelatinous plankton include shrinkage, the loss of pigmentation and diagnostic structures, and distortions of the body proportions that are caused by fixation (Möller 1980; Holst & Laakmann 2014; Laakmann & Holst 2014). The use of rhopalial lappet length, rhopalial lappet shape and body proportions could not be recommended as useful diagnostic characters for stage 0 ephyrae for either of the *Chrysaora* species investigated here. Large variation existed in the central disc diameter (CDD) and rhopalial lappet length (RLL) within *C. fulgida* (Fig. 3.6), which would compromise the calculation of associated body proportions – despite the fact that in this study, all measures were recorded after a standard 24 months in

preservation. The lengths of the rhopalial lappet and the stem lappet depend on the size of the central disc and their degree of contraction during preservation (Russel 1970). In addition, the sizes of these wild caught ephyrae would depend on the onset of their feeding (Russel 1970; Fu et al. 2014) and the size and nutritional status of their parental scyphistoma (Russel 1970; Wang & Li 2015).

Both the studies of Gröndahl & Hernroth (1987) and Straehler-Pohl & Jarms (2010) regarded the shape of the rhopalial lappet as useful in distinguishing species when the marginal lappets are undamaged. The ephyrae in this study were collected by a net with non-filtering cod-end precisely to minimize damage to their marginal lappets, despite this precaution the shapes of their rhopalial lappets were indistinct non-overlapping sharp ended points. An image of a 2-day post liberation *Chrysaora fulgida* ephyrae, from a polyp culture (Ras 2016) exhibited overlapping, round spatula-like rhopalial lappets, which is in contrast to the observations made from field-collected specimens. This discrepancy in appearance between field and laboratory collected specimens is not new. Images of laboratory reared ephyrae of the same species of *Chrysaora* exhibited sharp pointed vs. round pointed (*Chrysaora hysoscella* – Russel 1970: fig.53; Morandini & Marques 2010: fig. 36; Straehler-Pohl & Jarms 2010; Holst 2012b: fig. 4(g-i)) and non-overlapping vs. overlapping (*Chrysaora quinquecirrha* – Calder 1972: fig. 1; Morandini & Marques 2010: fig. 67) features on their rhopalial lappets. That said, Calder (1972) remarked in his study of *Chrysaora quinquecirrha* that "newly-liberated ephyrae from laboratory-reared strobilae were indistinguishable from those liberated from strobilae collected at West Point on the Corrotoman River" (Calder 1972, p. 41). Unfortunately, he did not elaborate on this observation. Aside from for the lack of pigmentation, cultured *Chrysaora lactea* ephyrae were reported to be identical to wild-caught specimens caught in the São Sebastião Channel, Brazilian coast (Tronolone et al. 2002). Similarly, Calder (1972) noted that cultured ephyrae of *Chrysaora quinquecirrha* did not develop pigmentation when compared to the wild caught specimens. Standardised laboratory culture/feeding conditions for the scyphistomae were recommended when pigmentation was used as a trait in the identification of jellyfish populations (Gambill & Jarms 2014).

The development of primary tentacles on the subumbrella near the bell margin, at the base of the aradial clefts, as observed here during the ontogenic development of both *Chrysaora fulgida* and *C. africana*, is typical for members of the family Pelagiidae (Morandini et al. 2004; Straehler-Pohl et al. 2011;

Holst 2012a). Obvious features that were maintained throughout the development of the more advanced stages (Stages 3–5), in this study, were the coloration patterns (when alive), the unique presence of branched canals on the periphery of velar and rhopalial canal tips on *C. fulgida* and the presence of broad "protrusions" – between the primary and secondary tentacles – in the periphery of velar canals on *C. africana*. Coloration was the most recognizable feature discerning all stages of *C. fulgida* (peach to pale pink) and *C. africana* (maroon-purple; Fig. 3.11). Regrettably, this feature faded almost completely within a year when the specimens were preserved.

The presence of small canals of the gastrovascular system penetrating the marginal lappets in *Chrysaora melanaster* assisted in differentiating it from *Chrysaora fuscescens* that lacked this feature. Both species, in this present investigation, illustrated the same ontogenic development of the tentacular lappets by the appearance of splits at the base of the marginal lappets opposite each secondary tentacle before the marginal lappets are parted, in Stage 4. The same sequence was illustrated for *Chrysaora hysoscella* (Russel 1970), which was contrary to observations on *Chrysaora fuscescens* and *Chrysaora lactea* whereby the embayments in their rhopalial lappets turned into slits in order to part the marginal lappets (Straehler-Pohl et al. 2011).

Chrysaora fulgida in Stage 5 resembled the general structural pattern (blueprint) of the adult medusa (Neethling 2009), with four marginal lappets per octant (32 lappets in total); 24 tentacles (3 per octant) arranged as 2-1-2 (primary tentacle central, secondary tentacles laterally); the unique pear-shaped radial septa and the aradial septa that enlarge at 1/5 distal part that terminated, in close proximity, at the periphery of the rhopalial lappets. Adult *Chrysaora africana* possessed six marginal lappets per octant (48 lappets in total); 40 tentacles (five per octant); and the aradial septa dilated distally which terminated at the cleft between rhopalial and velar lappets (Neethling 2009). *Chrysaora chinensis, C. lactea, C. pacifica, C. quinquecirrha, C. pentastoma* are species sharing the same morphological feature of forty-eight lappets (and 40 tentacles) from different geographical areas (Morandini & Marques 2010; Straehler-Pohl et al. 2011). In this study, *C. africana* in Stage 5 did not resemble the general structure of the adult medusa as described by Neethling (2009). It superficially bears a resemblance to the adult *C. fulgida* medusa by exhibiting the same number of tentacles and marginal lappets. However, there were morphological features present to clearly distinguish between *C. africana* and *C. fulgida* as shown in the

"Results" section, above. Thus, additional ontogenic stages as to resemble the adult medusa such as the development of tertiary tentacles and the splitting of the tentacular lappets in two above the tertiary tentacles as illustrated for *C. lactea* (Straehler-Pohl et al. 2011) would be expected to occur in *C. africana*. In addition, *C. lactea* revealed the absence of correlations between bell diameter and both gonad development and maximum tentacle number per octant while some individuals remained during their entire adult lifespan in the three-tentacle-per-octant stage (Morandini & Marques 2010). The sequence of tertiary tentacle development needs to be confirmed for *C. africana* since the arrangement of 2-3-1-3-2 was reported in *C. lactea* (Straehler-Pohl et al. 2011) whereas 3-2-1-2-3 was noted in *C. chinensis, C. pacifica* and *C. quinquecirrha (*Morandini & Marques 2010).

Deviations from the typical octoradiate symmetry in ephyrae and post-ephyrae of *Chrysaora fulgida* (reported in this study) is not an uncommon occurrence in other scyphozoan species (Berrill 1949; Gershwin 1999; Schiariti et al 2008), although in low frequency of 2–10% (Gershwin 1999). Typically, the 8:8 marginal:rhopalial lappet configuration is exhibited in most scyphozoans' ephyrae (Berrill 1949; Russel 1970; Arai 1997; Holst et al. 2007; Schiariti et al 2008), as the number of rhopalia serves as a blueprint for the adult medusa from liberation (Berrill 1949). Berrill (1949) reported that the position of the ephyral disc on the parental polyp during strobilation determined the symmetry of the ephyrae. The uppermost discs of a strobila are generally larger than the rest, and display up to 12 marginal lappets whereas the bottom discs are usually the smallest and are limited to two marginal lappets (Berrill 1949). Contrary, Schiariti et al. (2008) did not find any links between the number of marginal lappets and the position of ephyrae of *Lychnorhiza lucerna* in the strobili. In addition, the latter authors could not confirm the upkeep of the "blueprint" from liberation until adulthood of the medusa since the "ephyral deviations" displayed swimming disabilities and perished a few days after liberation. Abrams et al. (2015) observed that 9.5% of the *Aurelia aurita* ephyrae cultured in their laboratory were radially symmetrical non-octamers. In response to marginal lappet amputations, *Aurelia aurita* ephyrae go through a process of "symmetrisation" whereby their remaining marginal lappets are rearranged, their manubria re-centred and their muscular networks rebuilt, all accomplished within 12 hours to 4 days (Abrams et al. 2015). Hence, this self-repairing process when injured can result into non-octoradiate symmetry of ephyrae which are maintained throughout their adulthood (Abrams et al. 2015).

In the northern Benguela system, Neethling (2009) observed aberrations in the number of rhopalia present in the medusae of *Chrysaora fulgida* and *C. africana* while the number of primary tentacles varied accordingly with the number of rhopalia. From a total of 16 *C. africana* medusae, two had seven rhopalia and one specimen had nine, whereas out of 40 *C. fulgida* medusae, only one specimen held nine rhopalia (Neethling 2009). These observations suggest that "ephyral deviations" of *C. fulgida* and *C. africana* can reach adulthood in the northern Benguela system (Neethling 2009). It should be noted that morphological development of the ephyrae to young stage is a continuum and that the interim stages may account for the absence/presence of certain illustrated features of the "snapshot" specimens in this study. Due to the limited numbers of *C. africana* specimens, a detailed description with regard to its ontogenic development and a complete characteristic comparison with its counterpart stages *viz*. *C. fulgida* was not possible. The present study should be viewed as preliminary, in this regard.

The presence of Stage 0 ephyrae of *Chrysaora fulgida* (Table 3.4 & 3.6), with smallest diameter, suggests that strobilation of this species occurs in Walvis Bay over the period July (mid-winter) to the start of November (late spring). The development of *C. fulgida* ephyrae was not solely accompanied by alterations in morphology, but by growth in size as well (Table 3.7). In this study, the maximum total body diameter, of both years, showed that a size ≥100 mm (at Stage 5) could not be reached during the developmental period from Stage 0 (ephyra) to Stage 5 (juvenile). Ontogenic development and growth of *C. fulgida* ephyrae, in this study, seems to be characterised as slow, when compared with other species (Table 3.7), perhaps because of low water temperatures and poor food (abundance or quality). That said, suitable comparisons and interpretations of development rates among species in literature are hampered by the lack of standard definitions in the ontogenic development of ephyrae.

Growth of the ephyrae is reported to be controlled by the type of food (Lucas 1996; Olesen et al. 1996; Båmstedt et al. 1997; Zheng et al. 2015), food abundance (Lucas 1996; Møller & Riisgård 2007; Wang & Li 2015), food size (Båmstedt et al. 1994; Olesen et al. 1994; Lucas 1996; Lilley et al. 2014a), water temperature (Möller 1980; Hernroth & Gröndahl 1983; Møller & Riisgård 2007), resilience to starvation (Fu et al. 2014), irradiation (Hernroth & Gröndahl 1983); presence of certain phytoplankton bloom species (Huang et al. 2014) and population density (Schneider & Behrends 1994; Lucas 2001; Riisgård et al. 2010). Ephyrae of *Aurelia aurita* are freed from the strobilating benthic phase generally

during winter and early spring (Toyokawa et al. 2000, Lucas 2001), when the abundance and the production of their prey food are at their lowest. This is also the period whereby ephyrae overwinter in diapause and grow very slowly. However, this situation is quickly overturned with the onset of increase food availability, irradiation and water temperatures that promote rapid growth (Möller 1980; Hernroth & Gröndahl 1983). The feeding rate and morphological development of *Cotylorhiza tuberculata* increases with water temperature (Astorga et al. 2012). Similarly, the feeding rates of *Aurelia aurita* are influenced by water temperature (Olesen 1995; Møller & Riisgård 2007), and bell size (Olesen 1995).

Since water temperature and food availability/quality seem to be the main factors regulating the growth of ephyrae, in general, these factors might be the reason for the slow growth of the early phase of *C. fulgida* during winter and mid-spring. However, future studies should address the effect of food availability and quality on the growth of *C. fulgida* by investigating the abundance and temporal spatial distribution of possible prey species for ephyrae in the northern Benguela system. A growth experiment of *Pelagia noctiluca* ephyrae, fed *ad libitum*, exhibited a response of typical rapid growth increase for a period before stagnating and, in many cases, shrunk; until non-motile prey items were offered to improve their survivorship (Lilley et al. 2014a). Consequently, a mismatch between the availability of optimal food and the presence of developmental stages might substantially affect the growth and mortality rates of the young stages.

FIGURES

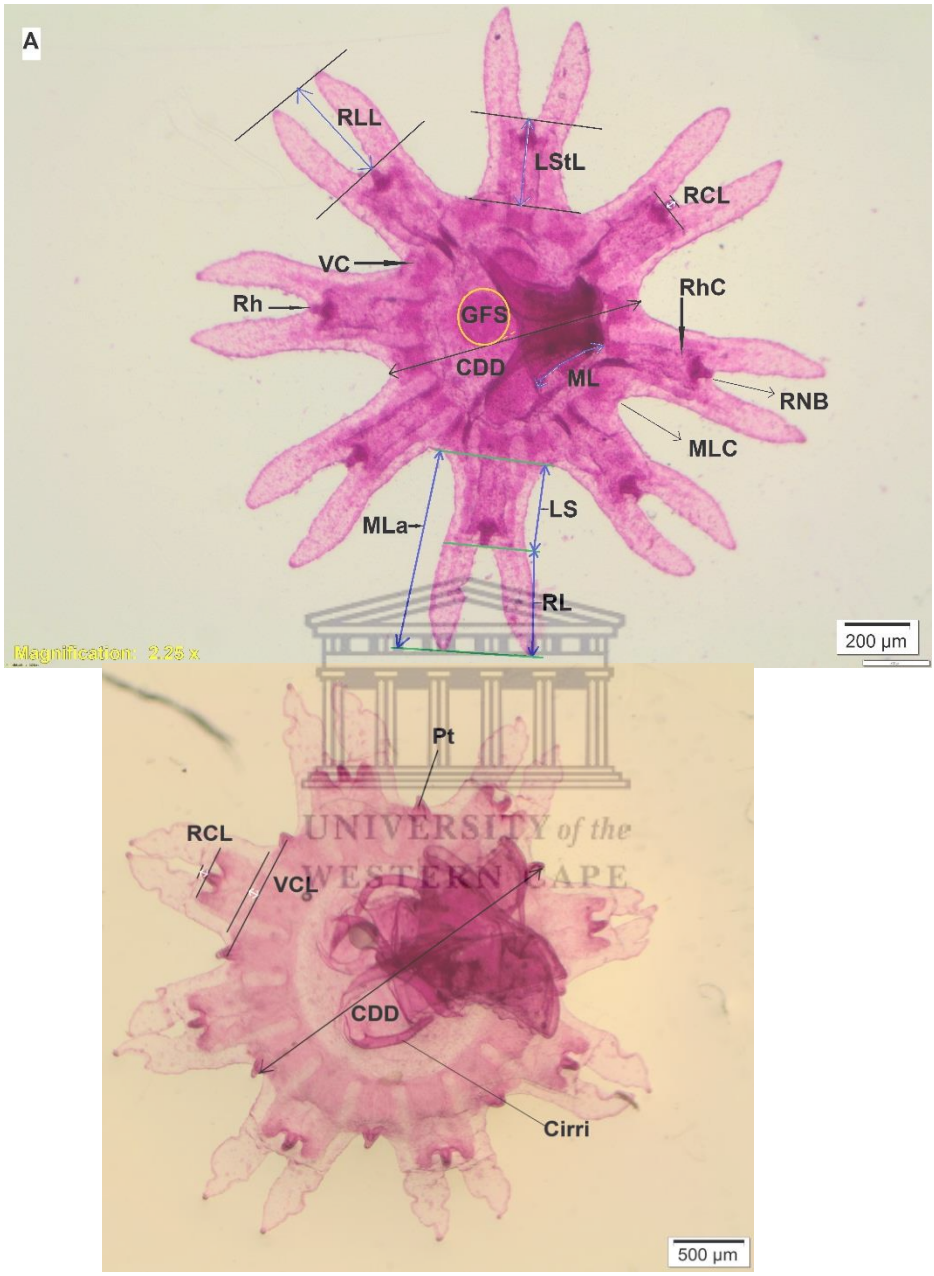


Figure 3.1. Images of measuring points taken for (A) ephyra and (B) post-ephyra. These samples were all stained with Rose Bengal to enhance contrasts between structural features. CDD: central disc diameter, Cirri: gastric filaments, GFS: gastric filament socket (yellow encircled), LS: lappet stem; LStL: lappet stem length, ML: manubrium length, MLa: marginal lappet; MCL: marginal lappet cleft; Pt: primary tentacle, RCL: rhopalial canal length, Rh: rhopalial; RhC: rhopalial canal; RL: Rhopalial lappet; RLL: rhopalial lappet length, RNB: rhopalial niche base; VC: velar canal; VCL: velar canal length

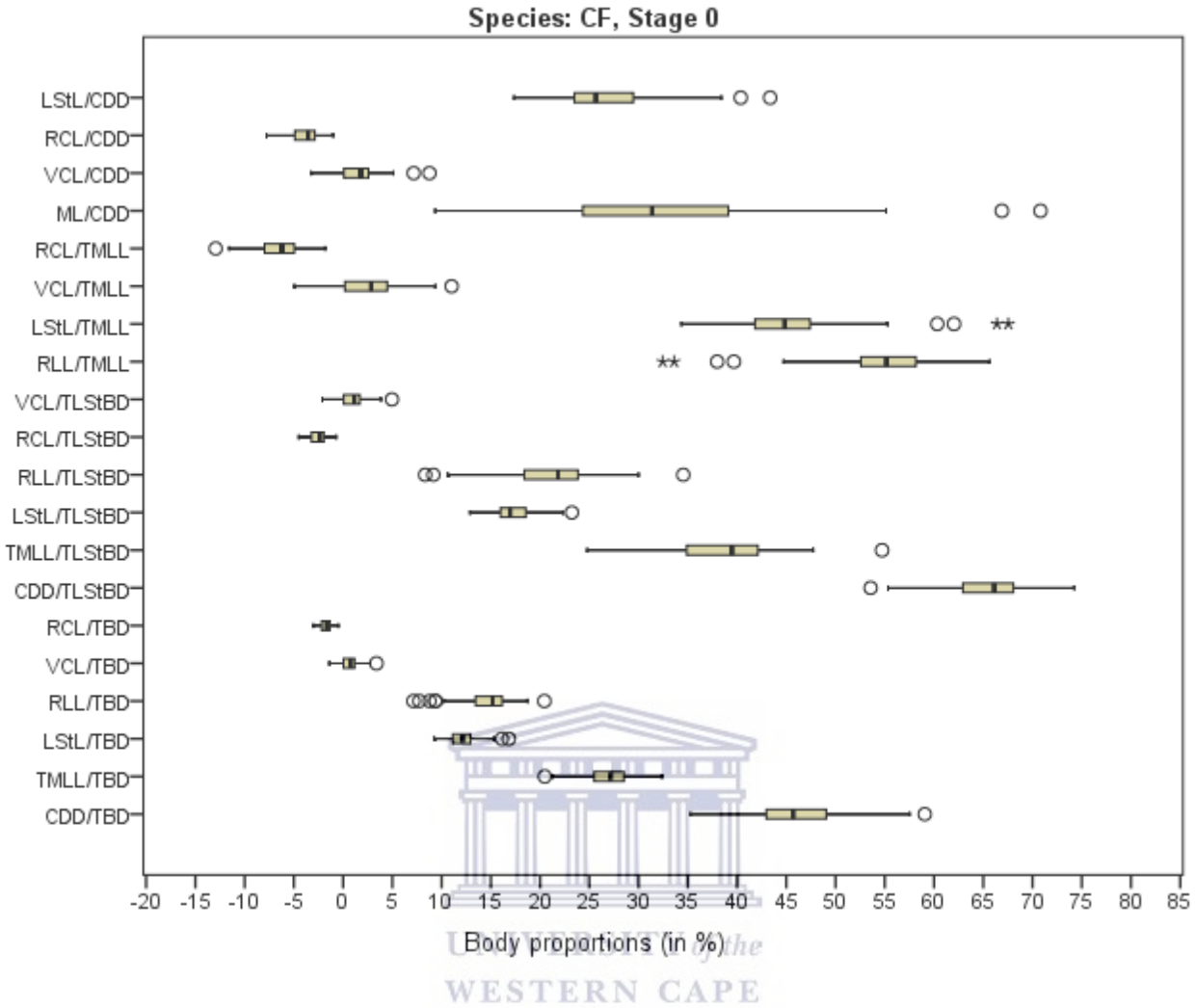


Figure 3.2. Box-and-whisker plots of body proportions (in %) for *Chrysaora fulgida* staged 0 ephyrae.

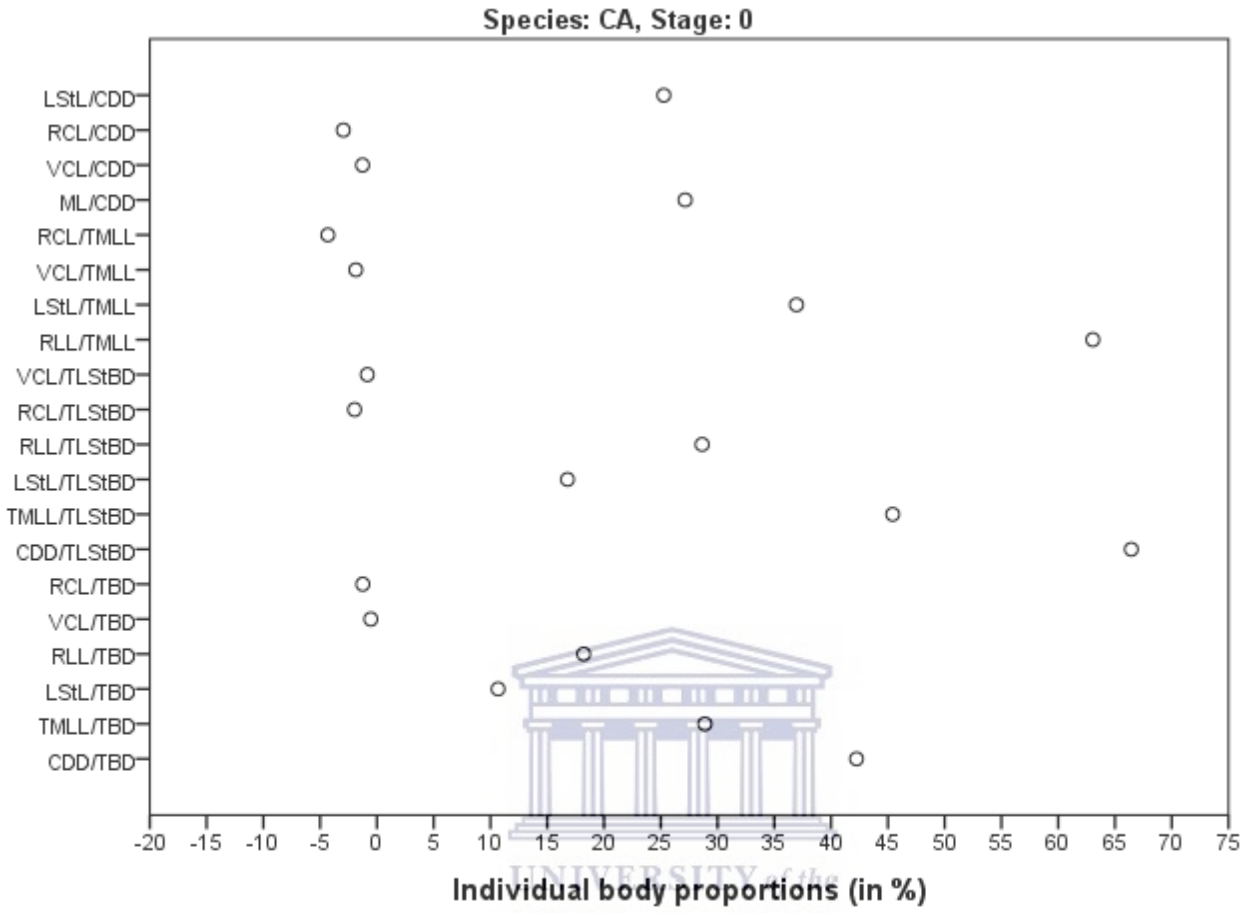


Figure 3.3. Individual body proportions (in %) of a *Chrysaora africana* ephyra.

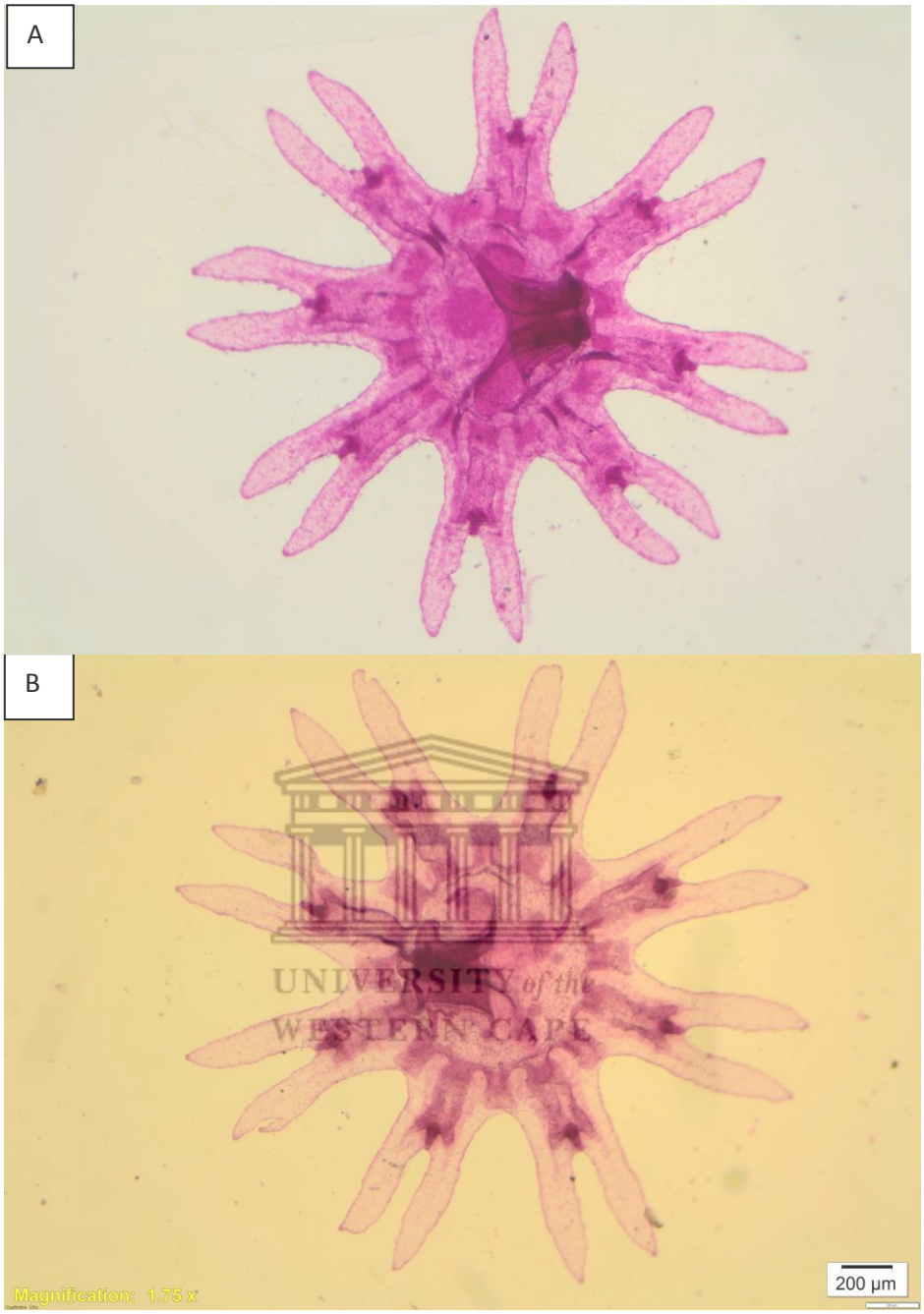


Figure 3.4. Stage 0 ephyrae images stained with Rose Bengal. A) *Chrysaora fulgida*, B) *Chrysaora africana.*

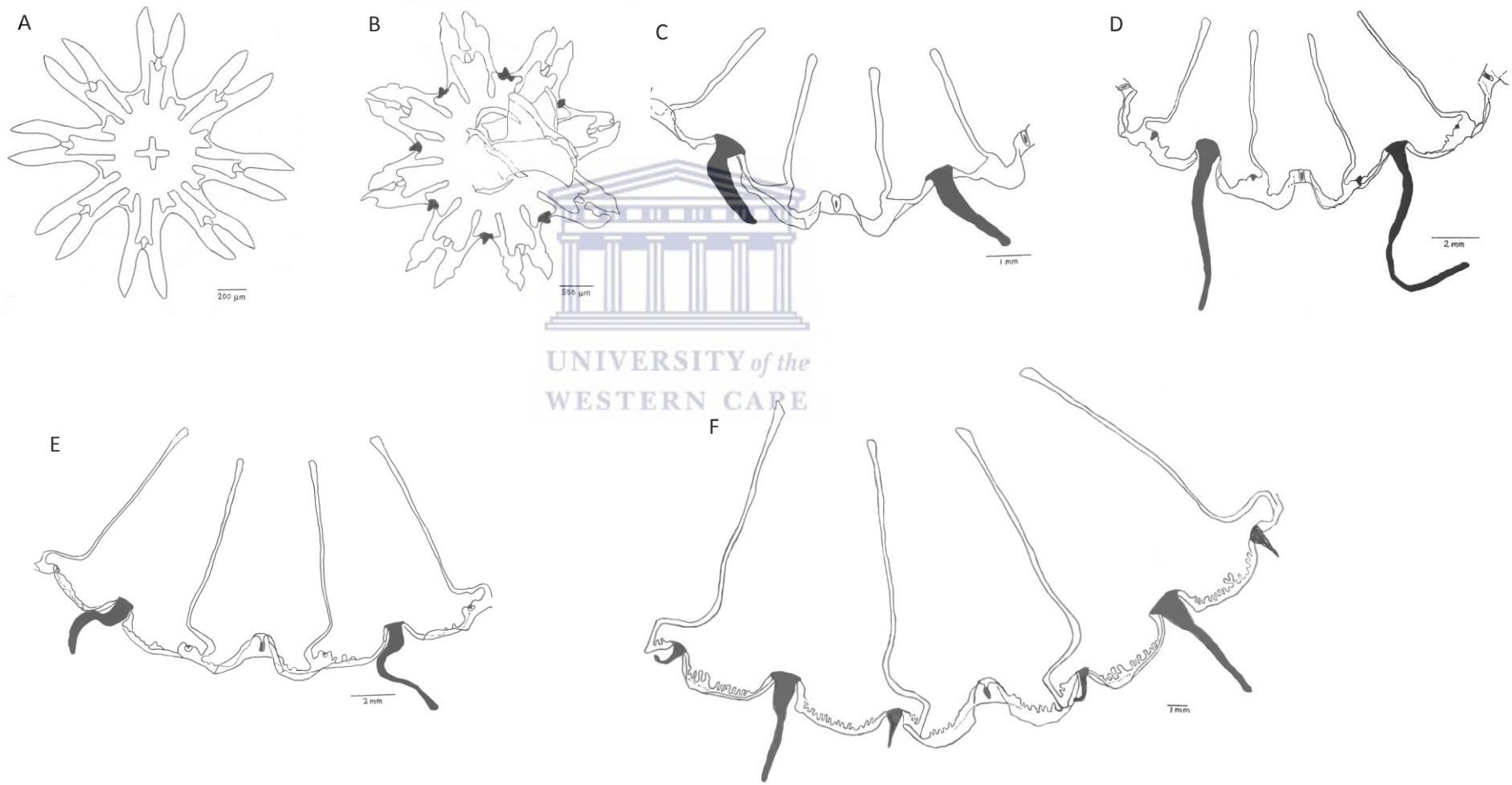


Figure 3.5. *Chrysaora fulgida*. Development of gastric system, marginal lappets and tentacles. A) Ephyra, Stage 0; B) Stage 1; C) Stage 2; D) Stage 3, illustrating the presence of secondary tentacle buds; E) Stage 4, showing the splitting of marginal lappets at its base; F) Stage 5 juvenile, illustrating final developed marginal lappets.

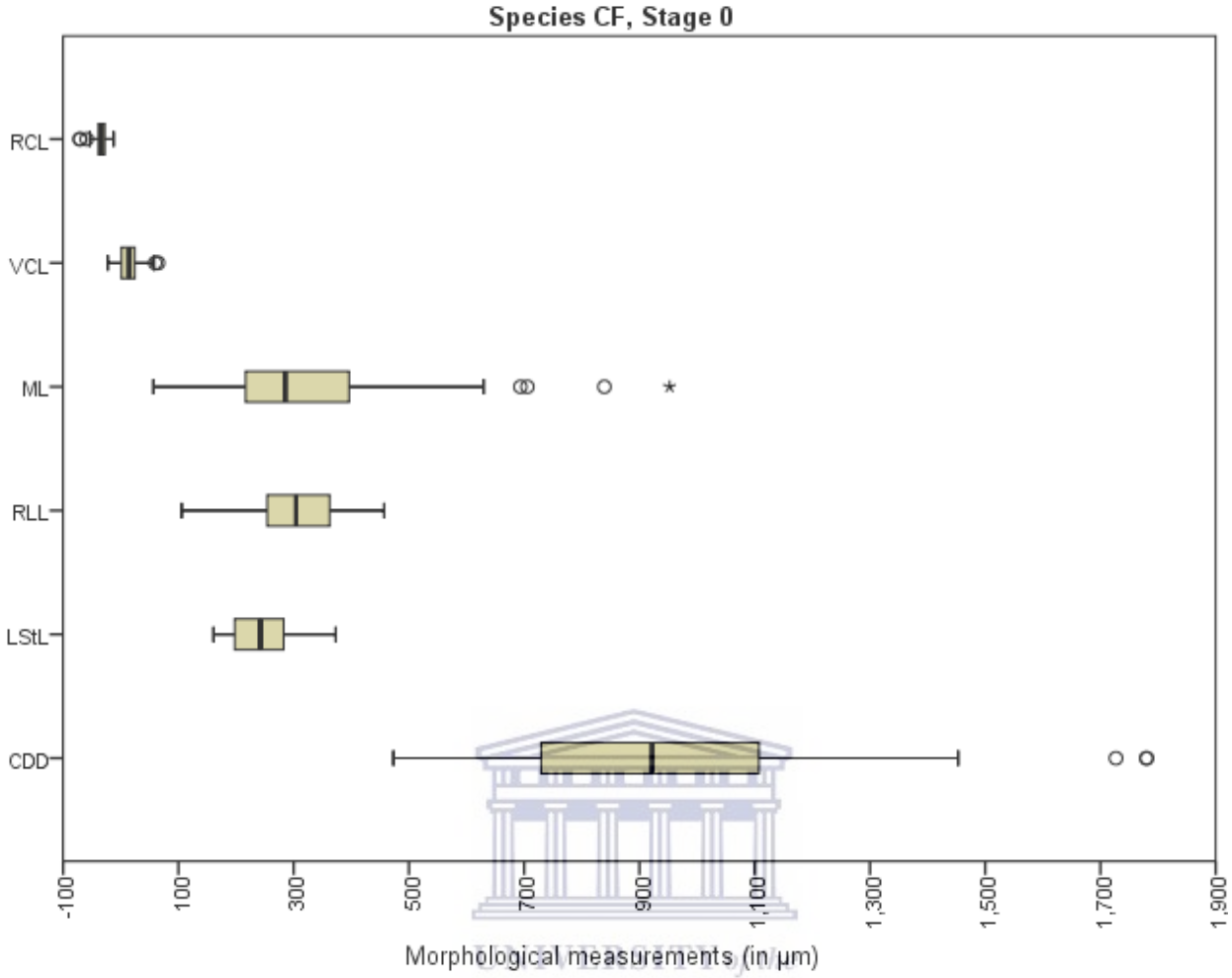


Figure 3.6. Box-and-whisker plots of morphological measurements (in µm) for *Chrysaora fulgida* staged 0 ephyrae.

Figure 3.7. Images of Stage 0 ephyrae to indicate natural coloration (subumbrella view) of *Chrysaora fulgida.*

Figure 3.8. Green arrows indicating the position of some of the nematocyst clusters present on *Chrysaora fulgida* Stage 0 ephyra.

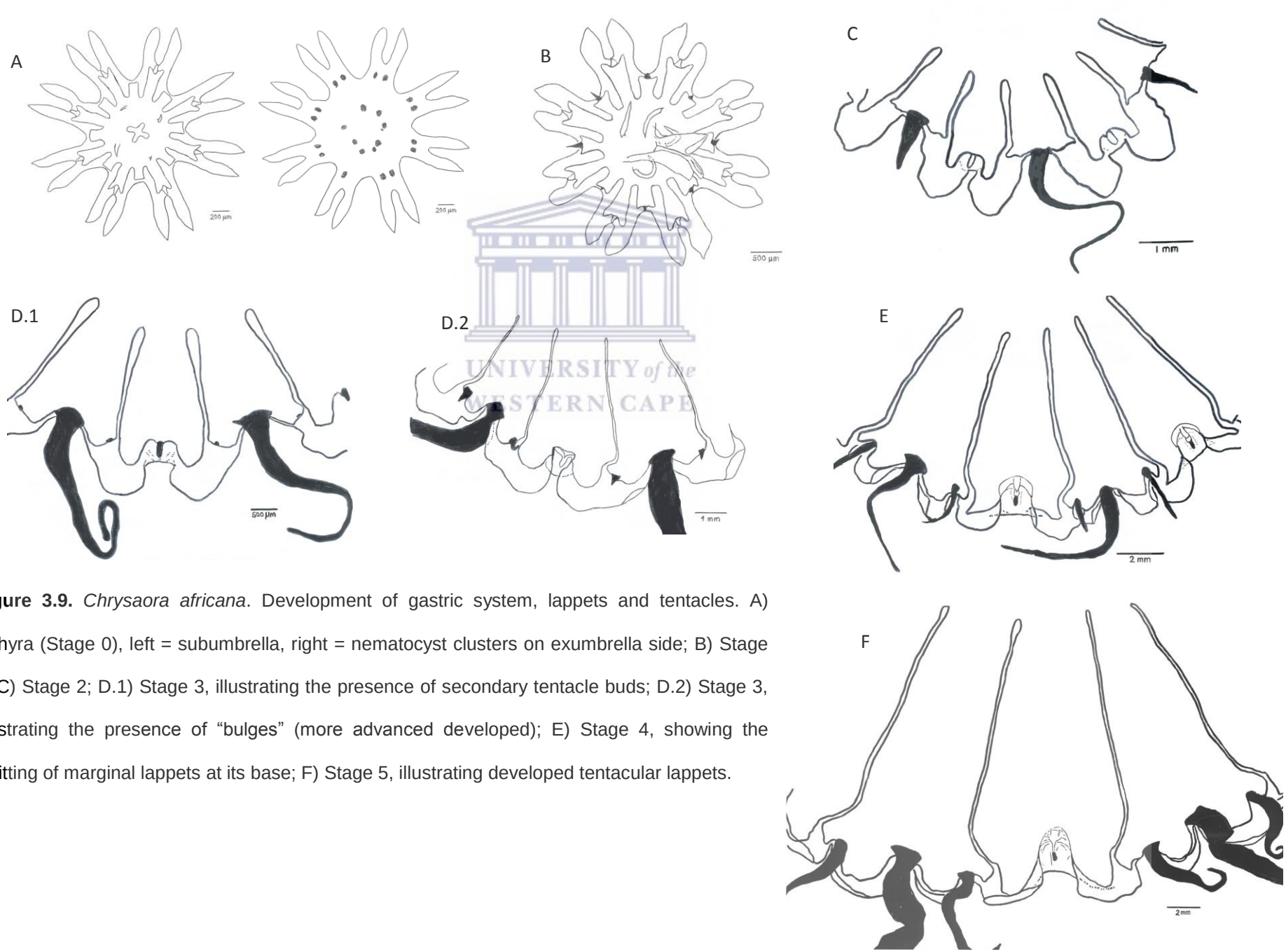


Figure 3.9. *Chrysaora africana*. Development of gastric system, lappets and tentacles. A) Ephyra (Stage 0), left = subumbrella, right = nematocyst clusters on exumbrella side; B) Stage 1; C) Stage 2; D.1) Stage 3, illustrating the presence of secondary tentacle buds; D.2) Stage 3, illustrating the presence of "bulges" (more advanced developed); E) Stage 4, showing the splitting of marginal lappets at its base; F) Stage 5, illustrating developed tentacular lappets.

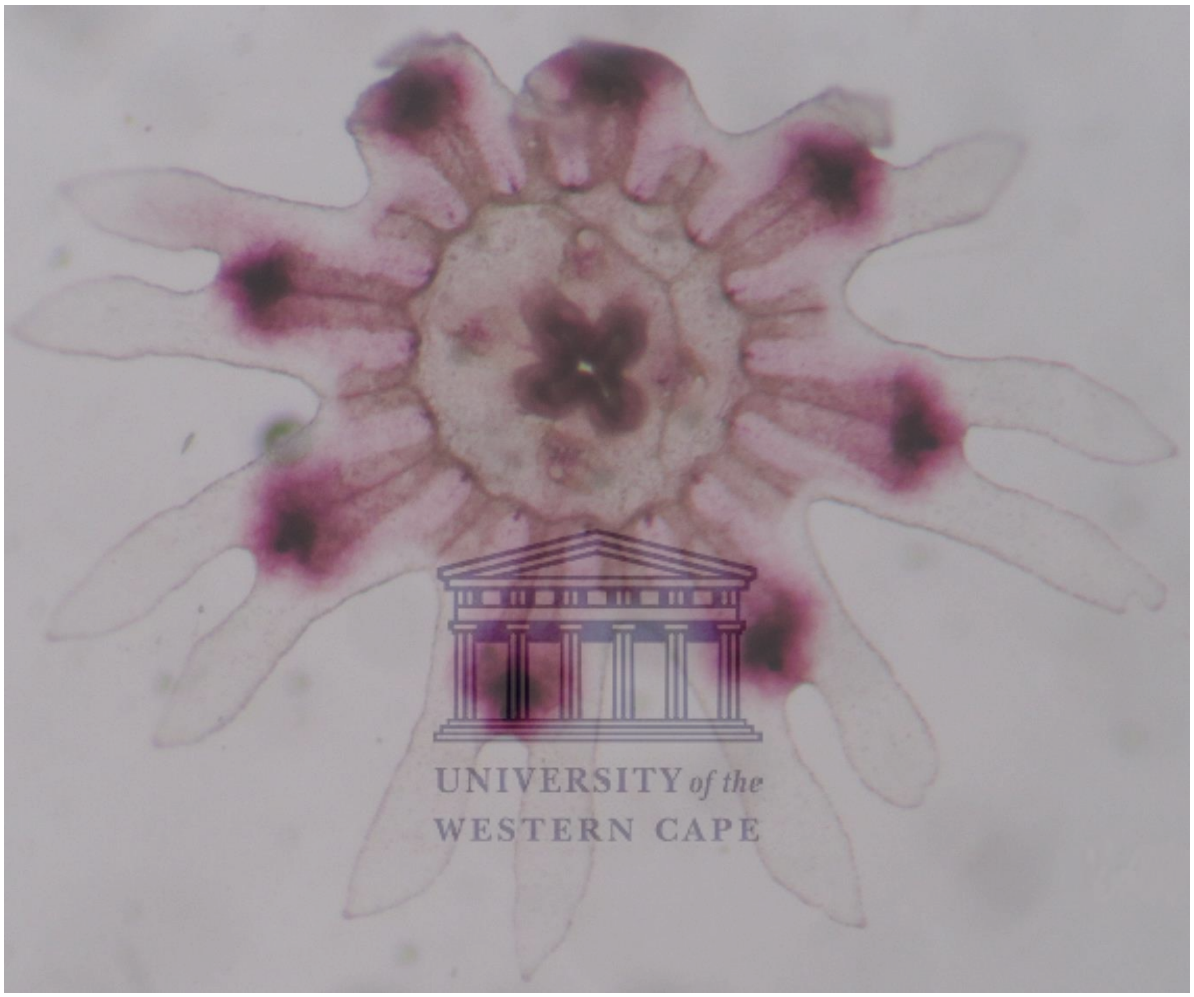


Figure 3.10. Photograph of Stage 0 ephyra of *Chrysaora africana* to indicate natural coloration (subumbrella view). Preserved specimen measured *ca*. 2.67 mm in total body diameter (TBD)

.

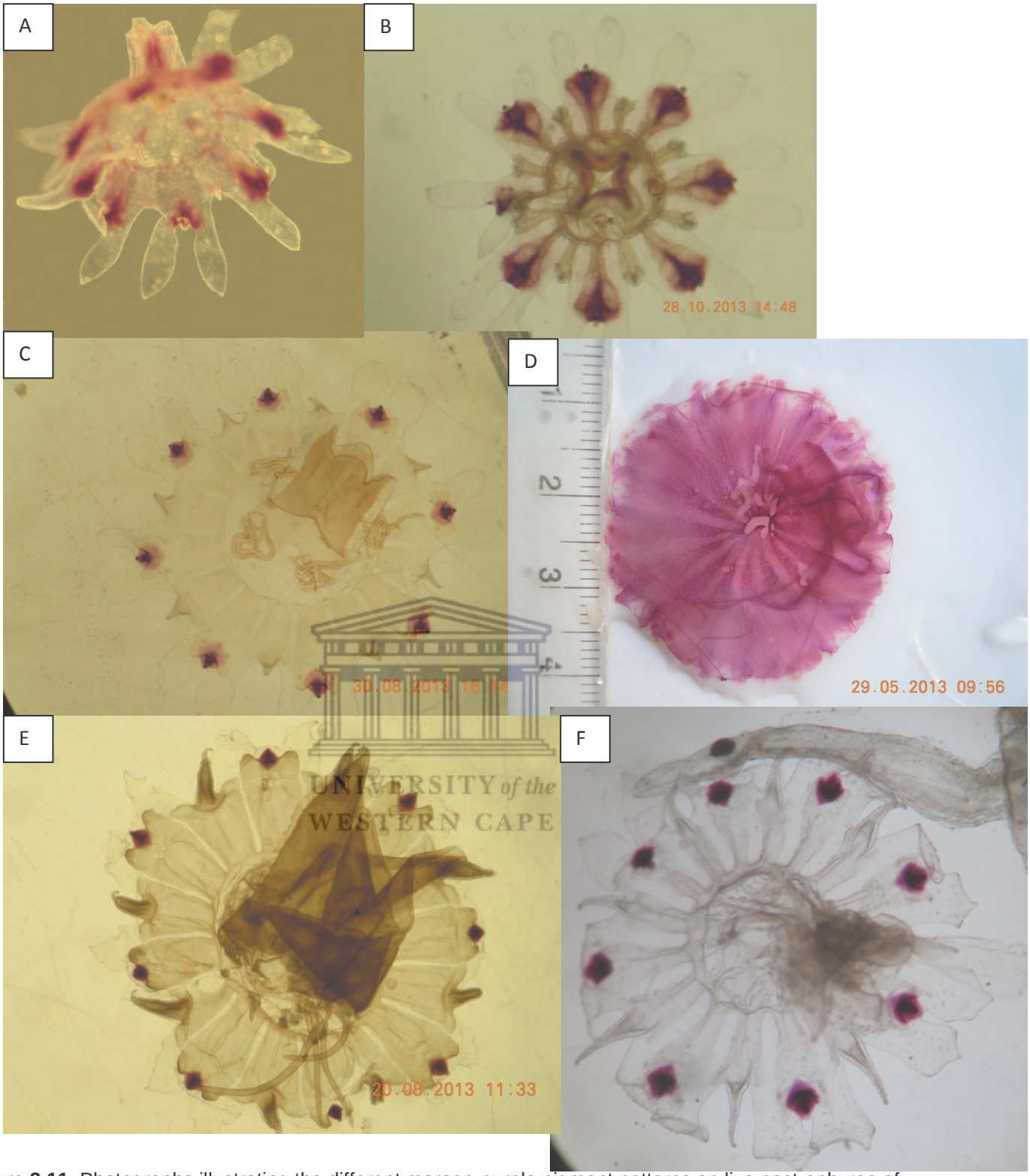


Figure 3.11. Photographs illustrating the different maroon-purple pigment patterns on live post-ephyrae of *Chrysaora africana*. Preserved specimens measured (total body diameter) and staged as following: (A) 4.14 mm at Stage 1; (B) 3.04 mm at Stage 1; (C) 6.03 mm at Stage 1; (E) 7.7 mm at Stage 1 and (F) 4.69 mm at Stage 1. (D) Live specimen measurement of *ca.* 35 mm at Stage 4.

TABLES

Table 3.1. Developmental shapes and descriptions of the manubrium

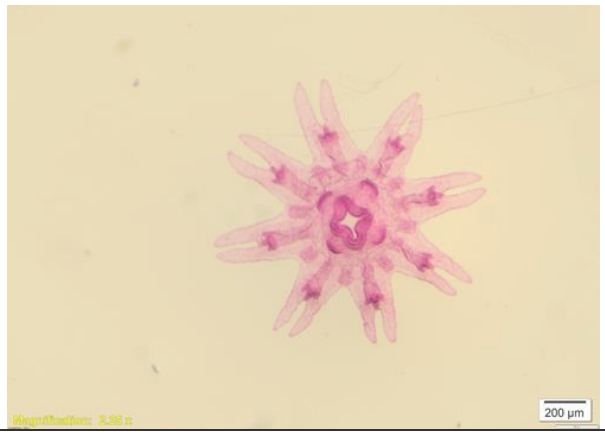
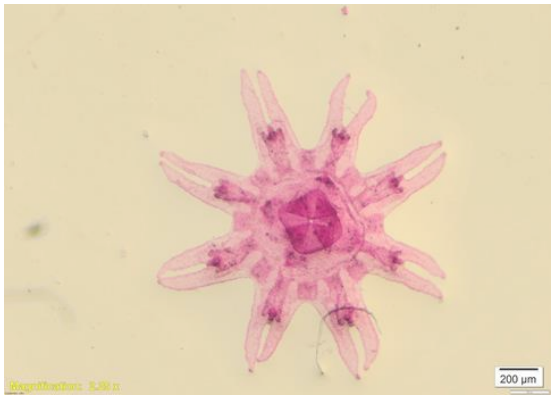
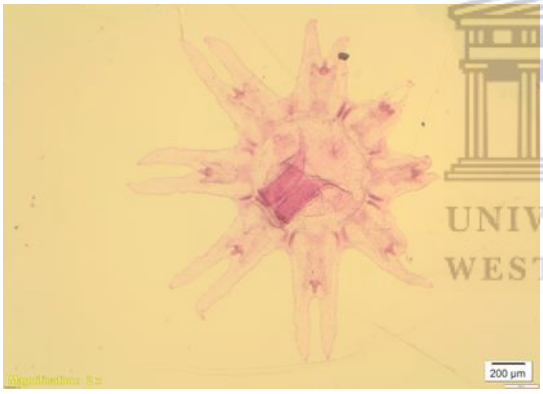
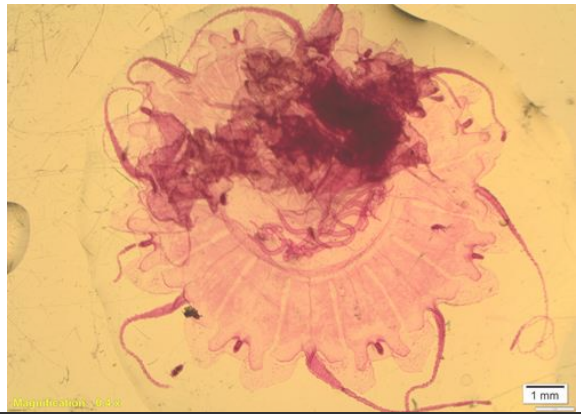
Shape 1: Simple, crusiform 	**Shape 2:** Rounded 
Shape 3: Straw-like (narrow and long) 	**Shape 4:** four distinct oral arms 
Shape 5: Highly folded sheet-like and frilled oral arms 	

Table 3.2. Standard measurements (in mm) of the different "ephyrae" stages of *Chrysaora fulgida* and *Chrysaora africana.*

Species	Stage	Characteristics	N*	Min	Max	Mean	Median	SD
Chrysaora fulgida	0	CDD	96	0.37	1.78	0.96	0.92	0.29
		LStL	96	0.11	0.37	0.25	0.24	0.056
		$TMLL_b$	95	0.33	0.81	0.55	0.55	0.12
		TBD[b]	95	1.18	3.35	2.07	2.10	0.48
		TLStBD[b]	96	0.61	2.53	1.45	1.46	0.38
		RLL	95	0.10	0.46	0.30	0.31	0.08
		ML	92	0.06	0.95	0.32	0.28	0.16
		VCL[e]	96	-0.02	0.06	0.01	0.01	0.02
		RCL[f]	96	-0.07	-0.01	-0.04	-0.03	0.01
	1	CDD	618	0.64	8.82	2.85	2.54	1.46
		LStL	617	0.182	0.94	0.47	0.46	0.01
		TMLL[b]	611	0.34	1.54	0.94	0.93	0.21
		TBD[b]	611	1.55	11.16	4.72	4.45	1.77
		TLStBD[b]	617	1.07	10.34	3.79	3.50	1.67
		RLL	611	0.12	0.86	0.47	0.46	0.11
		ML	544	0.13	9.25	1.62	1.29	1.13
		VCL[e]	616	-0.04	0.58	0.12	0.09	0.10
		RCL[f]	616	-0.11	0.17	-0.03	-0.04	0.04
	2	CDD	48	5.86	20.80	10.95	10.07	3.44
		LStL	47	0.56	1.53	1.05	1.04	0.22
		TMLL[b]	45	0.83	2.22	1.66	1.59	0.32
		TBD[b]	45	7.52	24.89	14.24	13.08	4.03
		TLStBD[b]	47	6.98	23.10	12.99	12.11	3.80
		RLL	45	0.27	0.90	0.61	0.59	0.13
		ML_c	10	1.24	9.31	5.16	3.89	2.58
		VCL[e]	47	0.37	1.21	0.73	0.67	0.25
		RCL[f]	47	0.00	0.41	0.013	0.10	0.10
	3	CDD	16	13.28	36.10	20.98	19.67	6.05
		LStL	16	1.02	2.22	1.51	1.43	0.31
		TMLL[b]	16	1.67	3.50	2.46	2.42	0.47
		TBD[b]	16	17.91	43.09	25.91	24.40	6.84
		TLStBD[b]	16	16.38	40.29	24.00	22.58	6.50
		RLL	16	0.65	1.41	0.95	0.87	0.25
		ML[c]	0	-	-	-	-	-
		VCL[e]	16	0.82	2.40	1.37	1.33	0.44
		RCL[f]	16	0.01	0.80	0.37	0.31	0.22

	4	CDD	10	15.68	34.76	26.94	28.00	6.03
		LStL	10	1.37	2.21	1.82	1.75	0.31
		TMLL[b]	10	2.26	3.65	2.94	2.92	0.44
		TBD[b]	10	20.20	42.07	32.82	34.01	6.83
		TLStBD[b]	10	18.41	39.19	30.57	31.77	6.42
		RLL	10	0.86	1.44	1.12	1.11	0.23
		ML[c]	0	-	-	-	-	-
		VCL[e]	10	0.72	2.49	1.63	1.72	0.50
		RCL[f]	10	0.28	1.99	0.63	0.47	0.50
	5	CDD	3	43.38	72.93	54.30	46.60	16.21
		LStL	3	2.03	3.15	2.49	2.27	0.59
		TMLL[b]	3	3.80	5.82	4.55	4.04	1.11
		TBD[b]	3	50.97	84.56	63.41	54.68	18.42
		TLStBD[b]	3	47.44	79.23	59.27	51.15	17.38
		RLL	3	1.76	2.67	2.07	1.77	0.52
		ML[c]	0	-	-	-	-	-
		VCL[e]	3	2.28	3.94	2.97	2.69	0.86
		RCL[f]	3	0.49	1.88	1.23	1.317	0.70
Chrysaora africana	0	CDD	1	1.13	1.13	1.13	1.13	-
		LStL	1	0.28	0.29	0.29	0.28	-
		TMLL[b]	1	0.77	0.77	0.77	0.77	-
		TBD[b]	1	2.67	2.67	2.67	2.67	-
		TLStBD[b]	1	1.70	1.70	1.70	1.70	-
		RLL	1	0.49	0.49	0.49	0.49	-
		ML[c]	1	0.31	0.31	0.31	0.31	-
		VCL[e]	1	-0.01	-0.01	-0.01	-0.01	-
		RCL[f]	1	-0.03	-0.03	-0.03	-0.03	-
	1	CDD	12	1.42	6.15	3.10	2.60	1.72
		LStL	12	0.35	0.80	0.51	0.47	0.16
		TMLL[b]	11	0.71	1.61	1.07	1.03	0.27
		TBD[b]	11	2.96	9.22	5.28	4.58	2.28
		TLStBD[b]	12	2.13	7.74	4.12	3.54	2.01
		RLL	11	0.36	0.81	0.56	0.56	0.01
		ML[c]	10	0.62	4.54	1.91	1.53	1.33
		VCL[e]	12	0.03	0.34	0.10	0.08	0.09
		RCL[f]	12	-0.14	0.00	-0.07	-0.08	0.04

		CDD	1	6.24	-	-	-	-
		LStL	1	0.62	-	-	-	-
		TMLL[b]	1	1.28	-	-	-	-
		TBD[b]	1	8.80	-	-	-	-
	2	TLStBD[b]	1	7.47	-	-	-	-
		RLL	1	0.66	-	-	-	-
		ML	1	5.38	-	-	-	-
		VCL[e]	1	0.09	-	-	-	-
		RCL[f]	1	0.06	-	-	-	-
		CDD	1	9.30	-	-	-	-
		LStL	1	0.95	-	-	-	-
		TMLL[b]	1	1.55	-	-	-	-
		TBD[b]	1	1.24	-	-	-	-
	3	TLStBD[b]	1	1.12	-	-	-	-
		RLL	1	0.60	-	-	-	-
		ML	1	6.19	-	-	-	-
		VCL[e]	1	0.61	-	-	-	-
		RCL[f]	0	-	-	-	-	-
		CDD	2	14.76	24.14	19.45	19.45	6.64
		LStL	2	1.37	1.73	1.55	1.55	0.26
		TMLL[b]	2	2.26	2.44	2.35	2.35	0.13
		TBD[b]	2	19.63	28.66	24.14	24.14	6.38
	4	TLStBD[b]	2	18.22	26.88	22.55	22.55	6.12
		RLL	2	0.70	0.89	0.80	0.80	0.13
		ML[c]	0	-	-	-	-	-
		VCL[e]	2	1.03	1.05	1.04	1.04	0.01
		RCL[f]	2	0.00	0.17	0.09	0.09	0.125
	5	BD[d]	2	43	54	-	-	-

*Some measurements omitted due to damaged structures

[b]Calculated from measurements

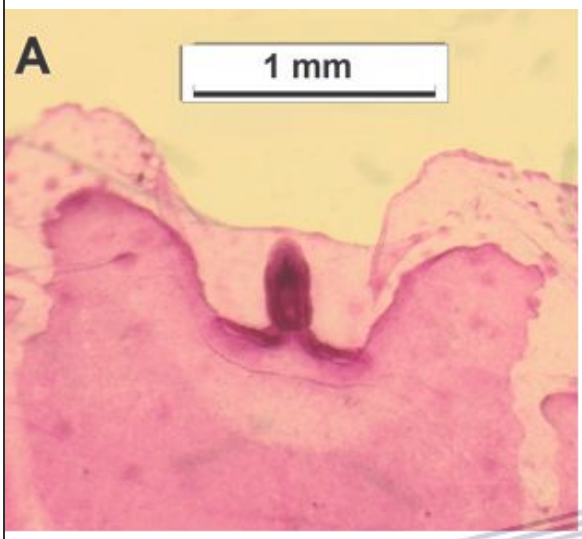
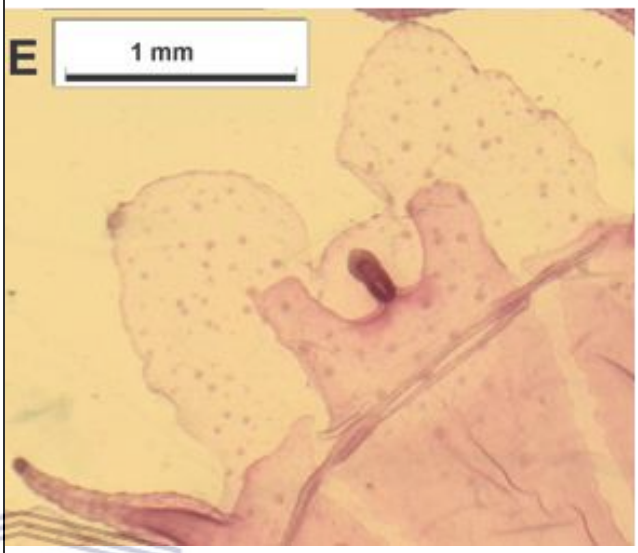
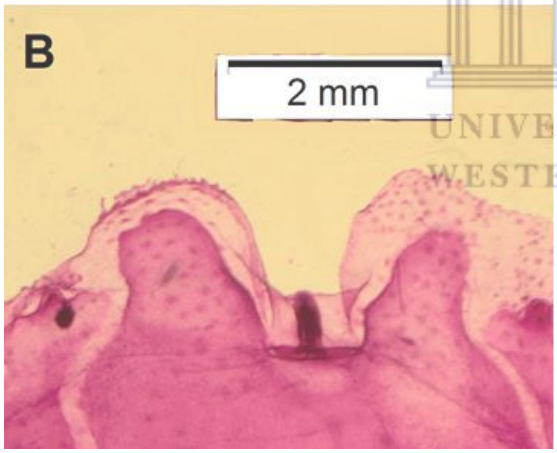
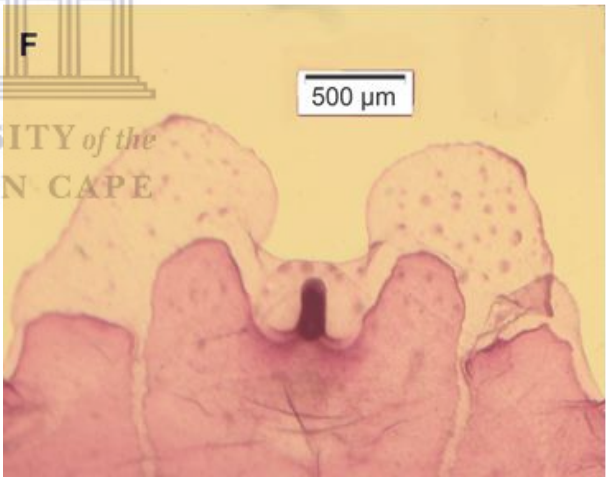
[c]Manubrium length too long for measuring under microscope

[d]Bell diameter measured with ruler

[e]The position of the velar canals tips relative to the lappet base: minus (-) for below or plus (+) for extending beyond the lappet base

[f]The position of the rhopalial canal tips relative to the rhopalial niche base: minus (-) for below or plus (+) for surpassing the rhopalial niche base

Table 3.3. Developmental shapes of rhopalial between Stages 2–5.

STAGE	*Chrysaora fulgida*	*Chrysaora africana*
2		
3		

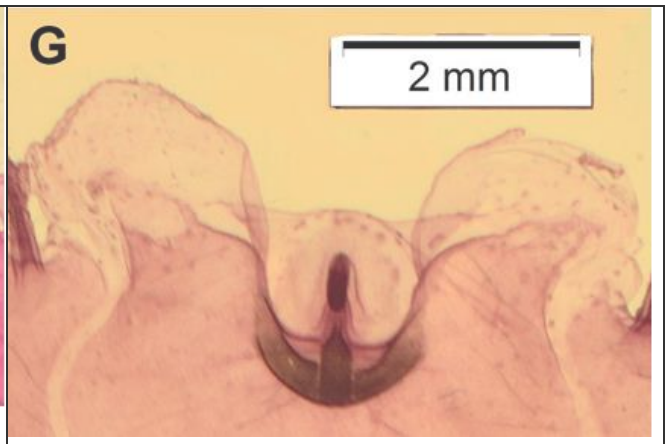
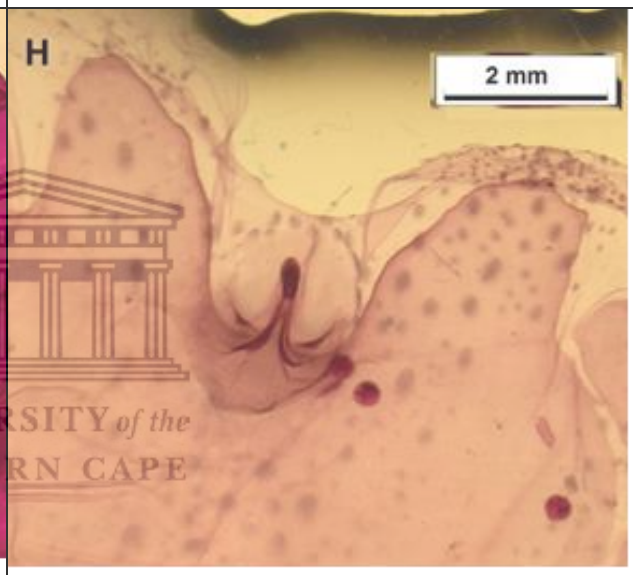
4		
5		

Table 3.4. The number (n) of *Chrysaora fulgida* and *Chrysaora africana* individuals present per stage per calendar week per year.

Stage	Week	*Chrysaora fulgida*			*Chrysaora africana*		
		n			n		
		Year 2012	Year 2013	Total	Year 2012	Year 2013	Total
4	21	-	-	-	-	1	1
1	27	-	-	-	1	-	1
2		-	-	-	1	-	1
0	28	1	-	1	-	-	-
1		2	-	2	2	-	2
0	29	37	-	37	1	-	1
1		13	-	13	1	-	1
1	30	-	11	11	-	-	-
3		-	-	-	-	1	1
4		-	-	-	-	1	1
0	32	-	2	2	-	-	-
1		50	50	100	-	1	1
2		-	3	3	-	-	-
3		-	-	-	1	-	1
1	33	48	-	48	-	-	-
2		2	-	2	-	-	-
0	35	-	1	1	-	-	-
1		-	49	49	-	1	1
0	36	4	-	4	-	-	-
1		46	-	46	-	-	-
0	37	-	2	2	-	-	-
1		-	50	50	-	-	-
0	38	21	-	21	-	-	-
1		43	-	43	-	-	-
0	39	-	3	3	-	-	-
1		-	46	46	-	-	-
2		-	1	1	-	-	-
5		-	-	-	-	1	1
0	41	5	2	7	-	-	-
1		37	27	64	1	-	1
2		8	-	8	-	-	-
3		1	-	1	-	-	-
0	43	12	5	17	-	-	-
1		35	42	77	1	4	5
2		5	3	8	-	-	-
3		2	-	2	-	-	-

0	45	1	-	1	-	-	-
1		42	20	62	-	-	-
2		5	2	7	-	-	-
3		2	-	2	-	-	-
1	47	-	3	3	-	-	-
2		-	3	3	-	-	-
3		-	1	1	-	-	-
1	49	-	2	2	-	-	-
2		-	6	6	-	-	-
3		-	3	3	-	-	-
4		-	1	1	-	-	-
1	51	2	-	2	-	-	-
2		4	6	10	-	-	-
3		3	4	7	-	-	-
4		6	3	9	-	-	-
5		2	1	3	-	1	1
0	Combined	81	15	96	1	-	1
1		318	300	618	6	6	12
2		24	24	48	1	0	1
3		8	8	16	1	1	2
4		6	4	10	-	2	2
5		2	1	3	-	2	2
Total		439	352	791	9	11	20

Table 3.5. Stage duration of the developing *Chrysaora fulgida* population.

Stage	Stage duration (in days)
0	0
1	6 - 12
2	16 - 36
3	57 - 105
4	14 - 68
5	< 14

Table 3.6. Rate of growth for post-ephyrae of *Chrysaora fulgida.*

Week	Total body diameter (mm)											
	Year 2012						Year 2013					
	Date	Min	Max	Mean	N	SD	Date	Min	Max	Mean	N	SD
28	11-Jul-12	1.79	3.97	2.88	3	1.53	-	-	-	-	-	-
29	18-Jul-12	1.18	7.87	2.711	50	1.73	-	-	-	-	-	-
30	-	-	-	-		-	28-Jul-13	2.33	6.25	4.35	11	1.30
32	7-Aug-12	1.54	8.77	4.13	50	1.71	11-Aug-13	1.73	12.62	4.96	55	1.98
33	16-Aug-12	2.62	10.47	5.49	50	1.50	-	-	-	-	-	-
35	-	-	-	-	-	-	28-Aug-13	2.18	7.45	3.50	50	1.00
36	5-Sep-12	1.65	5.68	3.63	50	0.91	-	-	-	-	-	-
37	-	-	-	-	-	-	11-Sep-13	1.37	9.30	4.79	52	1.55
38	19-Sep-12	1.47	6.83	3.26	64	1.10	-	-	-	-	-	-
39	-	-	-	-	-	-	29-Sep-13	1.76	11.72	5.04	50	2.42
41	12-Oct-12	1.50	24.88	7.07	51	5.57	9-Oct-13	1.77	9.64	4.66	29	1.90
43	26-Oct-12	1.65	35.31	6.52	54	6.05	27-Oct-13	1.32	7.20	3.69	50	1.61
45	7-Nov-12	1.72	43.10	8.27	50	5.87	10-Nov-13	2.03	10.96	5.30	22	2.02
47	-	-	-	-	-	-	24-Nov-13	4.56	27.37	12.10	7	7.78
49	-	-	-	-	-	-	8-Dec-13	6.53	33.80	17.09	12	9.30
51	19-Dec-12	8.53	84.56	29.52	17	18.24	22-Dec-13	11.54	54.68	23.61	14	12.28

Table 3.7. Overall growth rate (% d^{-1}) calculated for Scyphozoa. D_1 is the minimum diameter of ephyrae (in mm) and D_2 is the maximum diameter recorded (in mm). Days is the number of days elapsed between the measurements of D_1 and D_2.

Species	D_2	D_1	Days	Growth rate	Stage	cultured/wild	Description	Growth remarks	References
Aurelia aurita	88.0	0.8	217	6.50	Ephyrae are < 10 mm in diameter while larger ones (> 10) are named medusae	wild	Gullmar Fjord, Sweden, sampled in 1982/1983	Overwintering period spent in diapause of 4 months, followed by a period of rapid increase in bell diameter	Hernroth & Gröndahl 1983
Aurelia aurita			20 - 28		Newly liberated ephyrae to early young medusae as described by disc growth index	cultured	Tokyo Bay, ephyrae fed zooplankton prey collected from the surface waters in Tokyo Bay, kept at 15 °C	Food availability in the spring in Tokyo Bay is appropriate for ephyrae	Ishii et al. 2004
Aurelia aurita	53.8	3.4	182	4.57	Ephyrae to maximum mean bell diameter	wild*	Horsea Lake, England; population obtained maximum average bell diameter in September; overall specific growth rates were very low; release of ephyrae starts in December (winter) and occurred throughout winter and spring (7 months long); sampled during 1993	Overall specific growth rates were very low due to severely food limitations in the abundance and quality of the mesoplankton community	Lucas 1996
Aurelia aurita	187.8	7.4	152	6.38		wild	Kiel Fjord, Germany, sampled in 1978	Growth is characterised by a stagnation period in winter and early spring, by a rapid increase in summer and by a size reduction in September and October	Möller 1980
Aurelia aurita	197.0	1.8	273	5.16		wild	Kiel Fjord, Germany, sampled in 1979	Growth is characterised by a stagnation period in winter and early spring, by a rapid increase in summer and by a size reduction in September and October	Möller 1980
Aurelia aurita	37.0	2.0	133	6.58	First appearance of ephyrae up to maximum size in mean diameter of	wild	Kertinge Nor, Denmark, sampled in 1992	Food limited most of the season in Kertinge Nor, and this explains the poor growth observed	Olesen et al. 1994

					medusae				
Aurelia aurita	32.0	3.1	80	8.72	First appearance of ephyrae up to maximum size in mean diameter of medusae	wild*	Kertinge Nor, Denmark, sampled in 2009	Extremely high abundance of small jellyfish causing shortage of prey and thus restricting their own growth	Riisgård et al. 2010
Aurelia aurita	27.3	3.5	90	6.83	First appearance of ephyrae up to maximum size in mean diameter of medusae	wild*	Kure Port , the Inland Sea of Japan, sampled during 1990	Growth was slow in early spring, accelerated during the period from April to July, due to elevated temperature and food supply, and ceased in mid-summer.	Uye & Schimauchi 2005
Aurelia aurita	24.2	1.2	90	10.10	First appearance of ephyrae up to maximum size in mean diameter of medusae	wild*	Kure Port, the Inland Sea of Japan, sampled during 1990	Growth was slow in early spring, accelerated during the period from April to July, due to elevated temperature and food supply, and ceased in mid-summer.	Uye & Schimauchi 2005
Aurelia aurita	16.4	0.6	90	11.03	First appearance of ephyrae up to maximum size in mean diameter of medusae	wild*	Ondo Strait, the Inland Sea of Japan, sampled during 1990	Growth was slow in early spring, accelerated during the period from April to July, due to elevated temperaure and food supply, and ceased in mid-summer	Uye & Schimauchi 2005
Aurelia aurita sp. 1	10.4	3.7	12	25.85	Ephyra to juvenile medusa	cultured	18 °C, kept in dark, artremia fed at 2.2 x 10^2 ind L^{-1}	Significant growth rate when fed *Artemia* nauplii when compared with phytoplankton diet	Zheng et al. 2015
Catostylus mosaicus	160	60	21	14.012	Maximum growth recorded of cohort	wild*	Botany Bay, Australia	The growth rate of cohorts appeared to vary between Botany Bay and Lake Illawarra	Pitt & Kingsford 2003
Cephea cephea	33.0	1.9	42	20.58	Ephyra to juvenile medusa	cultured*	28 °C, continuously light, artemia fed once a day	Experiment to describe morphological development	Sugiura 1966
Chrysaora fulgida	29.5	2.9	161	4.34	Stage 0 - 5, mean diameter of ephyral stages	wild	Walvis Bay, Namibia		This study, for 2012
Chrysaora fulgida	23.6	4.3	147	3.45	Stage 0 - 5, mean diameter of ephyral stages	wild	Walvis Bay, Namibia		This study, for 2013

Chrysaora hysoscella	228.6	2.0	91	15.62	Ephyrae to adult medusa	cultured	Gonads visible at maximum diameter; aquarium temperature 42° F to 64° F; cannibalism mentioned		In Russel 1970, described by Delap (1901)
Chrysaora lactea	20.0	1.2	38	22.21		wild caught but reared in laboratory; N = 1	Kept in a constant temperature chamber at 20-21°C; fed daily with *Artemia* sp. nauplii and other planktonic organisms (especially copepods) and small pieces of muscle and gonads of mussels (*Perna perna*)	Species identification	Tronolone et al. 2002
Chrysaora quinquecirrha	75.0	3.8	64	14.04	First appearance of ephyrae up to maximum size in mean diameter of medusae	wild*	Tred Avon River tributary, Chesapeake Bay, USA, sampled in 1993	High growth rates in natural populations may be possible due to a bloom in *Mnemiopsis leidyi* in Chesapeake Bay	Olesen et al. 1996
Chrysaora quinquecirrha	171.0	3.9	33	34.37	First appearance of ephyrae up to maximum size	wild[$]	St. John Creek, Chesapeake Bay, USA, sampled in 1966	Very rapid growth rate in St. John Creek, reaching as much as 171 mm diameter in 4 weeks	Cargo & Schultz 1967
Cyanea capillata	25.8	2.9	39	16.77	Ephyrae to 42 days	cultured*	10 °C, on ctenophore diet (*Bolinopsis infundibulum*)	Ephyrae did not grow on either *Artemia* nauplii or copepod dominated mixed zooplankton, but grew with an average rate of 16.5 % day^{-1} on a ctenophore diet	Båmstedt et al. 1997
Cyanea capillata	10.0	2.0	14	34.49	ephyrae to "mid-tentaculate"	cultured[$]	Newly strobilated ephyrae were maintained at 19 °C in 0.2-µm-filtered seawater. The ephyrae were fed 3-day-old *Artemia* sp. nauplii five times per week untill adult morphology appeared (bell diameter > 1.0 cm).	Experiment to describe morphological development	Higgins et al. 2008
Cyanea species	66.6	22.0	89	3.73	Maturation occurs 43 days after the initial presence of medusae	wild*	Niantic River, Waterford, Connecticut, sampled during 1973-1986	Daily instantaneous growth rate is low	Brewer 1989
Lychnorhiza lucerna	14.0	1.9	20	29.96	Ephyrae to "advanced metephyra"	cultured	22 °C, salinity 17 psu, kept in dark, mixed diet fed of rotifers and newly hatched *Artemia franciscana* nauplii at 2-3 day intervals	Ephyrae developed into metephyrae 15 days after release at 19–22°C.	Schiariti et al. 2008

Rhizostoma octopus	9.5	4.5	21	10.67	Ephyra to 3 weeks	cultured	Fed *Artemia salina nauplii*	Ephyrae development was very slow compared to natural growth. Natural plankton was absent in the cultures, the prey fed was *Artemia salina* nauplii. The unnatural food and limited space may account for the slow and limited growth of ephyrae and young medusae in the laboratory	Holst et al. 2007
Rhizostoma octopus	25.0	4.5	90	5.72	Ephyra to 3 months	cultured	Fed *Artemia salina* nauplii	Ephyrae development was very slow compared to natural growth. Natural plankton was absent in the cultures, the prey fed was *Artemia salina* nauplii. The unnatural food and limited space may account for the slow and limited growth of ephyrae and young medusae in the laboratory.	Holst et al. 2007
Rhizostoma octopus	225.0	18.0	70	10.82	Mean diameter of ephyrae to medusae	wild	Elbe estuary, Germany, sampled during 1964		Russel 1970, observations from Thiel (1966a)

[$] Using maximum diameters

* Estimated from graph

Medusae of *Chrysaora fulgida* (left) and *Chrysaora africana* (right).

PICTURE

CHAPTER 4

SEXUAL REPRODUCTION AND MATURATION OF *CHRYSAORA FULGIDA* AND *CHRYSAORA AFRICANA* MEDUSAE

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INTRODUCTION

The medusa stage in Scyphozoa is responsible for sexual reproduction, creating genetic variability in the population that allows for evolutionary adaptation to the environment. It also allows for geographical range expansion of the benthic polyp, via planulae release (Giangrande et al. 1994; Arai 1997; Colin & Kremer 2002; Ramirez Llodra 2002; Dawson 2005; Dawson & Hamner 2009). The genders of most scyphomedusae are separate (gonochoristic), with the exception of *Chrysaora hysoscella* (Berrill 1949), which is a progressive hermaphrodite (male first, then hermaphrodite, followed by being female). Although sexual dimorphism is uncommon, some characteristics such as gonad colour (*Chrysaora quinquecirrha*; *Cyanea nozakii; Lychnorhiza lucerna; Pelagia noctiluca*), gonad morphology (*Atolla wyvillei*; *Periphylla periphylla; Pelagia noctiluca*), the presence/absence of brood structures (e.g. *Cotylorhiza tuberculata*) and bell size (*Aurelia*) occasionally enable gender identification (Littleford 1939; Kikinger 1992; Schiariti et al. 2008, 2012a, 2012b; Dawson & Hamner 2009; Lucas & Reed 2010; Milisenda et al. 2014; Liu et al. 2015). As noted in Chapter 1, fertilisation in Scyphozoa can take place within the female gonad, female gastrovascular cavity or outside the medusa in the open seawater (Aria 1997). Some female scyphozoans are brooders (such as species of *Aurelia*, *Chrysaora hysoscella*, *Rhopilema verrilli*, *Cotylorhiza tuberculata*) that retain their embryos within specialised brooding structures, liberating fully developed planulae: others are non-brooding (such as *Lychnorhiza lucerna*) and planula development occurs within the water column (Kikinger 1992; Arai 1997; Schiariti et al. 2012).

The life history strategy of an organism is a trade-off between fecundity, growth and survivorship in order to ensure maximum fitness (Stearns 1989, 2000). The fitness of a semelparous species depends on producing the maximum number of offspring, since reproduction is a once-off event. In the case of an iteroparous species fitness depends also on survival between multiple attempts at breeding (e.g. Bell 1980; Harman et al. 1989; Gaillard et al. 2000; Broussard et al. 2003; Isaac & Johnson 2005; Fisher & Blomberg 2011). Semelparous species are inclined to minimize the generation time (Lucas & Dawson

2014), except if their generation times have evolved to synchronise with a specific environmental factor such as a spring bloom (Troedsson et al. 2002). Comparatively little is known about the life-history trade-offs in gelatinous zooplankton due to the difficulty in measuring their generation time, the absence of age-determining structures, the poor correlation between body size and age and size at maturity, and the variability in individual growth responses to changes in the food environment (growth, degrowth and regrowth: Lucas & Dawson 2014). Nonetheless, schypozoans in general are considered as being semelparous: to reproduce at a population-specific upper size limit and die shortly thereafter (Lucas & Dawson 2014). Milisenda et al. (2016) reasoned that *Pelagia noctiluca* favours an iteroparous reproductive strategy on the basis that all female animals possessed oocytes at various maturation stages throughout the year; similar observations have been reported for *Periphylla periphylla* (Jarms et al. 1999); *Catostylus mosaicus* (Pitt & Kingford 2000) and *Lychnorhiza lucerna* (Schiariti et al. 2012).

The egg is one of the most "prized" single cells in the life history of most marine invertebrates, and in addition to contributing half of the genetic material and providing the entire mitochondrial DNA to the zygote, it also provides nutrients and structural material for the developing embryo. It is energetically expensive to produce (Olive 1985; Jaeckle 1995). Ramirez Llodra (2002) highlighted the importance of food availability to female reproductive output of marine invertebrates: high food quality/quantity boosts the production of fitter eggs. Conversely, periods of food deprivation or low food quantity/quality can decrease or even halt egg production. This characteristic is displayed by *Aurelia aurita,* which can direct nutrients towards somatic growth during high food abundance, enlarging the bell size, or towards reproduction during food scarcity, with a reduced bell size (Lucas 1996, 2001). As a result, reproductive output is affected, since the number of larvae produced per female medusa increases linearly with female medusa size (Lucas 1996, 2001).

The genotype (phylogenetic history, heritability and natural variation), environment (temperature, salinity, pollution, food) and developmental traits (maternal size, maternal age, maternal nutrition, maternal condition and population density) are the mechanisms that determine (singly or in combination) egg size (Moran & McAlister 2009). Although egg size is a highly variable trait amongst even closely related species and widely different marine taxa, it is one of most important life history characteristics given that it reflects the maternal energy investment, correlates with larval developmental mode and

affects the physiological performance and success of larvae (Moran & McAlister 2009). A holopelagic life history (direct development from egg to medusae with the absence of a benthic polyp stage) is associated with large egg producing scyphomedusae such as *Atolla wyvillei*, *Periphylla periphyll*a (Jarms et al. 1999; Lucas & Reed 2010) and *Pelagia noctiluca (*Rottini Sandrini & Avian 1991). Several species of medusa can reach maturity over an exceptionally short period ~2–7 months (Lucas & Dawson 2014), with generation times and life spans of <1 year, although by contrast individuals in captivity can often stay alive longer for ~2–4 years (Arai 1997).

Seasonality in reproduction can easily be recognised for species that have annual cycles of recruitment, growth and abundance while their reproduction is restricted to those periods when the adult component is present (Kon & Honma 1972; Brewer 1989; Kikinger 1992). When adult medusae are present for extended periods or throughout the year, seasonality is evident via the timing of reproduction (Lucas 1996; Albert 2005), a decline in the abundance of oocytes (Rottini Sandrini & Avian 1991), or an increase in the proportion of medusae with absent oral arms due to post-spawning mortalities (Omori et al. 1995; Möller 1980; Fancett 1986). Arai (1997: p. 145) suggested that oceanic scyphomedusae (*Atolla* species, *Poralia rufescens*) produce eggs at a low rate during the course of the year, while neritic temperate species display a strong seasonality in the production of ephyrae and eggs (*Cotylorhiza tuberculata*). The estuarine and neritic subtropical–tropical *Catostylus mosaicus* spawn continuously over a life span of 13 months (Pitt & Kingsford 2003). The neritic subtropical–tropical *Nausithoe aurea* produces gametes throughout the year (Morandini & Da Silveira 2001), whereas the mesopelagic *Periphylla periphylla* continuously spawn over several years (Jarms et al. 1999; Tiemann & Jarms 2010). These reproductive patterns are strategies to maximize the lifetime reproductive success via repeated spawning and could theoretically evolve towards shortened generation times relative to longevity; yet, in the vast majority of cases, most evidently in temperate coastal systems, generation time seems to be controlled by synchronisation with annual cycles of environmental variability (Lucas & Dawson 2014). Information regarding the sexual reproduction of *Chrysaora fulgida* and *Chrysaora africana* medusae is unknown in the Benguela system. Gonad maturation of medusae can be established via the histological examination and measurement of oocyte lengths of gonad tissues (Pitt & Kingsford 2000; Iguchi et al. 2010; Lucas & Reed 2010; Toyokawa et al. 2010).

The aims of this study were to: (1) investigate oocyte development, (2) establish a histological-based maturity scale for gonads, (3) investigate patterns in gonad development, and (4) determine differences within and between *Chrysaora fulgida* and *C. africana* medusae based on a histological examination of gonad tissue and oocyte sizes.

MATERIALS AND METHODS

Field sampling

Gonad samples of medusae of *Chrysaora fulgida* and *Chrysaora africana* were collected on an approximate biweekly basis, over a 25-month period from January 2012–February 2014 (see Table 4.1) off Walvis Bay. Additional material was collected in 2014 and 2015 from the same area. Dip-nets (mesh size: 5 mm; net mouth diameter: 600 mm) were used to collect medusae that were at or close to the sea surface, and animals were immediately placed into buckets filled with ambient seawater. Specimens were transported to the laboratory and kept at 16 °C overnight. Within 24 hours of sample collection, the maximum bell diameter of the specimen was measured (mm), exumbrella face-down, after the oral arms had been removed: the colour of the gonads was recorded and a sample was taken randomly from the individual's gonads and fixed in borax-buffered 4-percent formaldehyde filtered seawater solution (Harris et al. 2000). Small medusae were preserved whole.

Histology and image analysis

After a period of four weeks in fixative, tissue samples were dehydrated through an ethanol series, cleared in Xylene, embedded into paraffin wax blocks and sectioned at a thickness of 5 µm with a Leica RM2245 microtome (described in Annexture 2). Six slides were prepared per wax block at a minimum interval of 80 µm section divisions. The tissue ribbons were stained using Harris' Haematoxylin and Eosin (described in Annexture 3) and then cover-slipped with DPX mountant.

An Olympus CX41 microscope, with an Olympus SC100 camera attached, was used to examine and distinguish maturation stages of oocytes or spermatogenic follicles. Image analysis software, Olympus Stream, was used to capture all images and it was calibrated by a stage micrometer to an accuracy of 0.01 mm. The classifications of oocyte stage and the maturity of each medusa (MM) were

adjusted from descriptions made by Pitt & Kingsford (2000), Iguchi et al. (2010), Lucas & Reed (2010) and Toyokawa et al. (2010) – see below. As a starting point, a group of oocytes was chosen at random in the field of view and a minimum of 50 oocytes showing a clear nucleus was measured for length (*L*) and width (*W*). Because oocytes are not perfectly round in shape the maximum and minimum oocyte diameters were averaged.

Additional calculations

Size at maturity (L^{50}), refers to the size at which 50% of the females or males in the population are sexually mature. Female medusae were considered mature when 15% or more of the oocytes were in the late vitellogenic stage, whereas males were considered mature when 70% or more of the sperm follicles contained spermatozoa (Pitt & Kingsford 2000). In the case of female medusae maturity classes I, 1 and 2 were considered to be immature, whereas class 3 was considered to be mature (see Results). Male medusae maturity classes I and M1 were considered to be immature, whereas classses M2 to M4 were considered to be mature. The proportion of mature medusae per 50 mm bell diameter class interval was calculated for females and males, separately, using a non-linear binary logistic regression (immature = 0, mature = 1) on the following equation, adapted from King (2007):

$$P_i = \frac{1}{1 + e^{-(L_i - a)/b}}$$

Where P_i is the proportion mature medusae at each size class, L_i the observed length class, a (length at 50% maturity) and b parameters to be fitted to the data.

In order to illustrate the reproductive cycle of both *Chrysaora* species the proportional seasonal occurrence of maturity classes was plotted for sex-indeterminable (I) , female (F) and male (M) medusae. The months for season were considered as: summer (December, January and February); autumn (March, April and May); winter (June, July and August) and spring (September, October and November).

STATISTICAL ANALYSIS

The aim of this study was to collect a suitable sample of individual medusae to allow for balanced statistical comparisons (e.g. across years and months). Unfortunately, owing to the temporal variation in

abundance (and constraints in weather and logistics), this was not possible and the data have therefore been pooled, by species.

To test for differences in the size of animals, by sex and species, independent t-tests or Mann-Whitney tests were used, depending on whether the data were normally distributed or not (respectively). T-tests were used to test for significant differences in the mean oocyte diameter across oocyte stages (F1–F4, F6), whilst correlation coefficients were calculated between oocyte diameter and oocyte stage group, maximum oocyte diameter and female bell diameter, and bell diameter and medusa maturity. Pearson's r or Kendall's tau correlation coefficients were computed with a bias and corrected accelerated confidence interval (BCa) estimated from 1000 bootstrap samples. All statistical tests were conducted using IBM SPSS v23 Statistics software (SPSS Inc., Chicago, USA).

RESULTS

Bell diameter and maturity status

In the case of *Chrysaora fulgida*, observations were based on 352 specimens that ranged between 31–768 mm in bell diameter (Table 4.2), whilst for *C. africana* observations were based on 63 specimens (32–352 mm). Genders were separate in both species, only 24% of the *C. fulgida* (225–768 mm) and 84% of *C. africana* (115–352 mm) could have gender assigned (MAT) following histological examination. The balance of individuals (31–435 mm, *C. fulgida*: 32–197 mm, *C. africana*) lacked gonad development and thus, were sex-indeterminable (I).

The mean bell diameter of mature *Chrysaora fulgida* did not differ significantly (t (81) = 0.348; p = 0.729) between sexes (female 465.33 mm, SD = 113.67 mm; males 456.18 mm, SD = 124.82 mm). The median (*Mdn*) bell diameter (Figure 4.3) of mature (MAT) medusae (*Mdn* = 432.0) was significantly greater (U = 21913.5, p < 0.001) than that of immature (I) medusae (*Mdn* = 145.5). Male and female medusae occurred at equal frequencies ($\chi^2(1) = 0.190$, p = 0.663).

Similar results were observed for *Chrysaora africana*. There was no significant difference (t (51) = 0.283; p = 0.778) in the size of female (BD = 265.29 mm; SD = 48.58) and male (BD = 261.40, SD = 51.4) animals, and mature (MAT) animals (Figure 4.3) were significantly larger (U = 522.5, p < 0.001) (*Mdn* =

270.0) than immature (I) individuals (*Mdn* = 74.5). Male and female medusae did not significantly deviate from the expected 1:1 sex ratio ($\chi^2(1) = 0.170$, $p = 0.680$).

In all comparisons, specimens of *Chrysaora fulgida* were bigger than *C. africana*, regardless of sex or maturity (Table 4.3).

Oocyte development and maturity classification

The oocyte developmental stages (FS) were determined by the histological examination of individual oocytes (Table 4.4) which in turn, collectively determined the overall state or condition of the ovary's maturity (MM) (Table 4.5). Five oocyte developmental stages (F1–F4; F6) and five female maturity classes (1, 2, 3A, 3B, 3C) were identified, as summarised in Table 4.6. It should be noted that oocyte development is a continuum and that intermediate oocyte stages may account for the overlap in oocyte diameters between consecutive oocyte stages.

The onset of female gonad development was characterised by the first appearance of spherical pre-vitellogenic oocytes (F1), which were still embedded within the gastrodermis. These F1 oocytes (Fig. 4.4a; Fig.4.5a) lacked yolk granules and stained a deep blue/purple relative to the later developmental stages, as a result of their basophilic nature. The subsequent stage consisted of early vitellogenic oocytes (F2) that was associated with the first visible appearance of some yolk granules. These F2 oocytes were larger in size than the F1 oocytes, they also stained not as dark as the F1 oocytes, and they started to protrude into the mesoglea but kept in close contact with the thin walled gastrodermis, while facing the closest side of subgenital sinus (Fig. 4.4b; Fig. 4.5b). The nucleus of the F2 oocyte, contained a single spherical nucleolus, which faced the contact side closest to the gastrodermis. Mid vitellogenic oocytes (F3) had yolk granules scattered throughout the oocyte (without visible dense accumaltion of yolk granules yet) and their increased sizes stretched almost entirely into the mesoglea while maintaining contact with the gastrodermis. These F3 oocytes visibly stained towards a combination of light to red (acidophlilic) with some traces of purple/blue staining. The late vitellogenic oocytes (F4) could visibly be characterised by their dense granulated appearances as a result of the accumulation of yolk granules throughout the oocytes and stained deep red/pink. Specialised gastrodermal cell structures (NC) between the thin-walled gastrodermis and the F3 and F4 oocytes were clearly visible (Fig. 4.4c & d; Fig. 4.5c). In

the case of *Chrysaora fulgida*, the F4 oocytes had a pronounced, thicker stained band of yolk granules around their edges (Fig. 4.4c) and NC was more conspicuous than in *C. africana*.

The released oocyte (F6), refers to an F4 oocyte that is in the process of being ovulated or had lost contact with the gastrodermis due to its presence in the subgenital sinus or is present in the disintegration structures of the gastrodermis and subgenital sinus. During the ovulation process, the NC parted from the central position, and the F6 oocyte became compressed and seemed to evaginate through this opening into the subgenital sinus (Fig. 4.4d; Fig. 4.5d). All the oocyte stages, except F6, maintained close contact with the gastrodermis. After ovulation, the subgenital sinus and the gastrodermis showed features of disintegration (Fig. 4.4e; Fig. 4.5e) and the presence of F6 oocytes. Different oocyte stages occurred in the mature gonads with smaller and larger oocytes randomly intermixed. The F6 oocytes of *C. fulgida* were elliptical or hourglass-shaped while most of the nuclei were not clearly visible whereas *C. africana* had oval shaped oocytes.

The first female maturity class (MM) 1 could be identified in both *Chrysaora fulgida* and *Chrysaora africana*. This class was dominated (~80%) by F1 oocytes with a diameter (mean ± SD) of 13.2 ± 5.86 µm (n = 329), and 11.0 ± 2.0 µm (n = 40), with the balance (~20%) of F2 oocytes with a diameter (mean ± SD) of 28.5 ± 6.91 µm (n = 71), and 18.0 ± 5.7 µm (n = 10) for *Chrysaora fulgida* and *C. africana*, respectively (Fig. 4.4a; Fig.4.5a). The second female maturity class (MM = 2), in the case of both species, was dominated by F2 oocytes (*C. fulgida,* 81%, 40.8 ± 12.4 µm, n = 605: *C. africana*, 63%, 34.5 ± 9.4 µm, n = 378), though F3 oocytes were more common (27%), in *C. africana* (54.6 ± 7.8 µm, n = 139) than *C. fulgida* (8.4 %, 71.7 ± 8.4 µm, n = 63). The balance of oocytes consisted of F1 (*C. fulgida*, 10.9%, 16.7 ± 5.1 µm, n = 82: *C. africana*, 8.5%, 15.8 ± 4.0 µm, n = 51); F4 (*C. africana*, 4.5%, 72.3 ± 6.6 µm, n = 27) and F6 (*C. africana*, 0.8%, 82.8 ± 15.5 µm, n = 5).

The third female maturity class 3A was identified as “ripe/ovulating”: This class was dominated by F4 (41.4%, 132.0 ± 17.4 µm, n = 290) and F3 (38.4%, 97.8 ± 17.4 µm, n = 269) oocytes for *C. fulgida*; and F2 oocytes (45.5%, 35.9 ± 10.3 µm, n = 250) for *C. africana*. The balance of oocytes consisted of F1 (*C. fulgida*, 0.6%, 17.5 ± 4.8 µm, n = 4: *C. africana*, 5.6%, 11.4 ± 3.4 µm, n = 31), F2 (*C. fulgida*, 19.1%, 48.5 ± 14.1 µm, n = 134), F3 (*C. africana*, 23.5%, 57.2 ± 8.1 µm, n = 129), F4 (*C. africana*, 18.2%, 73.2 ±

6.2 µm, n = 100) and F6 (*C. fulgida*, 0.4%, 165.6 ± 11.8 µm, n = 3: *C. africana*, 7.3%, 78.7 ± 5.7 µm, n = 40).

The fourth female maturity class 3B was identified as “disintegration”: This maturity class was dominated by F6 (82%, 132.2 ± 16.7 µm, n = 82) oocytes for *C. fulgida*; and F2 oocytes (47.0%, 32.4 ± 11.1 µm, n = 94) for *C. africana*, respectively. The balance of oocytes for *C. fulgida* comprised of F2 (4.0%, 54.6 ± 6.5 µm, n = 4), F3 (4.0%, 86.0 ± 9.4 µm, n = 4) and F4 (10.0%, 102.1 ± 11.0 µm, n = 10) stages. The balance of oocytes for *C. africana* could be assigned to F1 (4.0%, 9.4 ± 2.1 µm, n = 8), F2 (4.0%, 54.6 ± 6.5 µm, n = 4), F3 (24.5%, 54.9 ± 9.6 µm, n = 49), F4 (4.5%, 76.6 ± 4.1 µm, n = 9) and F6 (20%, 79.2 ± 6.1 µm, n = 40) stages. In the case of *Chrysaora fulgida*, F6 oocytes were elliptical

In the case of *Chrysaora fulgida*, a fifth female maturity class 3C was identified as “partially spent”: Histological observations indicated that one female specimen (BD = 378 mm, MM = 3C, sampled on the 9 September 2015) was partially spent (Fig. 4.4f). An unusually high number of histological slides (20) had to be prepared for this specimen, in order to comply with the measurement of 50 oocytes per specimen, due to the scarcity of oocytes present in its gonads. Very noticeable features that emanated from its histological examination were the presence of a limited number of oocytes compared to the high abundance of NCs, visible empty “cavities” surrounded by NCs and the absence of visible signs in the degradation of the gastrodermis or subgenital sinus. This “partially spent” (3C) maturity class for this specimen was dominated by F4 oocytes (86%, 136.0 ± 14.1 µm, n = 34) whereas the balance of oocytes comprised of F1 (2%, 17.9 µm, n = 1), F2 (14%, 37.2 ± 10.7 µm, n = 7), F3 (12%, 123.0 ± 9.0 µm, n = 6) and F6 (4.0%, 123.5 ± 16.9 µm, n = 2) oocytes.

The profile of female maturity indicated that oocytes at different stages of vitellogenesis occurred simultaneously in all mature medusae examined histologically (Table 4.6; Fig. 4.6). Although, the sample size was too small to analyse robustly, the diameter of each oocyte stage did not appear to change across the female maturity classes. In the case of *Chrysaora fulgida*, F1 oocytes were present in all the female maturity classes, except 3B; F2 oocytes were present in all female maturity classes; F3 oocytes were present in all female maturity classes, except F1. F4 and F6 oocytes were only present in the 3A, 3B and 3C female maturity classes. For *C. africana*: F1 and F2 oocyte stages were present in all female

maturity classes but F3, F4 and F6 oocytes were only present in the 2, 3A and 3B female maturity classes.

Within each species, the maximum oocyte diameter was significantly correlated with female maturity class (Fig. 4.7): CF, τ = 0.792 [0.712, 0.844], n = 40, $p < 0.001$; and CA, τ = 0.451 [0.179, 0.686], n = 28, $p = 0.003$. In addition, oocyte diameter was significantly correlated with oocyte stage within each species: CF, $r = 0.897$ [0.890, 0.905], $p < 0.001$; and CA, $r = 0.852$ [0.840, 0.862], $p < 0.001$, and in all cases, for each oocyte stage the oocyte diameter was significantly bigger (Fig. 4.8; Table 4.7) in *C. fulgida* than in *C. africana*.

Spermatogenesis and maturity classification

Four classes of male maturity were evident from the histological observations, namely: (i) unripe male (M1), (ii) early ripe male (M2), (iii) active ripe male (M3) and (iv) disintegrating ripe male (M4), as described in Table 4.5. The process of spermatogenesis occurred within the sperm follicles, and the germinative zone of the sperm follicles was situated in the margin of the follicle walls. Several sperm follicles (Fig. 4.9a & b) developed through the invagination of the gastrodermis in long convoluted rows into the mesoglea of the gonads (M1). The developmental process of the sperm follicles progressed through a centripetal sequence pattern of (1) spermatogonia located on the margin of the follicle walls, (2) into spermatocytes that were liberated into the follicular cavity to finally mature from (3) spermatids into (4) spermatozoa (Fig. 4.9c & d). From histological observations, it seemed that as the M2 testis matured, the spermatozoa accumulated and filled the follicular cavities to such a degree that each individual follicle wall distended into and became fused with those of neighbouring follicles, thereby forming a continuous, condensed mass of spermatozoa (Fig. 4.9e & f). This gave rise to the M3 class. In order to spawn, the wall structures of these condensed areas disintegrate or rupture, which released the spermatozoa into the subgenital sinus. The M4 class appeared to be associated with the post-spawning degeneration of both the subgenital sinus and the gastrodermal structures (Fig. 4.9g & h). The degree of maturation within the male gonad seemed to be closely linked during the sequence of its development since M1 and M3 follicle stages were not observed to co-exist in the same gonad. The general follicle development and maturation

stages of both study species were similar and no distinctions could be made from the histological sections.

Size at maturity (L^{50})

The largest unripe female *Chrysaora fulgida* had a bell diameter of 590 mm and the smallest ripe female was 360 mm. Female bell diameter was moderately but significantly correlated with both its maturation stage (T = 0.410, [0.158, 0.623], n = 39, p = 0.001) and maximum oocyte size (T = 0.427, [0.187, 0.624], n = 39, $p < 0.001$). The largest unripe male *C. fulgida* had a bell diameter of 670 mm while the smallest ripe male was 225 mm. There was a low but significant correlation between male bell diameter and its maturation stage (T = 0.273, [0.069, 0.447], n = 44, p = 0.019).

The largest unripe female *Chrysaora africana* had a bell diameter of 352 mm and the smallest ripe female was 215 mm. Female bell diameter was not significantly correlated with either its maturation stage (T = 0.200, [-0.156, 0.509], n = 28, p = 0.190) or maximum oocyte size (T = 0.152, [-0.196, 0.454], n = 28, p = 0.259). The largest unripe male *C. africana* was 150 mm and the smallest ripe male was 213 mm. Male bell diameter was again not significantly correlated with its maturation stage (T = 0.247, [-0.235, 0.616], n = 25, p = 0.135).

The logistic regression model could neither predict the size at maturity for female or male medusa of either species (Fig. 4.10; Fig. 4.11). This can probably be explained by the large number and wide size range of immature specimens that overlapped with those of the mature animals (Table 4.2).

Observations on gonad colour

The following five gonad colours were identified in *Chrysaora fulgida*: brown, cream, pink, pink-cream and transparent (Fig. 4.12). Pink was the most frequent colour group and was dominated (80.3%) by the sex-indeterminable medusae (I). Transparent and cream gonads were exclusively present in sex-indeterminable (17 of 261) and male (2 of 43) medusae. Brown, pink-cream and cream were only present in mature medusae of both genders. Brown gonads were more characteristic of females (88.2%) than males (11.8%), whereas pink-cream gonads were more common in males (66.7%) than females (33.3%).

In summary, males and females could not be distinguished by the colour of their gonads, neither their female and male maturity classes (Fig. 4.13; Fig. 4.14).

In the case of *Chrysaora africana,* five gonad colours were also identified: brown, cream, brown-cream, grey and grey-brown (Fig. 4.15). Brown (female: 33.3%, male: 50%, sex-indeterminable: 16.7%) and grey (female: 65%, male: 25%, sex-indeterminable: 10%) gonads were the most frequent colour groups. Brown-cream was exclusively present in male medusae (2 of 25). Grey-brown, cream and brown-cream were only present in mature medusae of both genders. Cream gonads were more characteristic of males (80%) than females (20%), whereas grey-brown gonads were more common in females (75%) than males (25%). As in the case of *C. fulgida*, *C. africana* males and females could not be distinguished by the colour of their gonads, neither could their female and male maturity classes (Fig. 4.16; Fig. 4.17).

Observations on the reproductive cycle

Sex-indeterminable (I) specimens of *Chrysaora fulgida* dominated populations inshore throughout the year, with numbers peaking during autumn and reaching lowest densities during spring (Fig. 4.18 & 4.19) in the study site. Mature females (MAT) were present all year (pooled) around (Fig. 4.18), being most common in summer (45%) and least abundant in autumn (7.5%). The female maturity class 1 were prevalent in all seasons, being most common in spring and least common in autumn. The female maturity class 2 peaked in abundance during summer and were the scarcest in winter. The “ripe/ovulating” class (3A) was present all year, being most common in summer and least common in autumn. The partially spent class (3C; n = 1) was only present during spring, whilst the disintegrated class (3B; n = 2) was only found in summer. Mature *C. fulgida* males (MAT) could also be seen throughout the year (Fig. 4.19), and were most frequently caught during summer (54.5%) and followed by spring (31.8%), but were equally abundant in winter and autumn (6.8%). Both the unripe (M1) and early ripe (M2) classes were also found in all seasons, with the highest count in summer and the lowest count, in equal parts, in autumn and winter. The active ripe class (M3) was present only in the summer and spring. The disintegrated class (M4) was only represented during summer (33.3%).

As in *Chrysaora fulgida*, sex-indeterminable (I) *C. africana* medusae were also present all year around (Fig. 4.20; Fig. 4.21), peaking in abundance during spring and reaching lowest numbers in

autumn whereas only immature individuals represented all specimens caught in summer. No mature *C africana* females were recorded during summer (Fig. 4.20), and they were commonest during autumn (64.3%), less common in winter (28.6%) and scarce in spring (7.4%). The female matury class 1 (n = 1) was present only during spring whilst patterns in the abundance of female maturity class 2 reflected to be the most common class recorded over the years (autumn to spring). The “ripe/ovulating” class (3A) was only present in autumn (~60%), and the disintegrating animals (3B) were equally common during autumn and winter. As in the case of female *C. africana* medusae, no *C. africana* males were caught during summer (Fig. 4.21), and they were most common in autumn (44%), followed by winter (36%) and were otherwise the least abundant during spring (20.0%). Unripe *C. africana* males (M1; n = 2) were only recorded in spring whereas the early ripe class (M2; n = 1) was present in winter. Patterns in the abundance of active males (M3) followed that of *C. africana* females (MM = 3A), and they were most common in autumn (90.1%). The disintegrated classes (M4) illustrated a peak in the winter and a minimum, in equal parts, during autumn and spring.

DISCUSSION

The medusae of both *Chrysaora fulgida and C. africana* are gonochoristic, populations display a 1:1 sex ratio and exhibited no consistently clear sexual dimorphism: visible brooding structures are absent and gender cannot be assigned using gonad colour. In neither species is there a difference in the size of the two genders, though *C. fulgida* were consistently larger than *C. africana*. It is clear that there is no features to easily separate the two sexes of both *Chrysaora* species in the field, as in *Catostylus mosaicus* (Pitt & Kingsford 2000) and *Nemopilema nomurai* (Iguchi et al. 2010).

Gonad development

Oogenesis in both *Chrysaora fulgida* and *C. africana* resembles that of other Discomedusae (Kikinger 1992; Arai 1997; Eckelbarger & Larson 1988, 1992; Avian & Rottini Sandrini 1991; Eckelbarger 1994; Pitt & Kingsford 2000; Toyokawa et al. 2010; Ikeda et al. 2011; Schiariti et al. 2012; Milisenda et al. 2016) since the female germ cells that develop into oocytes originate from the gonadal gastrodermis. As the oocytes grow they gradually bulge into the gonadal mesoglea, but maintain close contact with

specialised ovarian epithelial cells (Arai 1997; Eckelbarger & Larson 1988, 1992; Eckelbarger 1994; Pitt & Kingsford 2000; Ikeda et al. 2011; Schiariti et al. 2012). The increase in oocyte size with development is mainly due to the accumulation of yolk in the ooplasm, which is made possible by these specialised ovarian epithelial cells (Arai 1997; Eckelbarger & Larson 1988, 1992; Eckelbarger 1994; Pitt & Kingsford 2000; Ikeda et al. 2011; Schiariti et al. 2012). By contrast, the oocytes in coronate medusae such as *Atolla wyvillei, Linuche unguiculata, Nausithoe atlantica* and *Periphylla periphylla,* migrate into the mesoglea and remain solitary as they develop in the absence of specialised gonadal gastrodermis cell associations (Eckelbarger & Larson 1992; Lucas & Reed 2010); with the exception of the deep water species *Periphylla periphylla* as reported by Tiemann & Jarms (2010). Ultrastructural descriptions of oocyte maturation indicated that yolk bodies are derived from the transfer of nutrients from the subgenital sinus via the oocyte-trophocyte contact (Eckelbarger & Larson 1988; Ikeda et al. 2011). Also from the adjoining mesoglea via coated pits, as well as from the combined synthetic efforts of the golgi complex and rough endoplasmic reticulum (RER) associated with intraooplasmic channels in the ooplasm (Eckelbarger & Larson 1988; Ikeda et al. 2011). Vitellogenesis has been reported for *Aurelia aurita* to take place within four days (laboratory conditions), whereby yolk is derived through both autosynthetic (Golgi complex and RER) and heterosynthetic pathways (Eckelbarger & Larson 1988). The vitellogenesis process in *Nemopilema nomurai* takes place within five days at 19–24 °C under laboratory conditions (Ikeda et al. 2011).

The basic structure of sperm follicles in both species did not differ from that described for *Aurelia aurita* (Kon & Honma 1972; Arai 1997), *Catostylus mosaicus* (Pitt & Kingford 2000), *Lynchnorhiza lucerna* (Schiariti et al. 2012) and *Nemopilema nomurai* (Toyokawa et al. 2010; Ikeda et al. 2011). Sperm follicles are formed by invagination of the epithelium into the mesoglea of the male gonads. Spermatocytes arise near the wall of the sperm follicles and migrate inwards whereby maturation proceeds in the follicle cavities (Arai 1997; Ikeda et al. 2011; Schiariti et al. 2012).

Chrysaora fulgida

Based on the (released) egg sizes reported for other Pelagiidae, mature oocytes (F6) of *Chrysaora fulgida* (100.4–174.7 µm) are larger than those reported for *C. hysoscella* (47 µm), but smaller

than those of *Pelagia noctiluca* (300 µm). They are similar in size to those of *Chrysaora quinquecirrha* (70–190 µm), as well as *Cyanea capillata* (120–150 µm) (Morandini & Da Silveira 2001). Although a number of different oocyte stages could often be identified in each gonad maturity class, synchronous development of the female gonad was notable. This was reflected by the dominant grouping of oocyte stages (Table 4.6), in line with the maturity progression of the female gonad: female maturity class 1 (F1 = 82%) → female maturity class 2 (F2 = 80.7%) → ripe/ovulating (3A) class (F3 = 38.4%; F4 = 41.4%) → partially spent (3C) class (F4 = 68%) or disintegrating (3B) class (F6 = 82%). As noted by Iguchi et al. (2010) for *Nemopilema nomurai*, female maturity of *Chrysaora fulgida* was strongly related to maximum oocyte diameter. A sequence in vitellogenesis related to increased oocyte size was also histologically observed for *Pelagia noctiluca* from the central and northern Adriatic Sea (Rottini Sandrini & Avian 1991). Synchronous oocyte development reflects the organisation of the ovary itself, whereby all the oocytes present in the gonad (after synthesis) grow and ovulate in unity. This would imply that further replenishment of earlier oocyte stages cannot take place, and that spawning is a once-off event followed by death (Murua & Saborido-Rey 2003). The evidence presented here suggests that medusae of *C. fulgida* presented gonadal development characteristics of a semelparous organism. The data obtained from the ripe males also support this, through the merging of sperm follicles and the deterioration of follicle walls, gastrodermis and subgenital sinus of the gonads. Semelparity has been associated with several medusae species whereby reproduction happens at a population specific upper size range and death ensues shortly after a period of spawning (Hamner & Jenssen 1974; Brewer 1989; Mills 1993; Lucas & Lawes 1998; Lucas 2001).

Light microscopy revealed the existence of specialised gastrodermal cell structures that maintained an intimate relationship with F3- and F4-stage oocytes, when they were in the “ripe/ovulating” (MM = 3A) class or where ≥50% of mid vitellogenic oocytes (F3) were in the MM = 2 class. These specialised gastrodermal cell structures were absent in the 3B class but were present in high numbers in the 3C class. Most studies have used an electron microscope in order to describe the different specialised cell types found in close association with oocytes during development. These include: trophocytes, nurse cells, paraovular bodies, contact plate, follicle cells, gamete-releasing pores, mucus cells and resorption cells (Eckelbarger & Larson 1988, 1992; Avian & Rottini-Sandrini 1991; Eckelbarger

1994; Tiemann & Jarms 2010; Ikeda et al. 2011; Adonin et al. 2012; Schiariti et al. 2012; Milisenda et al. 2016). The use of standard paraffin histology (as here) is believed to physically disrupt the delicate oocyte-trophocyte connections and cause fracturing of the developing oocytes from the inner gastrodermal wall. However, the existence of possible oocyte-trophocyte connotations can be deduced from the histological images of light microscopy when developing oocytes in close contact with the gastrodermis are observed (Eckelbarger & Larson 1992). Close associations between developing oocytes and the gastrodermis are illustrated in Fig. 4.4(b–d; f), thus indicating the possibility that trophocytes are present. Trophocytes have a nutrient supportive function and their presence has been reported for a variety of scyphozoans (Eckelbarger & Larson 1988, 1992; Pitt & Kingsford 2000; Tiemann & Jarms 2010; Ikeda et al. 2011; Schiariti et al. 2012) and in some anthozoans (order Actinaria) (Larkman & Carter 1982; Wedi & Dunn 1983). Trophocytes are unique accessory cells that have not been discovered outside the phylum of Cnidaria (Shikina & Chang 2016).

During the process of ovulation (spawning), oocytes are compressed through a pit opening (the weakest point of the gastrodermis) close to where the oocytes appear to be in contact with the specialised cells/structure of the gastrodermis (Fig. 4.4d). These results are in agreement with the observations of Ohtsu et al. (2007), Tiemann & Jarms (2010), Toyokawa et al. (2010), Ikeda et al. (2011) and Schiariti et al. (2012). Following Ikeda et al. (2011), a gap appears between the maturing oocytes and the putative trophocytes that include large vesicles and a large mass structure of trophocytes forms containing “filled” vesicles in their cytoplasm (Fig. 4.4c).

Morphological deterioration associated with post-spawning of *Chrysaora fulgida* medusae was evidenced by sites of necrosis and irregular holes on the bodies; reduced or absent oral arms; constricted shaped medusae and the presence of air bubbles inside their bells. The presence of disintegrating gonads (maturity classes 3B and 4M) in animals that are visually deteriorating morphologically strongly suggests post-spawning mortality. Mortality and/or similar morphological degradation characteristics after reproduction have been described for a variety of medusae including the scyphozoans *Aurelia aurita* (Hamner & Jenssen 1974; Möller 1980; Lucas & Williams 1994; Lucas 1996), *Cyanea* species (Fancett 1986; Brewer 1989; Liu et al. 2015) and *Lychnorhiza lucerna* (Schiariti et al. 2012), as well as the hydrozoan *Aglantha digitale* (Pertsova et al. 2006) and the cubozoan *Alatina moseri* (Chiaverano et al.

2013). Pitt et al. (2014) have suggested that the majority of post-spawning deaths can be attributed to starvation caused by morphological disintegration. Obviously, weakened individuals are likely to be more susceptible to parasitism too, and the issue of post-bloom senescence is generally poorly understood (Gibbons & Richardson 2013). Interestingly, there might be a possibility for the disintegrating individuals of *Chrysaora fulgida* to continue with oocyte maturation and egg release given the high percentage of F6 oocytes in the gonads of such animals. Hamner & Jenssen (1974) reported that the gonads of pre-death *Aurelia aurita* continued to produce gametes despite somatic tissue deterioration. Mechanical damage to medusae can induce rapid gonad maturation (within several days for immature medusae) as reported for *Nemopilema nomurai,* where healthy active swimming medusae with immature gonads were present offshore whilst damaged drifting medusae with mature gonads were found closer inshore (Ohtsu et al. 2007; Ikeda et al. 2011).

One of the major differences between the histological results obtained here and the literature, was the identification of a partially spent class (3C) of *C. fulgida* female gonads; albeit from one specimen out of an overall total of forty females spanning two constantly (and two intermittently) sampled years. This class has not been described histologically for female gonads until now, and it is characterised by the presence of a high number of specialised gastrodermal tissue structures compared to the low number of oocytes, visibly high numbers of empty cavities surrounded by specialised gastrodermal tissue structures and the absence of any visible deterioration in either the subgenital sinus or the gastrodermis. These features indicate that this medusa was not in a pre-death mode and suggested that some female *Chrysaora fulgida* medusae might in fact continue to live longer after reproduction; to spawn more than once in their life time. This phenomenon is supported by Hamner & Jenssen (1974) who reported that populations of *Aurelia aurita* (which is also considered to be a semelparous, annual spawner) in Tomales Bay, California, did not all die off after reproduction during the summer of 1970, but continued to grow and reproduce for another full season in the field. Some laboratory studies have also indicated that gonad and somatic tissue deterioration after spawning are not mandatory for *Aurelia aurita* during favorable food conditions (Hamner & Jenssen 1974; Goldstein & Riisgård 2016), while aquarium-reared specimens are reported to have lifespans of 2-4 years (Raskoff et al. 2003).

Chrysaora africana

This species was much less common off Walvis Bay than *Chrysaora fulgida*, an observation made similarly by a number of authors (Uanivi et al. 2012, 2016; Uanivi & van der Plas 2013, 2014). The reason for this is likely to be a reflection of the fact that Namibia represents the southern limit of distribution for this species, which otherwise appears to be most common along the west coast of Africa and in the Gulf of Guinea (Kramp 1961).

The ovulated oocyte sizes (F6) of *Chysaora africana* (66.0–100.3 µm) are larger than those of *Chrysaora hysoscella* (47 µm); but smaller than those of *Pelagia noctiluca* (300 µm), *Chysaora fulgida* (100.4–174.7 µm) and *Cyanea capillata* (120–150 µm); they fall within the range of *Chrysaora quinquecirrha* (70–190 µm) (Morandini & Da Silveira 2001).

As in the case of *Chrysaora fulgida* there appears to be a close association between the developing oocytes and the gastrodermis, and the presence of NC. As argued previously for *C. fulgida*, it is possible that these NC might represent trophocytes (Fig. 4.5b–d). The ovulating process of *Chrysaora africana* via pit openings (Fig. 4.5d) is also supported by the observations of Ohtsu et al. (2007), Toyokawa et al. (2010) and Ikeda et al. (2011) in *Nemopilema nomurai*; Tiemann & Jarms (2010) in *Periphylla periphylla*, and Schiariti et al. (2012) in *Lychnorhiza lucerna*. The presence of a gap between the maturing oocyte and NC that included large vesicles was similar as described by Ikeda et al. (2011) during trophocyte development.

Although different oocyte stages could be identified in each female maturity class, a group-synchronous pattern of oocyte development is illustrated (Table 4.6). But only a fraction of oocytes are (albeit continuously) recruited from the population of small-yolked oocytes (F2 and F3) to advance, increase in size by accumulating yolk and to be released (ovulation: release of F6 oocytes). Group-synchronous development reflects the organisation of the ovary itself when at least two oocyte populations are developing at once, in synchrony but at different rates so that the ovary is populated by both advanced oocytes and another more heterogeneous smaller oocyte population from which the clutch is recruited (Murua & Saborido-Rey 2003). *Chrysaora africana* seemed to uphold the same two dominant oocyte stages (F2 and F3), throughout the development classes (growing, ripe/ovulating and disintegration) of the ovaries, and this could explain the poor relationship between maturity stage and

mean oocyte size, especially as large oocytes may constantly be lost through ovulation. The sustained high dominance percentage of these small oocytes (F2 and F3) suggests that *Chrysaora africana* continuously release their eggs in batches (there are a limited number of mature oocytes in 3A and 3B gonads). This strategy seems to be in stark contrast to that of *Chrysaora fulgida*, and implies some form of limited iteroparity. Similar spawning observations have been reported in the laboratory for *Nausithoe aurea* and *Aurelia aurita* (Hamner & Jenssen 1974; Morandini & Da Silveira 2001). Field observations revealed similar spawning strategies for *Catostylus mosaicus* (Pitt & Kingsford 2000) and *Nemopilema nomurai* (Iguchi et al. 2010; Toyokawa et al. 2010). Batch spawning, as a strategy, is seen to be beneficial in unpredictable environments and might be linked to limitations of the adult (Murua & Saborido-Rey 2003). Quite what those limitations might be for *Chrysaora africana* are unknown, but they might be related to the relatively small size of the adults which are able to maximize reproductive output better through serial, than by once-off batch, spawning.

Reproductive maturity and strategy

Chrysaora fulgida

Although there was no relationship between size at maturity and bell size (but see below), the largest specimens collected were always mature. Sex-indeterminable medusae dominated samples throughout the year: mature medusae were relatively uncommon. This is in agreement with the observations of Fearon et al. (1992) and Buecher et al. (2001), who noted that larger specimens of this species were more common offshore than inshore and the sampling site here was a very shallow lagoon. Suggesting, perhaps, that the majority of spawning takes place offshore rather than inshore.

Similarly unclear observations about the size at maturity have been reported by Lucas & Williams (1994), Lucas (1996), Lucas & Lawes (1998) and Iguchi et al. (2010). Collectively these authors have suggested this may reflect an individual's growth response (growth, degrowth and regrowth) towards food availability (Hamner & Jenssen 1974; Lucas 2001; Goldstein & Riisgård 2016) and medusa population density (Lucas 2001). Variations in size and reproductive status are likely to occur since ephyrae are released over an extended area and period (Chapters 2 and 3; Pagès & Gili 1991; Flynn et al. 2012), and while drifting away from their source area, they would likely encounter a variety of food and water

temperature conditions. Controlling factors such as day-length, water temperature, aggregative behaviour of medusae and mechanical damage to medusae have all been linked with gonad maturity, spawning and fertilisation of medusae (Rottini Sandrini & Avian 1991; Hamner et al. 1994; Lucas & Lawes 1998; Ohtsu et al. 2007; Tiemann et al. 2009; Ikeda et al. 2011; Liu et al. 2015).

It could be argued that *Chrysaora fulgida* displays a seasonal trend in population maturity (male and female), as greatest numbers of mature medusae were present inshore during early-spring (September) and mid-to-late summer (January and February). These results would partly support the observations of Buecher et al. (2001), who suggested that spawning of *Chrysaora fulgida* may occur during "early spring"[1], as evidenced by the high incidence of parasitism (the amphipod *Hyperia medusarum*) and their increased presence on the gonads of larger medusae during this period. Similar aggregative behaviours of medusae have been observed during spawning/breeding events for *Aurelia aurita* (Hamner et al. 1994), *Periphylla periphylla* (Tiemann et al. 2009), *Cyanea nozakii* and *Rhopilema esculenta* (Liu et al. 2015). That said, given that some mature medusae were present in the population throughout the year, it is possible that larger, sexually mature animals could simply have been preferentially advected into the study area at these times of the year. After all, medusae of *Chrysaora fulgida* are found throughout the year off Namibia (Fearon et al. 1992; Buecher et al. 2001; Sparks et al. 2001; Flynn et al. 2012), and larger individuals are found further offshore than smaller individuals – throughout the year. If the results of this study apply to the offshore part of the population, an assumption that is not unreasonable, then sexually mature individuals are found there persistently. Alternatively, mature individuals could have been advected into the nearshore region at this time of year.

The distribution (aggregation, appearance or disappearance) of medusae can be influenced by the hydrography, physical processes and the animal's behavioural reaction towards the prevailing environment (Graham et al. 2001). Dense accumulations of jellyfish in the surface waters along coastal margins can reflect the direction and speed of prevailing winds and surface currents that condense these animals along the shoreline (Shenker 1984; Larson 1990). Stranding events of *Physalia physalis* and

[1] Buecher et al. 2001 defined the sampling period of 31 August - 6 September 1999 as a winter cruise over the Namibian shelf. However, for the purpose of consistency, the latter mentioned date would be described as "early spring" here.

Velella velella are common, typically seasonal and driven by onshore winds (Graham et al. 2001). In addition, local hydrology can interact with topography or projecting coastal features to retain and entrain aggregations, as described for *Chrysaora fuscescens* in northern Monterey Bay, California (Lenarz et al. 1995; Graham & Largier 1997). Other mechanisms responsible for the formation of medusae aggregations are: upwelling fronts (Graham et al. 2001), areas of flow discontinuity (Purcell et al. 2000), Langmuir circulation cells (Larson 1992), as well as eddies, currents and tides (Arai 1992a; Graham et al. 2001). Behavioural responses of medusae towards their food environment (Bailey & Batty 1983; Arai 1992b; Costello & Colin 1995; Ford et al. 1997; Matanoski et al. 2001; Hays et al. 2012) are reported, which may account for their swarming presence in high density patches of prey. The jellyfish *Rhizostoma octopus*, in the Bay of Biscay, can actively change their swimming direction with respect to current drift and changing current flows and this behaviour plays a key role to bloom formation and a reduction in the incidence of strandings (Fossette et al. 2015).

The results of previous studies indicate that the size structure of populations of *Chrysaora fulgida* (as assessed using various fishing gears) does not change materially throughout the year (Brierley et al. 2001; Buecher et al. 2001; Brierley et al. 2005). If we accept that small individuals will be variously under-represented in the gear (meaning that seasonal changes in the recruitment of smaller individuals to the population is unknown), the bias in the size structure of the balance of the population that can be caught is a constant. In other words, the size structure of the populations of *C. fulgida* that can be assessed is constant: some large ones and some small ones persistently. Given then that mature *C. fulgida* can be found throughout the year, reproduction by the adult population is ongoing: release of planulae is ongoing. Whilst an individual *C. fulgida* may be semelparous, the population is not behaving in synchrony and thus this species population departs from what is known about the biology of most other scyphozoans. This could be a consequence of the weakly seasonal nature of upwelling off (especially central) Namibia (Shannon 1985), and the year-round high productivity of zooplankton that precludes the observation of seasonal changes (Shannon & Pillar 1986, Hutchings et al. 1991, 2009). Or alternatively, the asynchronous population behaviour can be explained by the manifestation of variation in age at reproduction. Theoretical models indicate that semelparous populations tends to synchronise when age at reproduction is homogeneous (Mjølhus et al. 2005) with a high extinction risk (Allen et al. 1993) and

that heterogeneity in age at reproduction is said to result in a higher viability of populations because it "buffers the negative impact of environmental stochasticity by reducing the covariation of life histories among individuals" (Acker et al. 2014). In addition, heterogeneity in age at reproduction with asynchronisation can buffer negative density-dependent processes in order to reduce intraspecific competition (Acker et al. 2014).

The other interesting issue that these results highlight is this: if an individual is semelparous and dies after spawning, why are some reproductively mature animals small (225 mm male, 360 mm female) whilst others are very much larger (737 mm male, 768 mm female)? Unlike an iteroparous species, where big is often better for reasons of sexual selection (Hosken & House 2011) or absolute fitness (Orr 2009), if a semelparous individual can reproduce at a small size, what is the evolutionary value of putting additional resources into somatic growth? Hence, the manifestation of variation in age at reproduction (as discussed in the paragraph above) or probably to survive and ensure another reproduction opportunity in order to increase its lifetime reproductive success. Research provides evidence that the two alternative modes of parity *viz*. semelparous and iteroparous, can coexist within a population and are likely to be condition -, seasonal - , environmental - or genetically dependent (Leggett & Carscadden 1978; Grosberg 1988; Iguchi & Tsukamoto 2001; Seamons & Quinn 2010; Meunier et al. 2012). Some semelparous species such as capelin *Mallotus villosus*, anadromous American shad *Alosa sapidissma* and crab spiders *Lysiteles coronatus* are physiologically capable of an iteroparous reproductive mode (Leggett & Carscadden 1978; Futami & Akimoto 2005; Christiansen et al. 2008) whereby intra-specific variations within the semelparity-iteroparity continuum is demonstrated – which is called "facultative iteroparity" (Hughes 2017). For example, the proportion of American shad individuals that exhibit iteroparity increases towards the higher latitudes where the natal rivers are subjected to a highly variable environment which strongly influences the survival of eggs and larvae (Leggett & Carscadden 1978). Capelin is typically associated with semelparity, however it demonstrates iteroparity (regardless of sex) during beach spawning events opposed to absolute semelparity (death of both genders) during offshore spawning events owing to subtle interactions between the spawning habitat, physical forcing and predatory pressure (Christiansen et al. 2008). The semelparous crab spider *Misumena vatia* typically lays and guards a single egg brood (Morse 1979). However, a successful second brood can be induced

experimentally through extra feeding of the adult female individual during pre- and post-egg laying and the removal of the brood shortly after laying (Morse 1994). In this situation, semelparity seems to be driven by the environment (Morse & Stephens 1996). Under favourable conditions a small percentage of male Chinook salmon *Onchorhynchus tshawytscha*, which typically are semelparous, have the ability to survive and reproduce in 2-3 consecutive seasons in New Zealand (Unwin et al. 1999). Two alternative life-history strategies for *Neotoma* inhabiting the extreme environment of Death Valley, California, are proposed (Smith & Charnov 2001): females can either have a large body size and hence higher fecundity, but die in early summer (semelparous), or they can remain minuscule, have restricted fecundity, but can carry on to a second reproductive session (iteroparous). In a comparative study of fitness outcomes of semelparity vs. iteroparity in the same fish population, Seamons & Quinn (2010) indicated that individual female steelhead trout *Oncorhynchus mykiss* that exhibited iteroparity (survived for two years and spawned twice) accomplished nearly twice the lifetime reproductive success of semelparous individual females, since a second season of growth increased their body size which corresponds with an increase in egg production that results in an average increase in fecundity of 10% (~400 eggs).

Chrysaora africana

This species was recorded throughout the year off Walvis Bay but unlike *Chrysaora fulgida*, the majority of medusae collected were mature, though immature individuals were found in all seasons. No mature animals were caught during summer, and both oocyte and maturity stages revealed that gamete production was limited to a 6-month period from mid-autumn (May) to early spring (September) and there was an apparent decline in the abundance of mature female medusae with the progression of the season from spring to summer. The presence of the ripe/ovulating (3A) and disintegrating (3B) maturity classes suggests a primary breeding season for *Chrysaora africana* that commences in mid-autumn (April), peaks in late-autumn (May), and starts to decline through winter and spring (Fig. 4.22). This is evidenced by the high prevalence of unripe females and the complete absence of mature female medusae and the exclusive presence of sex-indeterminable medusae during the summer.

I acknowledge that the results are inconclusive owing to the very small sample sizes, and that abundances may reflect the vagaries of advective and oceanographic processes (Shenker 1984; Larson

1990; Larson 1992; Lenarz et al. 1995; Graham & Largier 1997; Purcell et al. 2000; Graham et al. 2001), but ephyrae of *Chrysaora africana* are found in plankton samples off Walvis Bay (Chapter 2 and 3) suggesting that populations have a resident base. If we assume that the individuals collected are representative of the wider population then the start, peak and demise of the breeding season of *Chrysaora africana* all coincide with the local peaks in productivity observed off central Namibia, driven by upwelling (Louw et al. 2016). These latter authors have shown three seasonal peaks of Chlorophyll-a are generally observed off Walvis Bay during i) August (upwelling peak), ii) December (an early-summer primary peak) and iii) April (late secondary summer/autumn peak). Chlorophyll-a concentrations are markedly reduced during June and July due to a combination of low nutrient concentrations, the presence of upwelling unfavourable winds and high cloud coverage, as well as lower solar radiation, all of which negatively impact phytoplankton growth. Elevated phytoplankton abundances are generally followed by peaks in zooplankton abundances (Kollmer 1962, 1963), following a period of between 3 - 8 weeks (Postel et al. 1995).

The link observed here between reproduction and environmental conditions (productivity etc.) is commonly observed for medusae in temperate environments (Rasmussen 1973; Lucas 1996; Lucas & Lawes 1998), and many species have been documented to spawn during autumn and winter and to die off subsequently. The data collected for *Chrysaora africana* support the idea that animals die subsequent to reproduction: i) disintegrating classes (3B and M4) are present in the population during late-autumn (May) after the start of spawning during mid-autumn (April), ii) there is a visible breakdown of the gastrodermis and subgenital sinus, identified from histological slides for this class and iii) there is decline in the abundance and bell diameter of mature medusae with the progression of the season from autumn to summer (Fig. 4.22 & Fig. 4.23). The decline (bell size and abundance) and disappearance of the adult component of the *Chrysaora africana* medusae population might be caused by a combination of stressors acting in synergy, as suggested by Pitt et al. (2014).

Interspecies comparisons

Comparing the data collected here for the two investigated species reveals a number of similarities. Both show the same basic gametogenesis, gonad development progression and process of

ovulation. In both species there are specialised gastordermal cellular structures (NCs) (though these are less conspicuous in *Chrysaora africana*), and there is a close association between the developing oocytes and the gastrodermis. Some differences were apparent between the two species, however, with the oocytes of *Chrysaora africana* being smaller than those of *C. fulgida* (but *C. africana* bell size is smaller than *C. fulgida*) and having a slightly different shape. However, partially-spent females were not observed in *C. africana*. Comparative species-level phylogenetic studies in the determination of the evolution of semelparity and life history in salmonid fishes associated semelparity with larger sized species producing larger eggs (larger eggs are associated with higher juvenile survivorship) than iteroparous species (Crespi & Teo 2002). The evolutionary transformation towards semelparity in salmonids is linked with the combination of relative high juvenile survivorship and relative low adult survivorship, and that a low degree of repeated breeding is associated with higher reproductive investment per breeding event (Crespi & Teo 2002).

Perhaps the biggest difference however is seen in the spawning strategy taken by both species. *Chrysaora fulgida* are batch spawners and appear to die soon after spawning, though there is the possibility that some individual females may reproduce more than once. Individuals within the population can reproduce at different sizes (Fig. 4.23) and reproduction appears to take place by the population all year around. No clear seasonal peak in reproductive activity is apparent. By contrast, individual *C. africana* females appear to be able to reproduce in a serial fashion over a more protracted period of time before dying, so that reproduction by the population takes place across much of the year too (possibly six months). That said, unlike *C. fulgida*, the population seems to show a spawning peak in autumn and winter while following the general rule expected in temperate systems: i) the initial appearance of sexually mature individuals occurs when the maximum average size of the population has been reached (Rasmussen 1973; Lucas 1996; Lucas & Lawes 1998), ii) although the onset of sexual maturation occurs first in the largest medusae, ultimately all medusae mature, even those that are relatively small (Fig. 4.23) (iii) with the subsequently disappearance of the adult component of the population disappears after the onset of sexual reproduction as a result of senescence (Arai 1997) as well as mortality caused by a seasonal change in physical water parameters such as temperature/salinity that exceed beyond the physiological tolerance limits of the species (Pitt et al. 2014). In addition, the weakening pulsation rates

associated with a decline in temperature could lead to the sinking of medusae (Sexton et al. 2010) that make them more predisposed to starvation, disease, parasitism, predation and physical processes of removal (Mills 1993; Albert 2005; Pitt et al. 2014). The longevity of *Aurelia aurita* medusae in temperate regions is closely associated with a seasonal reduction in bell size, which occurs synchronously with sexual reproduction (Goldstein & Riisgård 2016). Due to the limited sample size for *C. africana*, it is not possible to infer a seasonal trend between bell size and maturity.

FIGURES

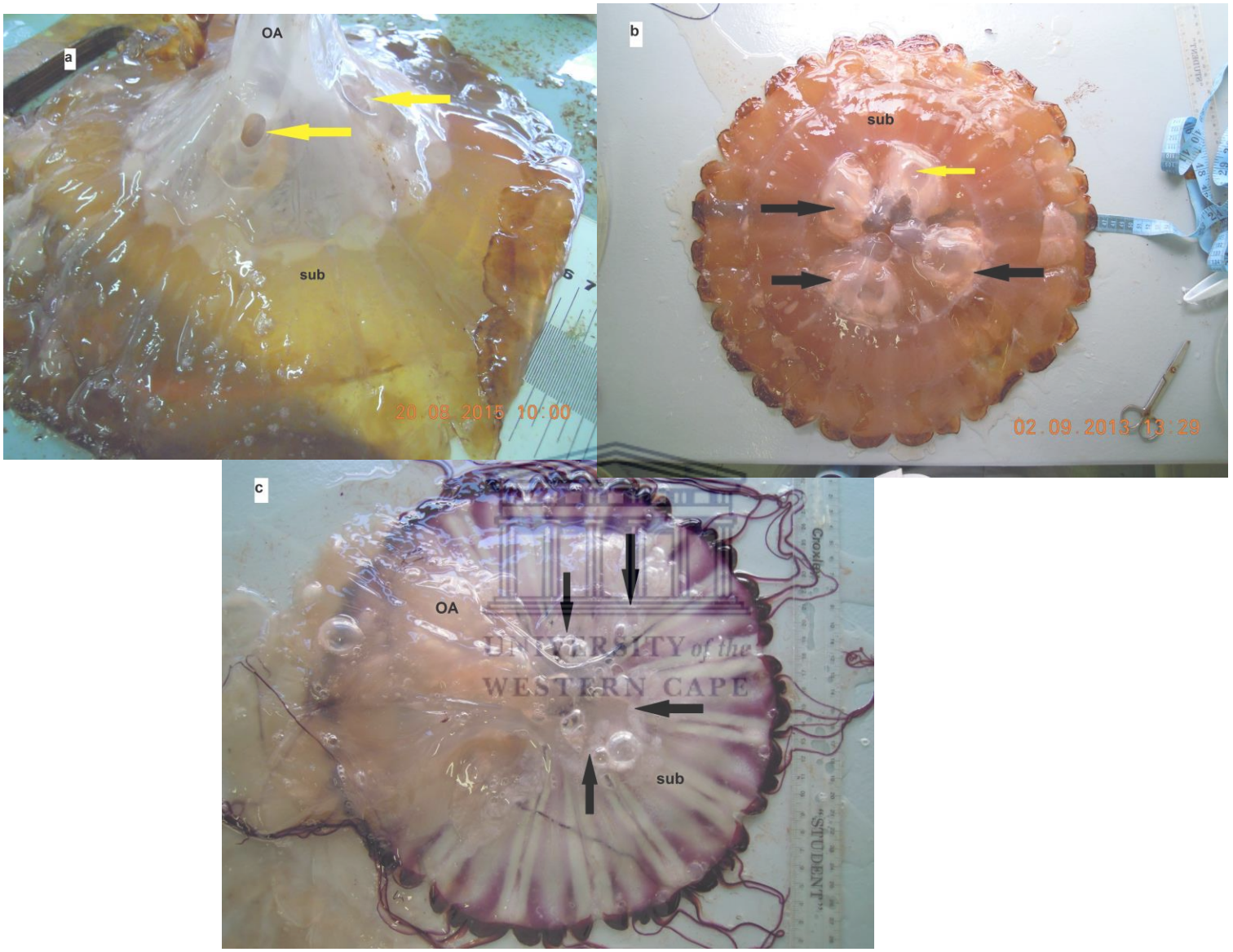
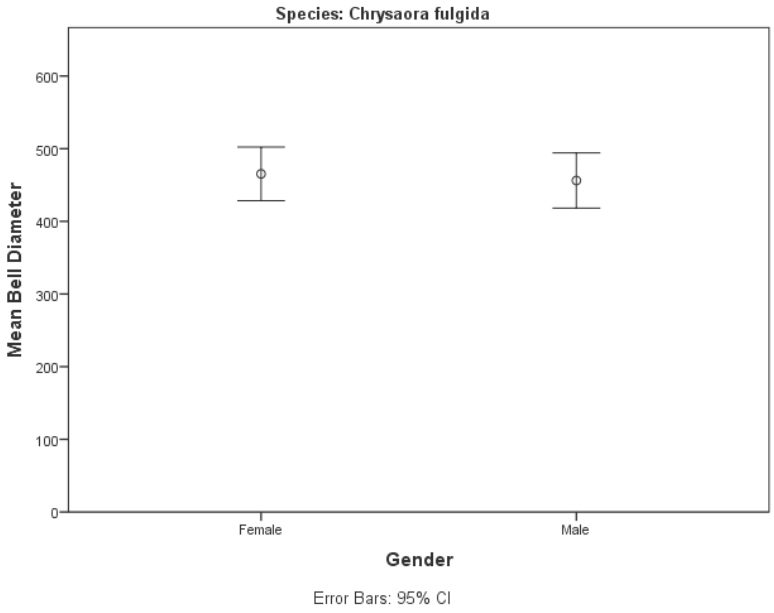


Figure 4.1. Subumbrellar (sub) view of *Chrysaora fulgida* (a) ~850 mm (bell diameter) and (b) ~460 mm (bell diameter) with oral arms removed and (c) *Chrysaora africana* ~285 mm (bell diameter) medusae showing the positions of the gonads (black arrows), oral arms (OA) and pouch openings (yellow arrows).



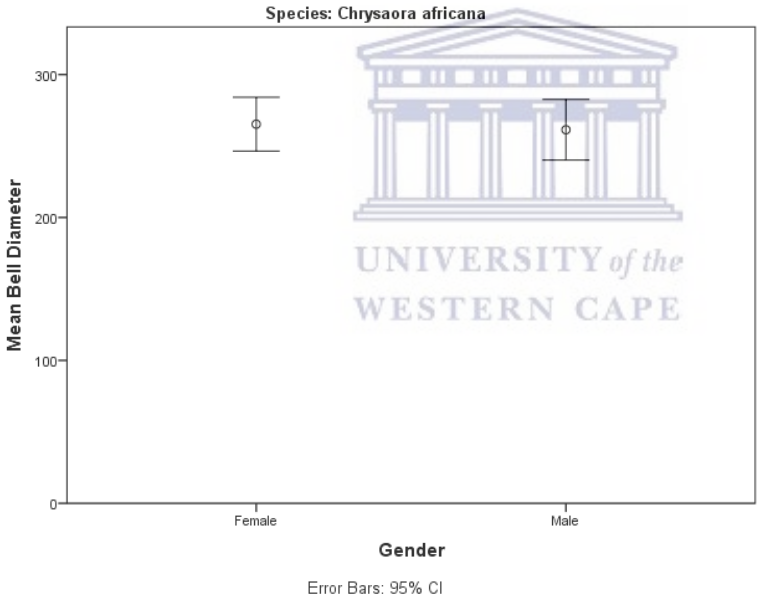


Figure 4.2. Mean bell diameter (in mm) and 95% confidence intervals by gender (female; male) per *Chrysaora* species.

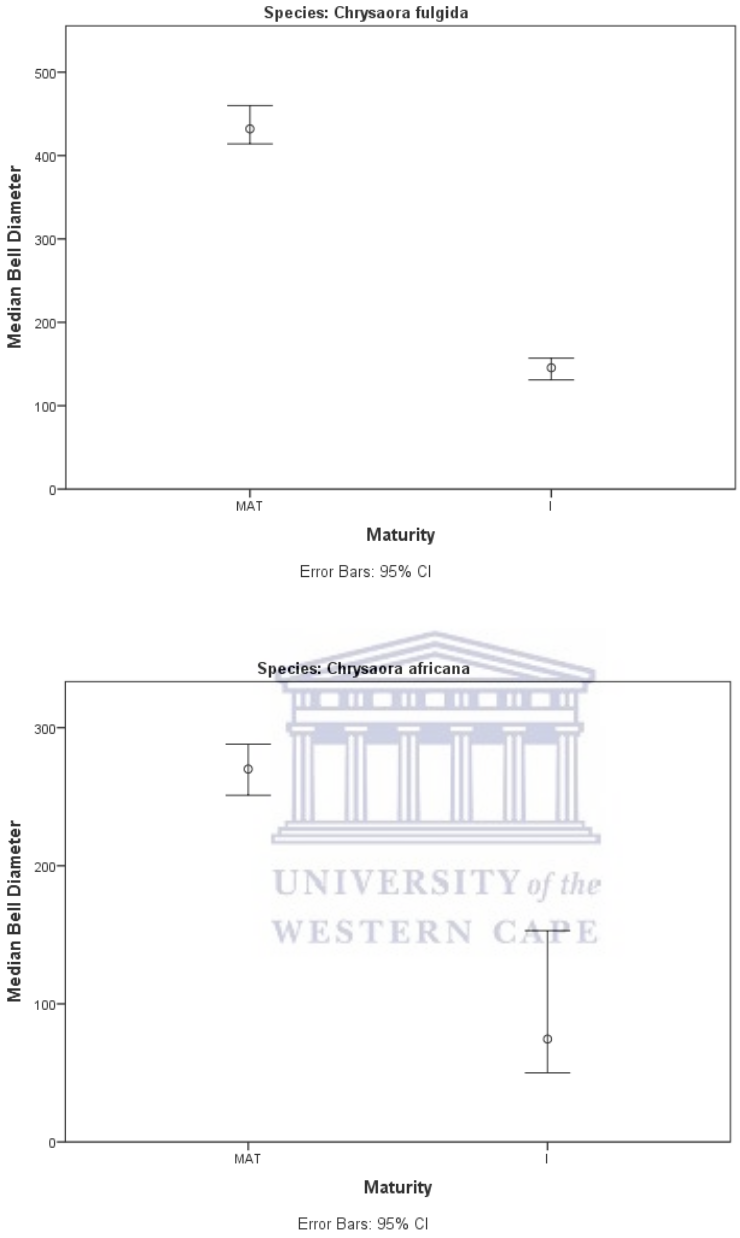


Figure 4.3. Median bell diameter (in mm) and 95% confidence intervals for sex-determinable (MAT) and sex-indeterminable (I) per *Chrysaora* species.

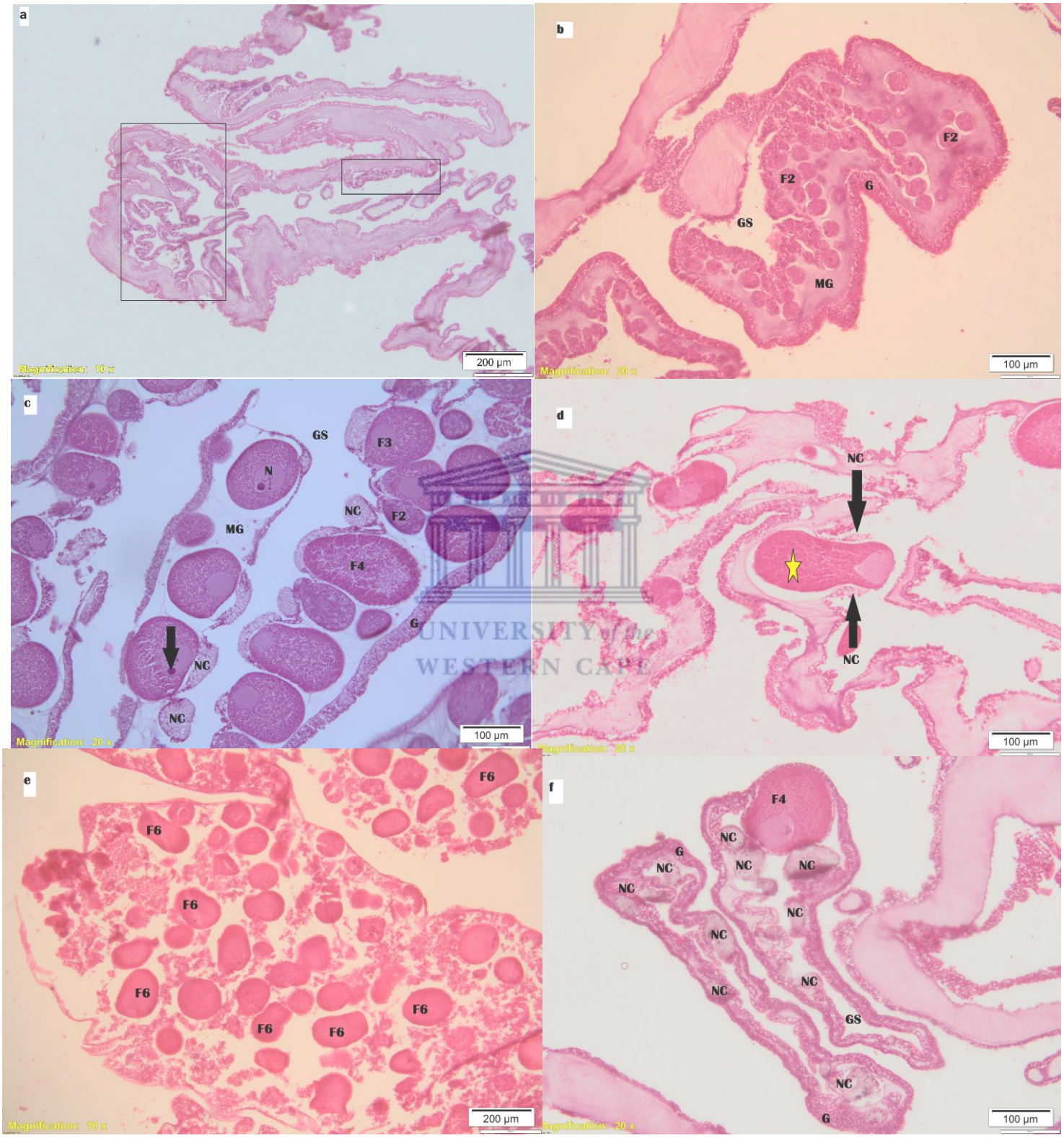


Figure 4.4 Cross section of the female gonad of *Chrysaora fulgida*, observed under light microscope, depicting the processes of oogenesis (Table 4.4). Maturity classes are defined in Table 4.5. (a) Maturity class 1 (unripe female); rectangular areas indicate the presence of pre-vitellogenic oocytes (F1). (b) Maturity class 2 (unripe female); showing early vitellogenic oocytes (F2). (c) Oocytes of a ripe female (Maturity class 3A) with different oocyte stages from F2 to F4. Black arrow: nucleolus of oocyte. (d) An ovulating oocyte (F6) indicated by a yellow star. Black arrows indicate the parted specialised gastordermal cellular structure to enable the evagination of an oocyte. (e) Disintegration of subgenital sinus and gastrodermis of the gonad (Maturity class 3B). Various elliptical and hourglass shaped F6 oocytes are visible. (f) Partially spent gonad (3C); showing the “empty cavities” surrounded by numerous *NC*s.

G gastrodermis, *GS* subgenital sinus, *MG* mesoglea, *N* nucleus, *NC* specialised gastrodermal cellular structures

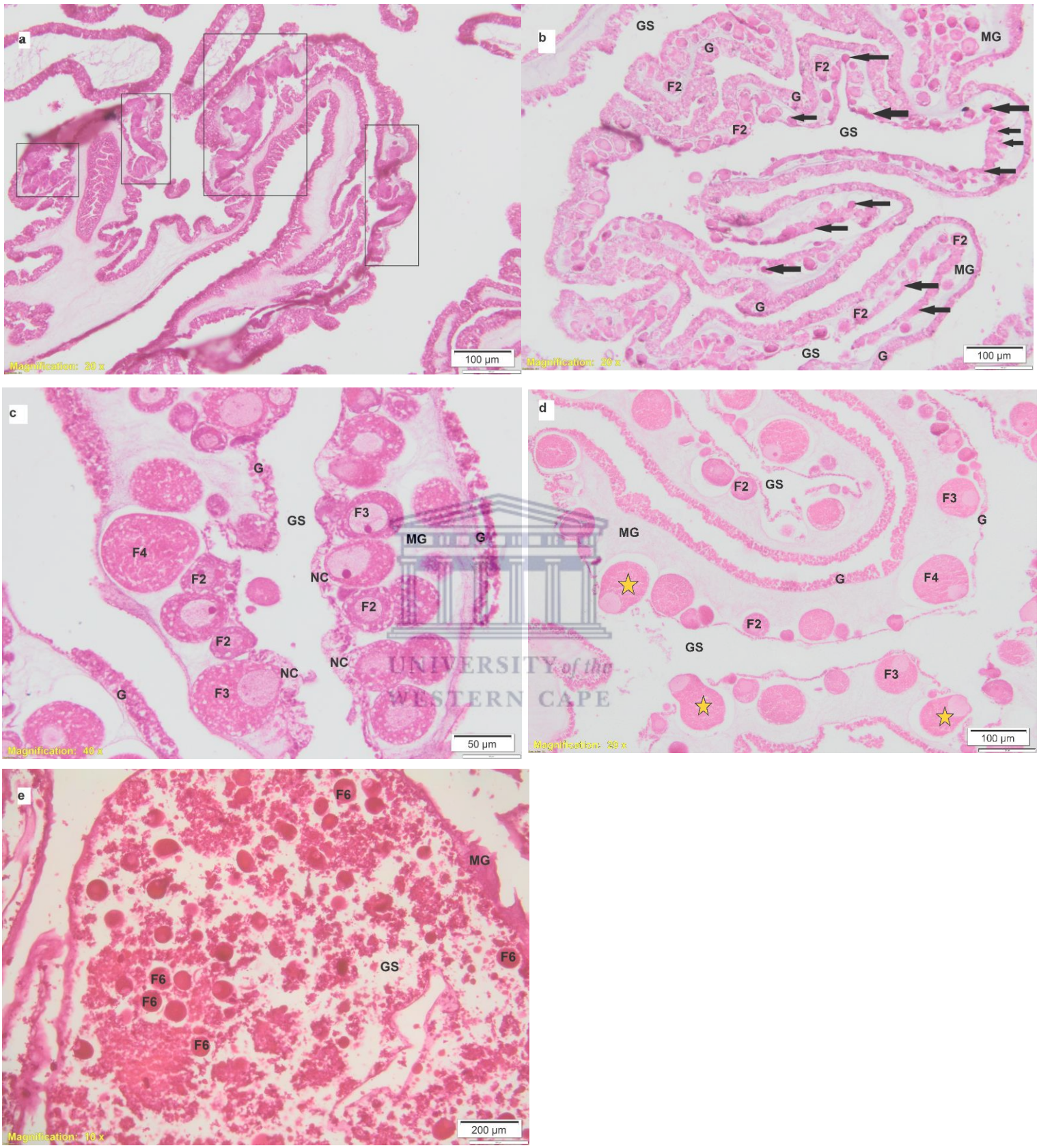


Figure 4.5. Cross section of the female gonad of *Chrysaora fulgida*, observed under light microscope, depicting the processes of oogenesis (Table 4.4). Maturity classes are defined in Table 4.5. (a) Maturity class 1 (unripe female); rectangular areas indicate the presence of pre-vitellogenic oocytes (F1). (b) Maturity class 2 (unripe female); showing early vitellogenic oocytes (F2). Black arrows point to F1 oocytes. (c) Oocytes of a ripe female (Maturity class 3A) with different oocyte stages from F2 to F4. (d) An ovulating oocyte (F6) indicated by a yellow star. (e) Disintegration of subgenital sinus and gastrodermis of the gonad (Maturity class 3B). Oval shaped F6 oocytes.

G gastrodermis, *GS* subgenital sinus, *MG* mesoglea, *NC* specialised gastrodermal cellular structures

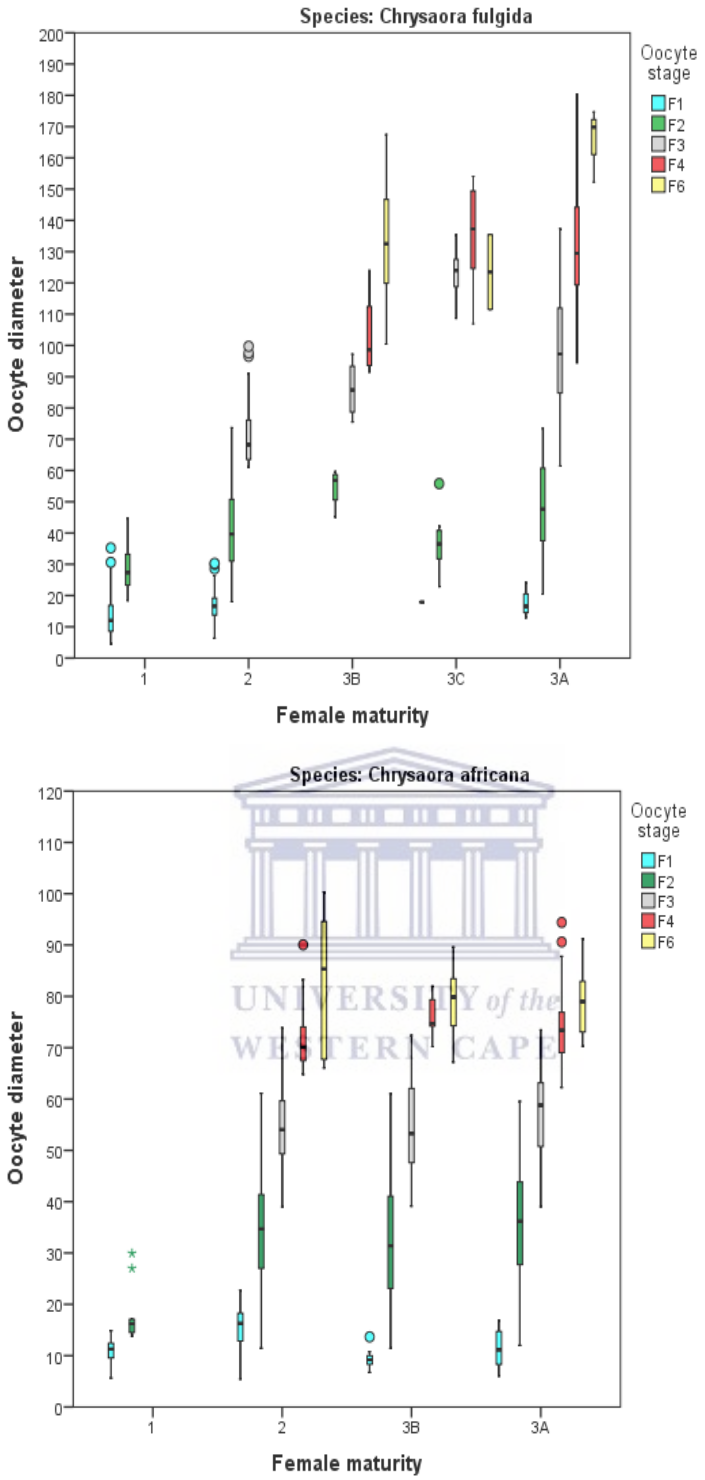


Figure 4.6. Box-and-whisker plots of the oocyte diameters (µm) grouped by oocyte stage for female maturity of *Chrysaora fulgida* and *Chrysaora africana* medusae.

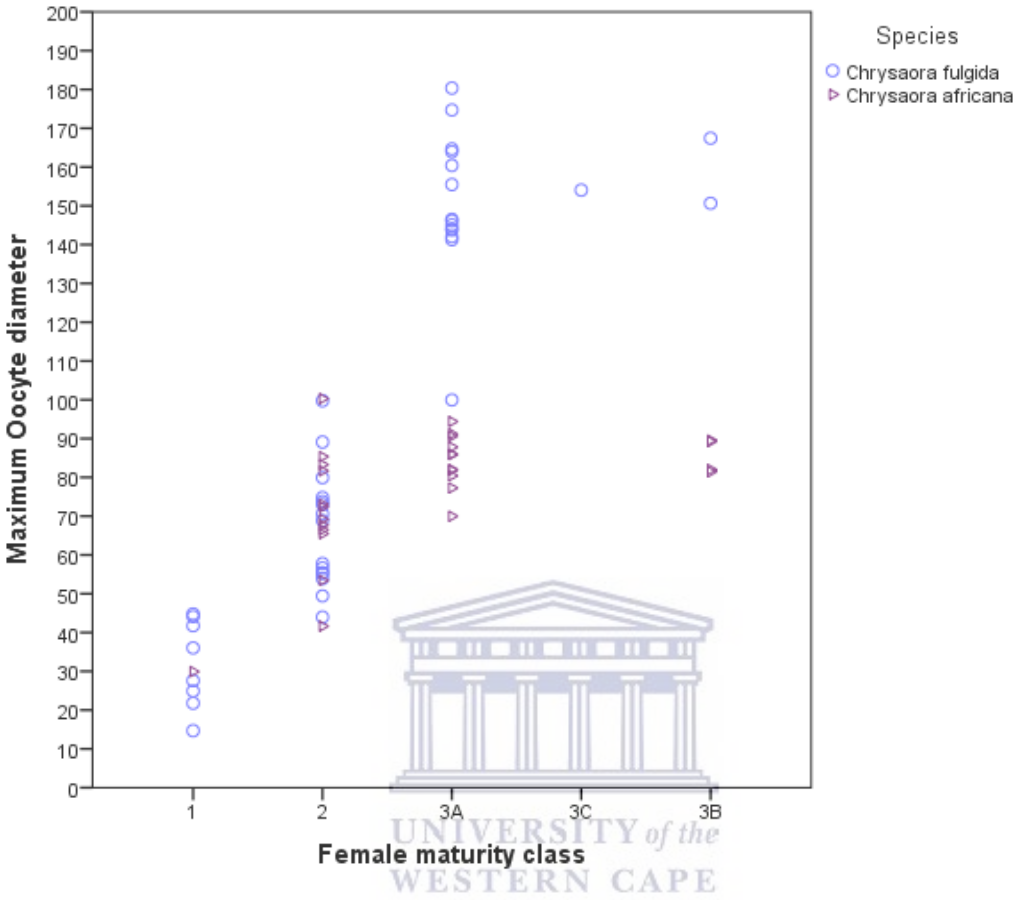


Figure 4.7. Maximum oocyte diameter (in µm) versus female maturity classes for *Chrysaora fulgida* and *Chrysaora africana.*

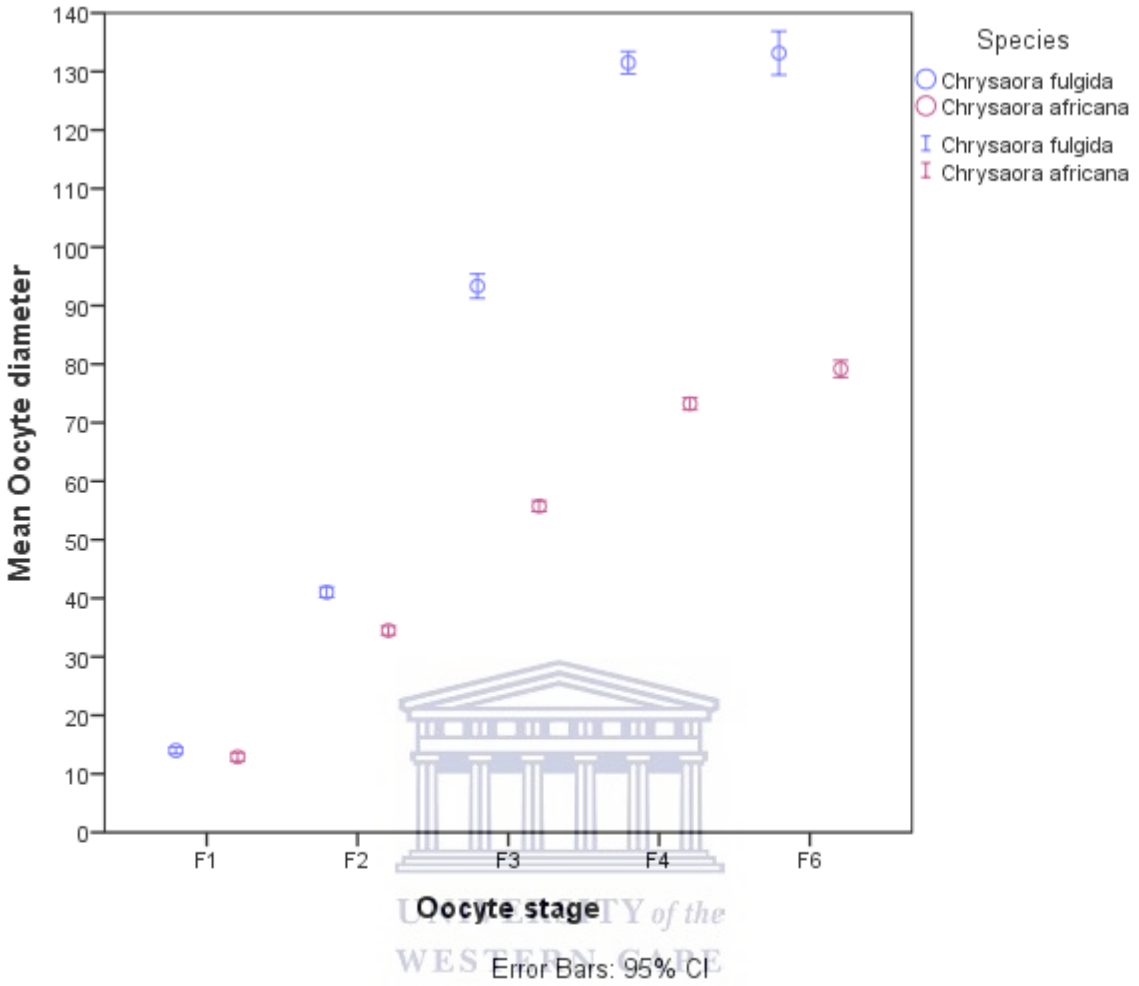
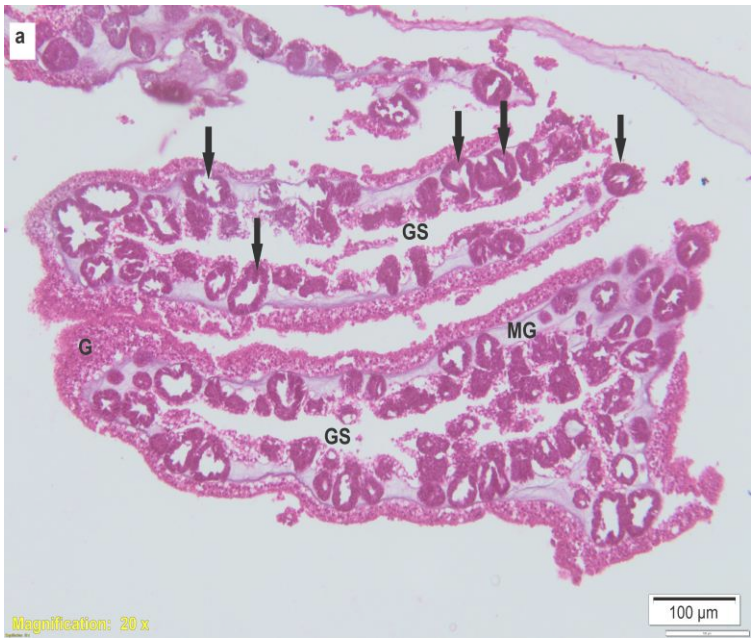
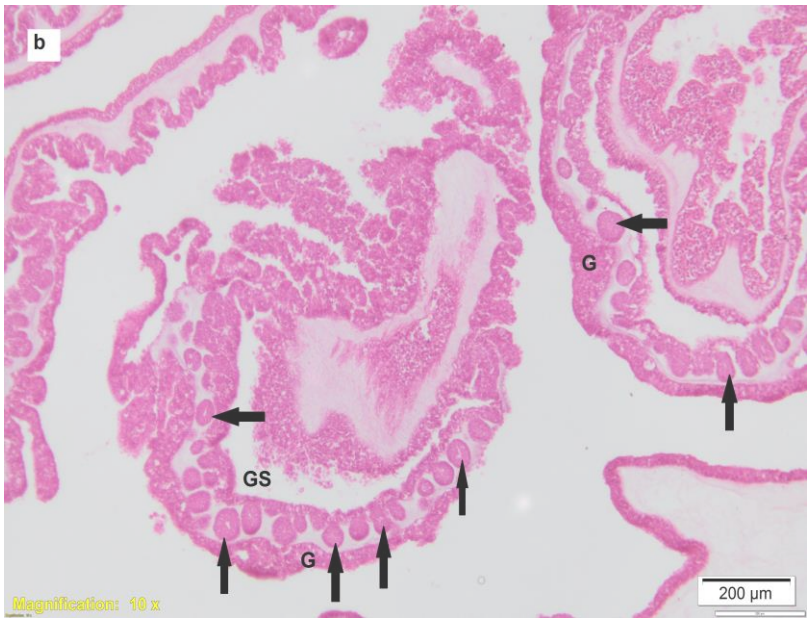
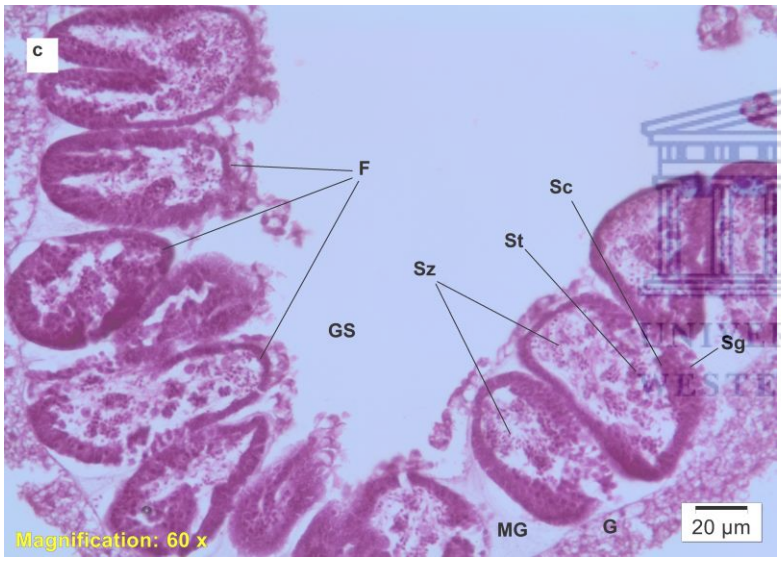
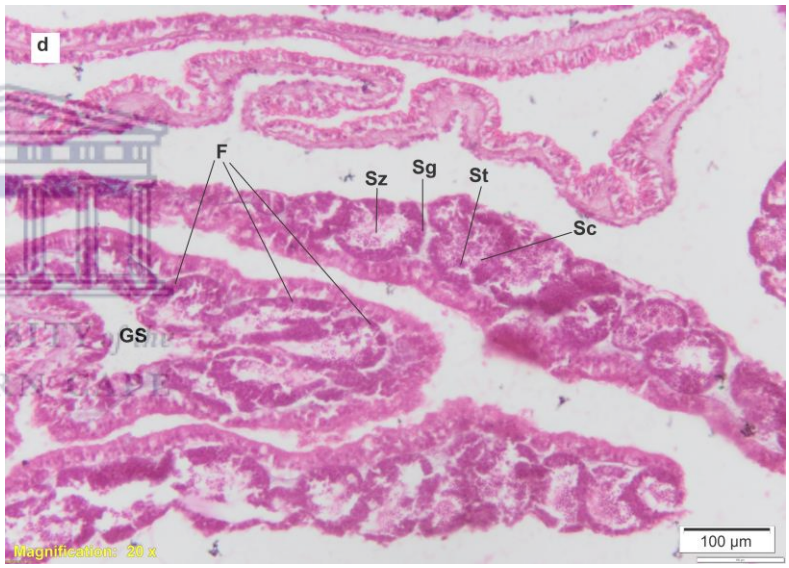


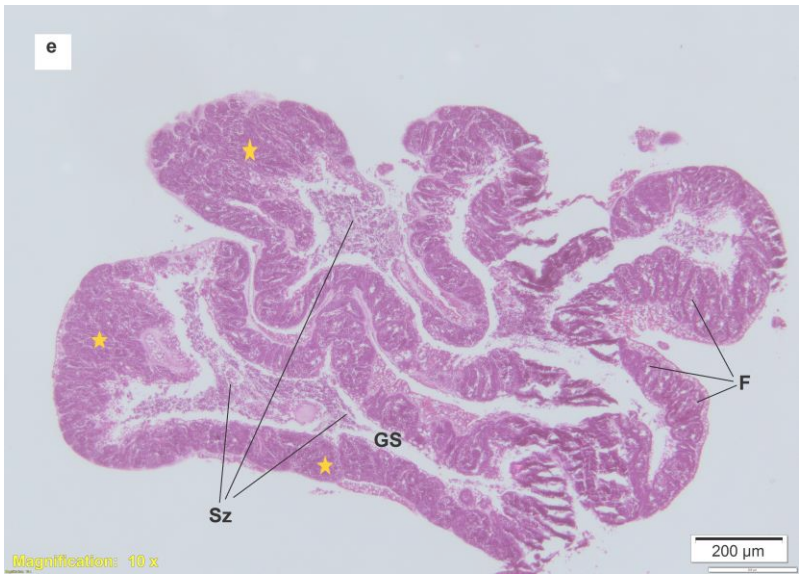
Figure 4.8. Mean oocyte diameter (in µm) and 95% confidence intervals per oocyte stage group per *Chrysaora* species.

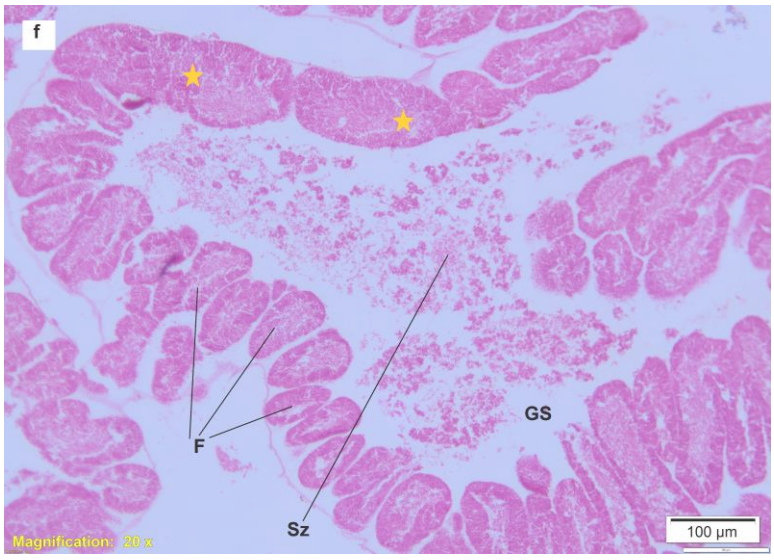












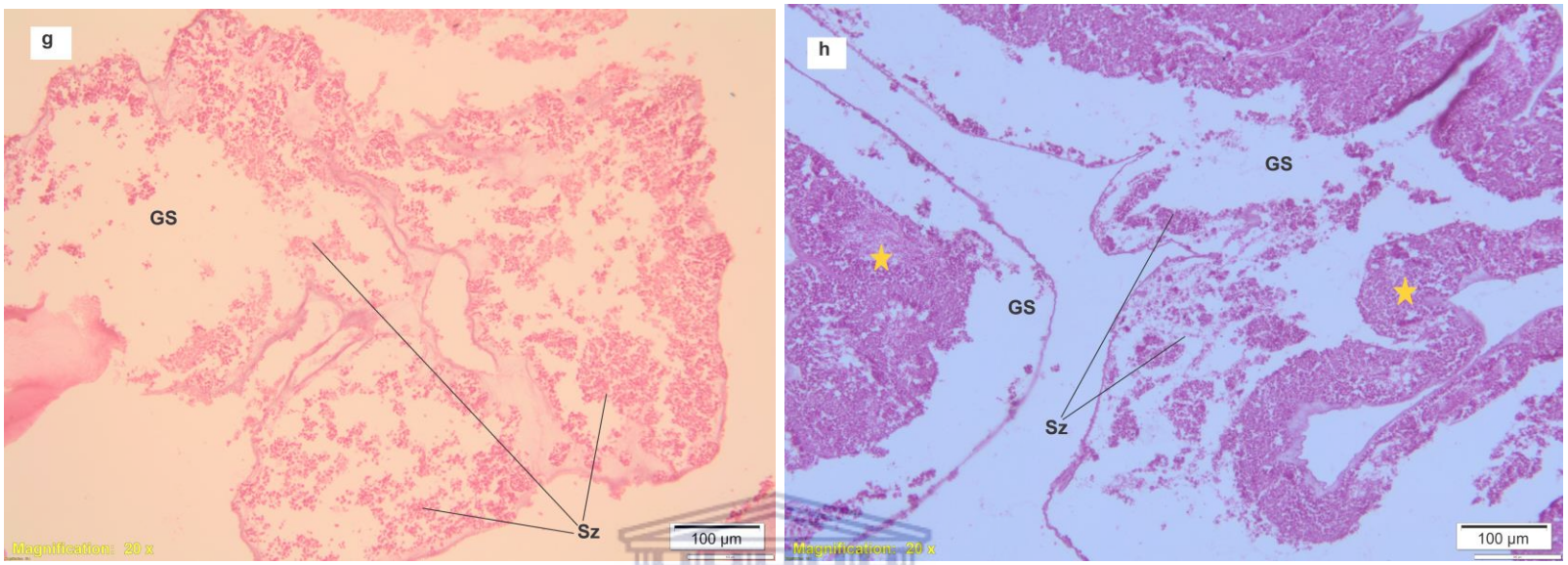


Figure 4.9. Structures of the testis of *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA) observed under light microscope; maturity classes for the male gonad are defined in Table 4.5. Development of sperm follicles within testis showing: unripe males (M1) for (a) CF and (b) CA; spermatozoa (*Sz*) are absent in the sperm follicles (black arrows). M2 ripe males of (c) CF and (d) CA, spermatozoa (Sz) present; *Sz* stains lighter than *Sg*. Gonad of M3 ripe male for (e) CF and (f) CA; spermatozoa (Sz) released in subgenital sinus (*GS*). The gonad of M4 ripe male for (g) CF and (h) CA depicting the disintegration of subgenital sinus and gastrodermis structures. The yellow stars indicate the areas of tightly packed spermatozoa (*Sz*).

F sperm follicles, *G* gastrodermis, *GS* subgenital sinus, *MG* mesoglea, *Sc* spermatocyte, *Sg* spermatogonium, *St* spermatid, *Sz* spermatozoa

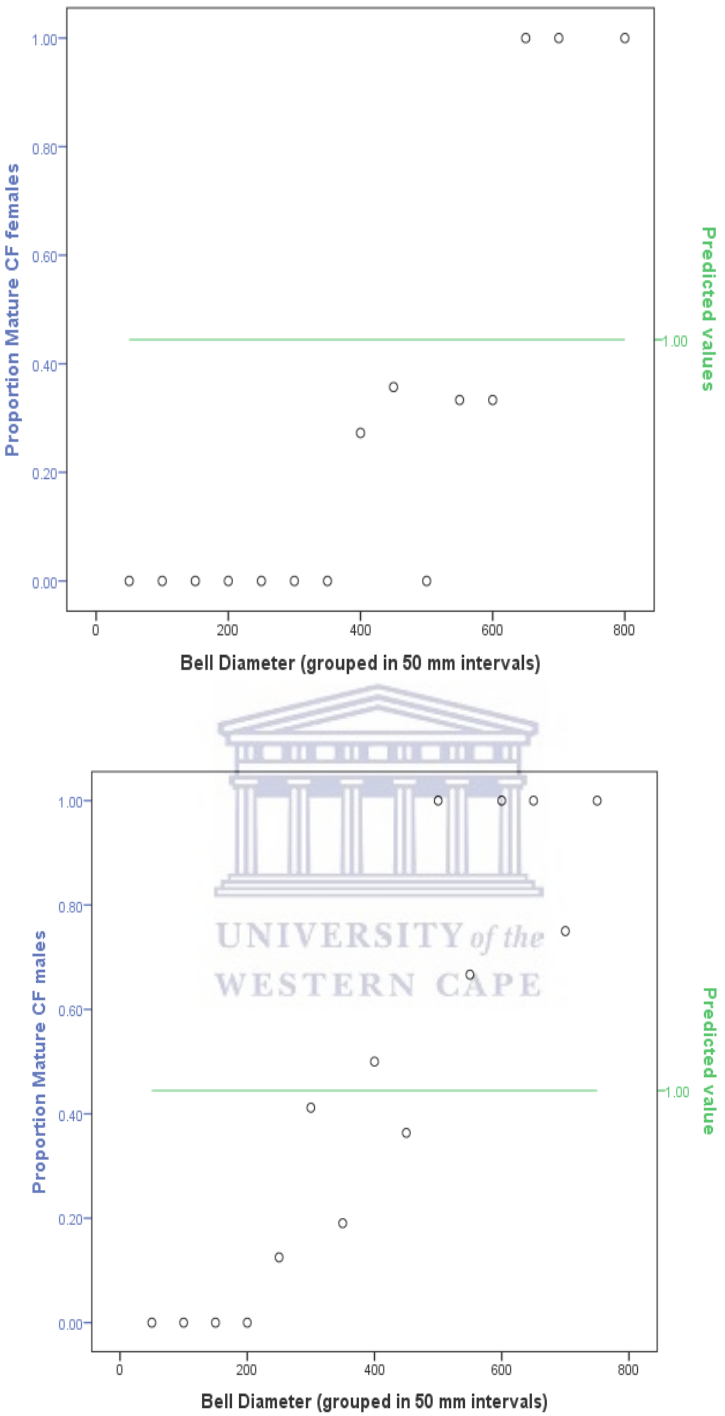


Figure 4.10. *Chrysaora fulgida*. Maturity ogives for bell diameter (grouped in 50 mm intervals) for females (n = 39) and males (n = 44). The L^{50} could not be calculated by the non-linear binominal regression model.

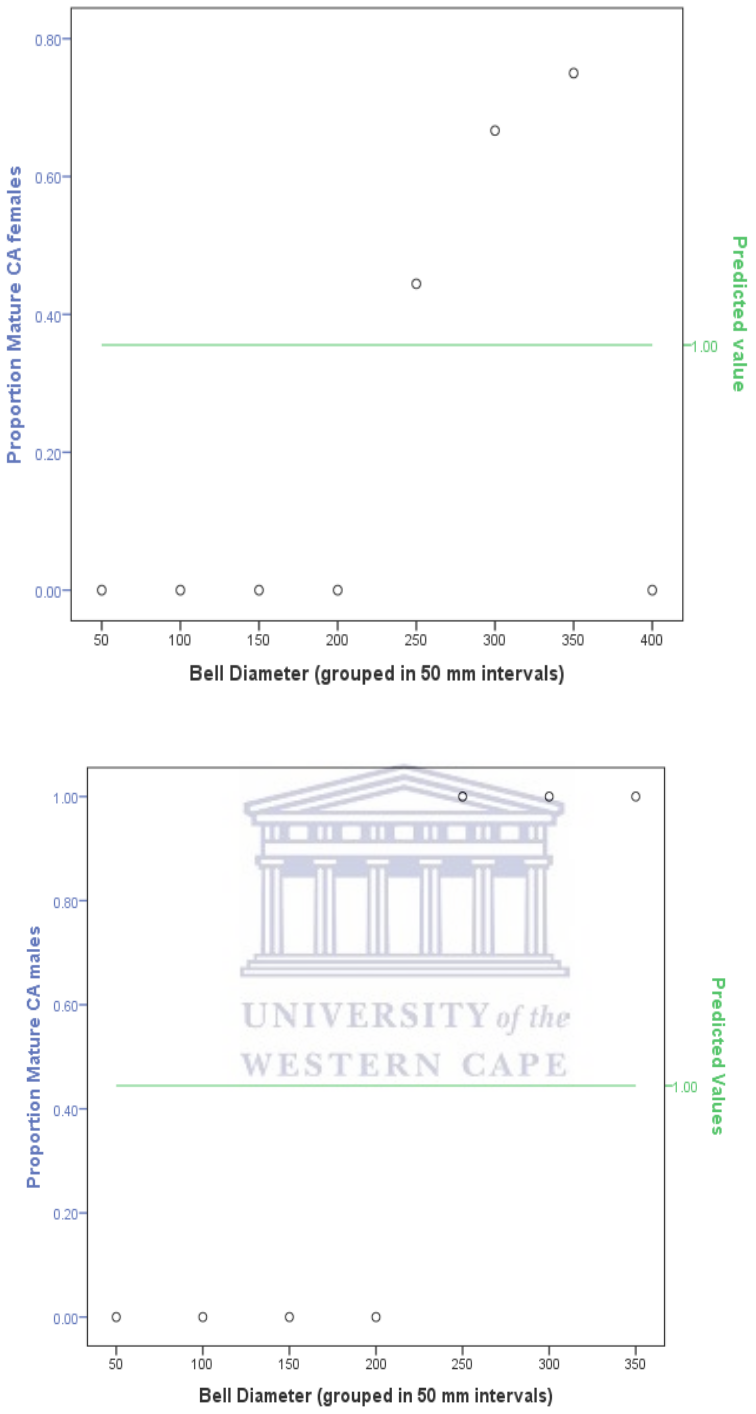


Figure 4.11. *Chrysaora africana*. Maturity ogives for bell diameter (grouped in 50 mm intervals) for females (n = 28) and males (n = 25). The L^{50} could not be calculated by the non-linear binominal regression model.

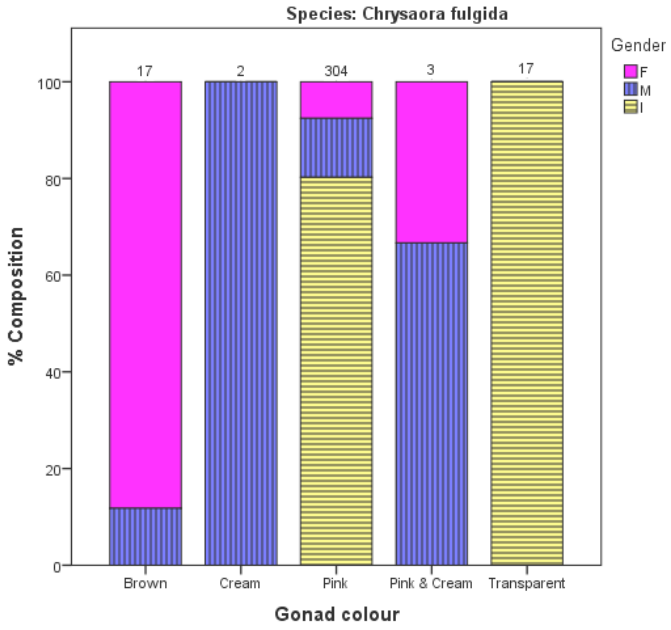


Figure 4.12. Variation in gonad colour of female (F), male (M) and sex-indeterminable (I) medusae of *Chrysaora fulgida* collected in the Walvis Bay area. The number on top of each bar is the total number of individuals in the sample.

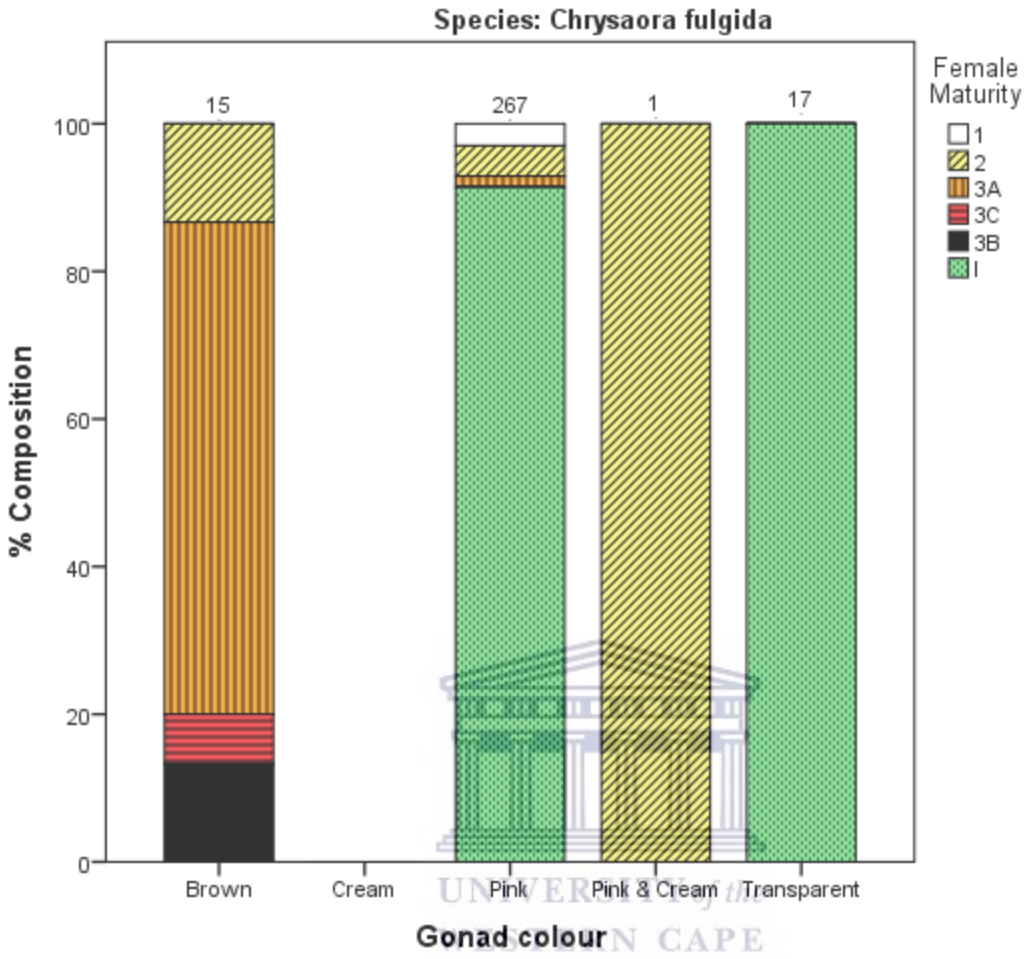


Figure 4.13. Variation in gonad colour classed according to female maturity (1, 2, 3A, 3B and 3C) and sex-indeterminable (I) *Chrysaora fulgida* medusae collected in the Walvis Bay area. The number on top of each bar is the total number of individuals in the sample.

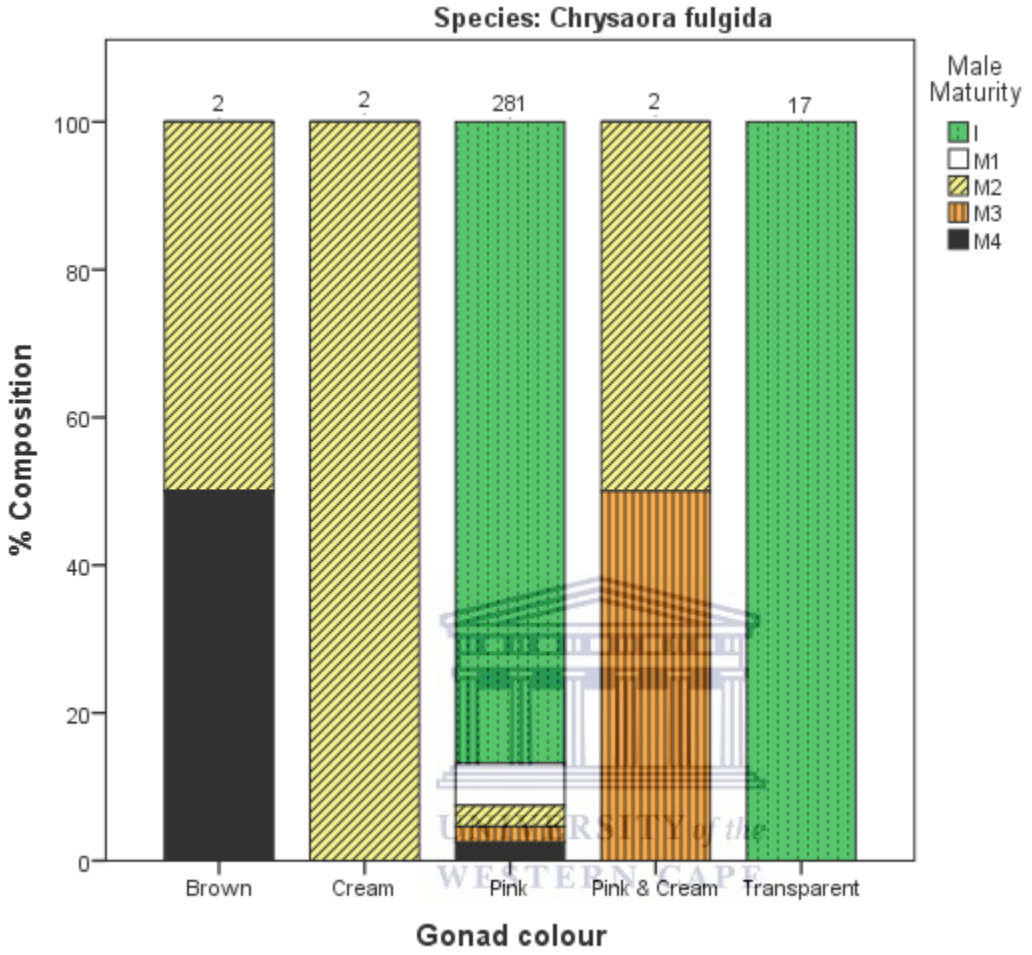


Figure 4.14 Variation in gonad colour classed according to male maturity (M1 to M4) and sex-indeterminable (I) *Chrysaora fulgida* medusae collected in the Walvis Bay area. The number on top of each bar is the total number of individuals in the sample.

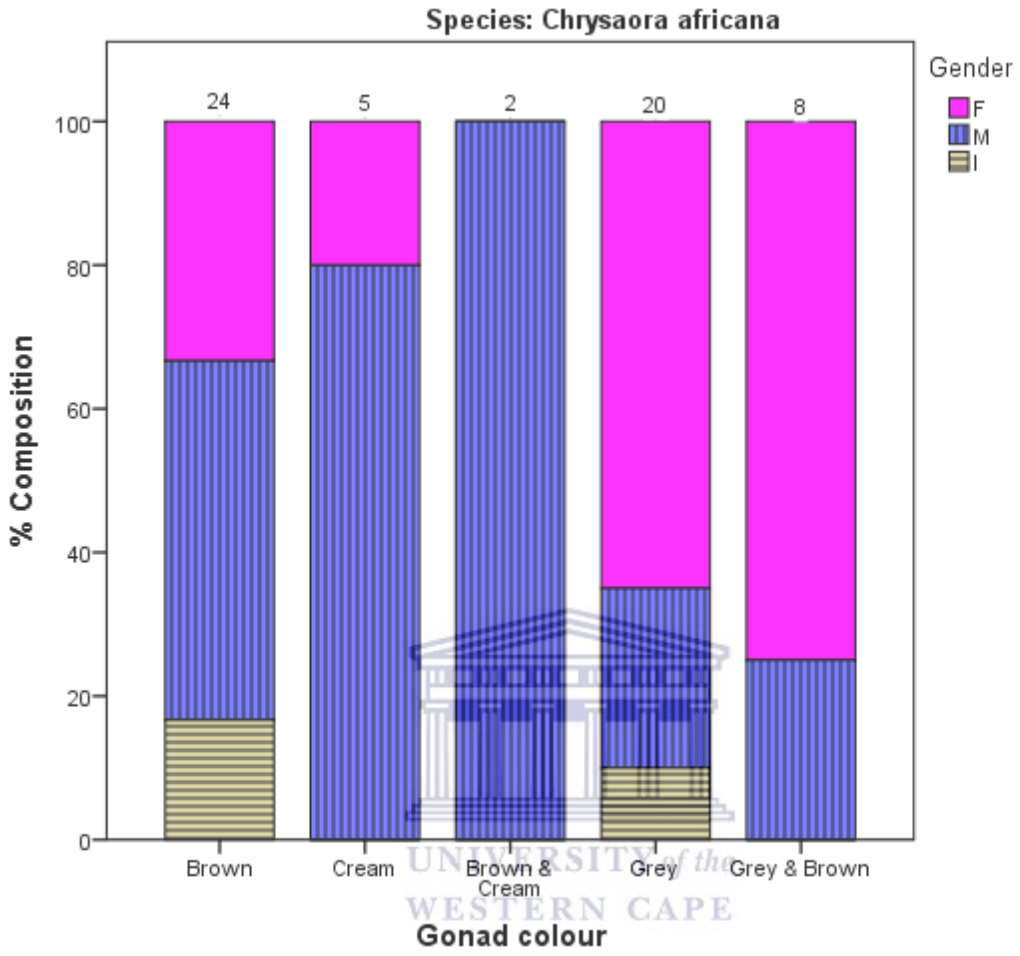


Figure 4.15. Variation in gonad colour of female (F), male (M) and sex-indeterminable (I) medusae of *Chrysaora africana* collected in the Walvis Bay area.The number on top of each bar is the total number of individuals in the sample.

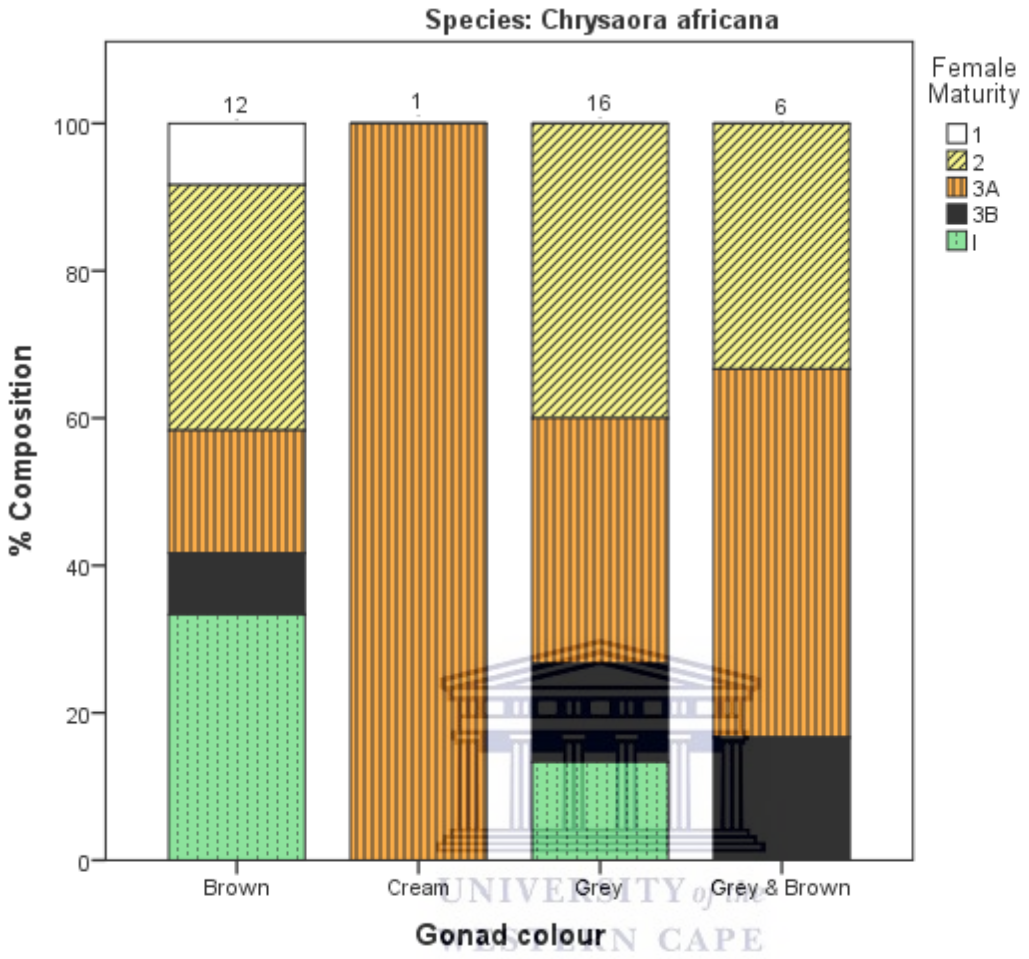


Figure 4.16. Variation in gonad colour classed according to female maturity (1, 2, 3A and 3B) and sex-indeterminable (I) *Chrysaora africana* medusae collected in the Walvis Bay area. The number on top of each bar is the total number of individuals in the sample.

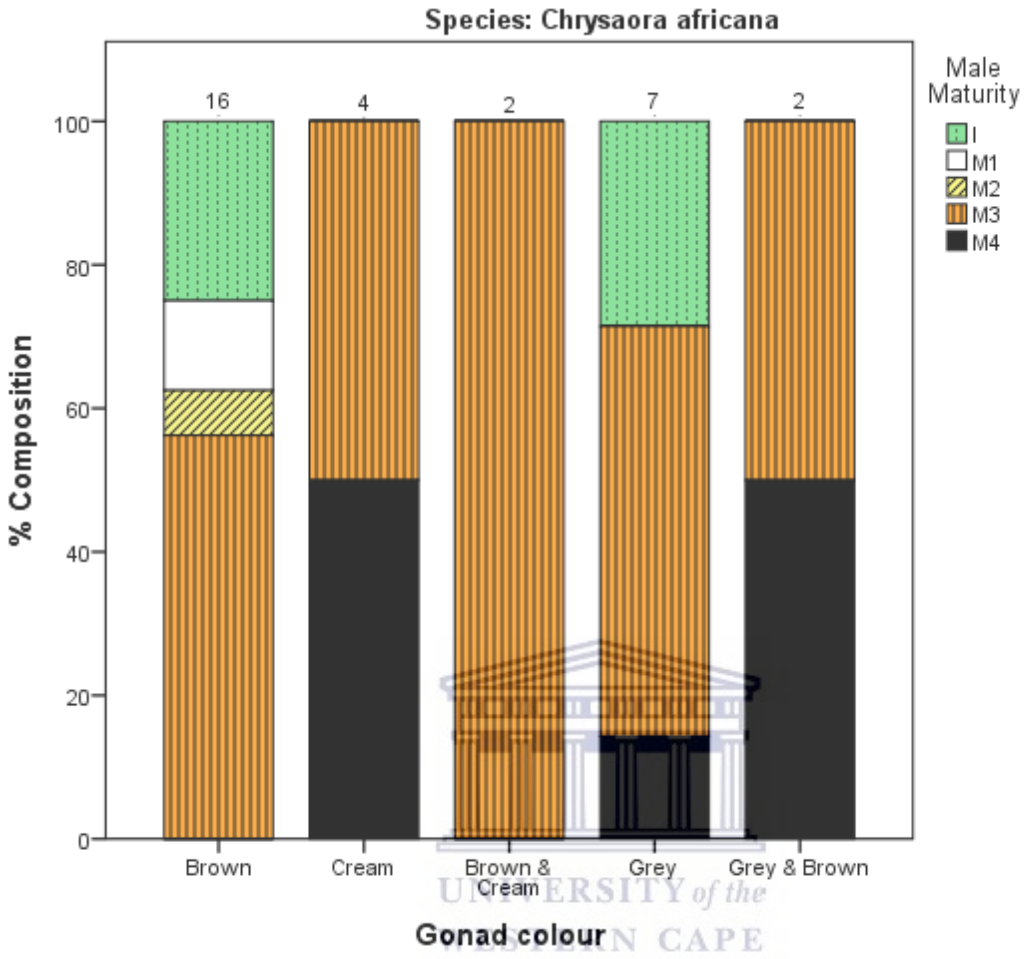


Figure 4.17. Variation in gonad colour classed according to male maturity of *Chrysaora africana* medusae collected in the Walvis Bay area. The number on top of each bar is the total number of individuals in the sample.

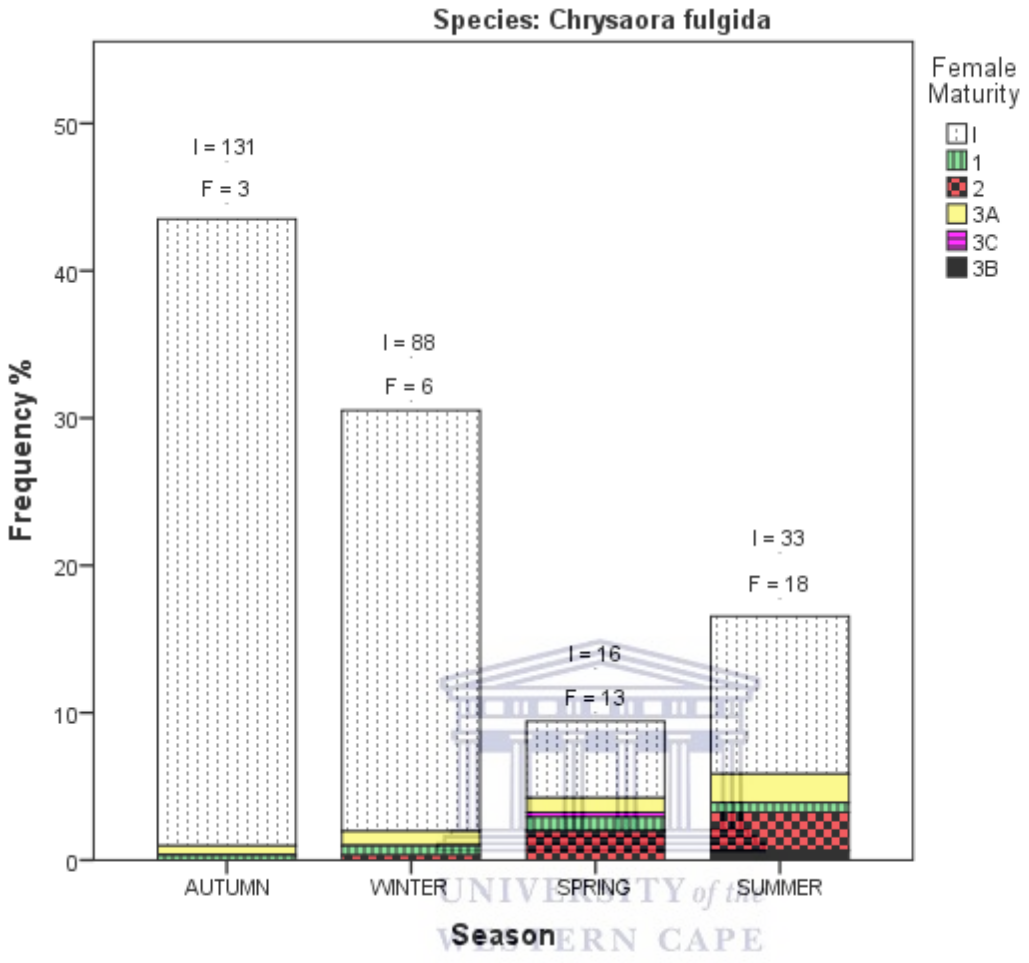


Figure 4.18. The seasonal occurrence of female (F) maturity classes (1, 2, 3A, 3B and 3C) and sex-indeterminable (I) medusae of *Chrysaora fulgida* for the period 2012–2015 (pooled years). The numbers on top of each bar is the total number of individuals in the sample.

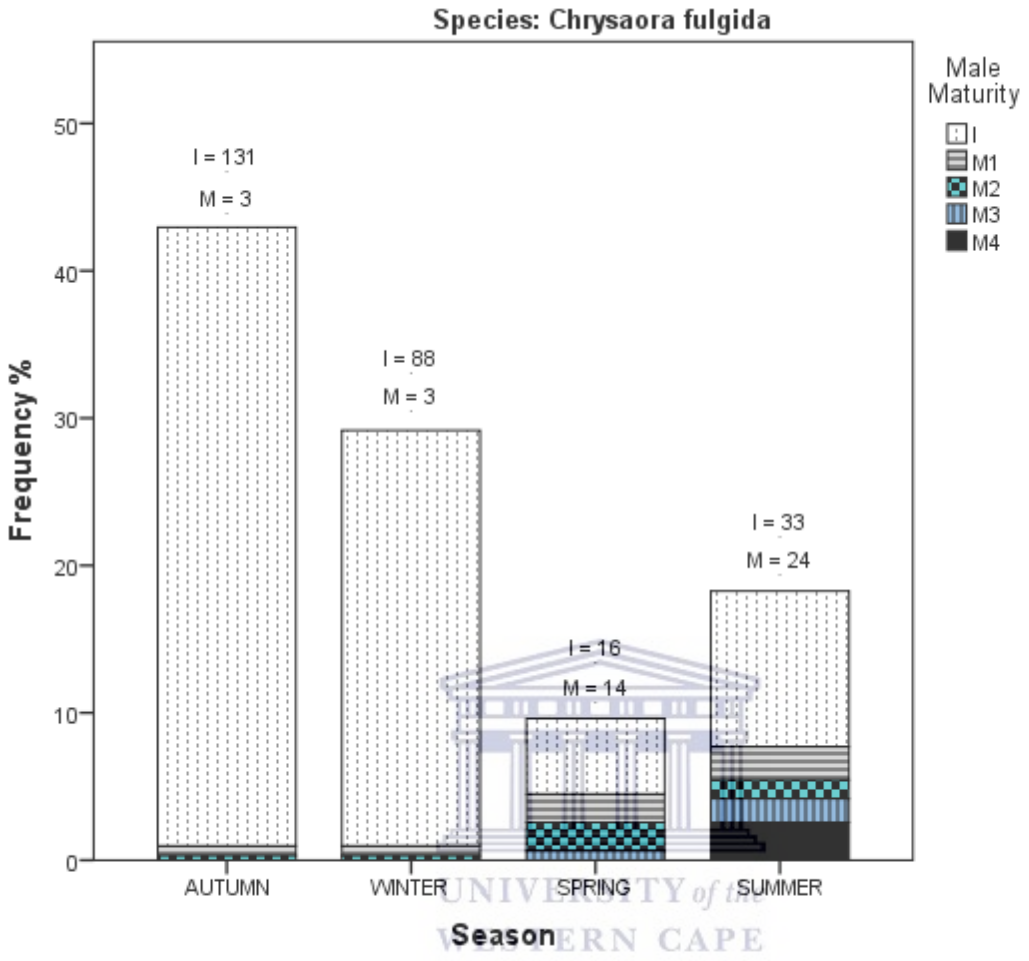


Figure 4.19. The seasonal occurrence of male maturity classes (M1–M4) and sex-indeterminable (I) medusae of *Chrysaora fulgida* for the period 2012–2015 (pooled years). The numbers on top of each bar is the total number of individuals in the sample.

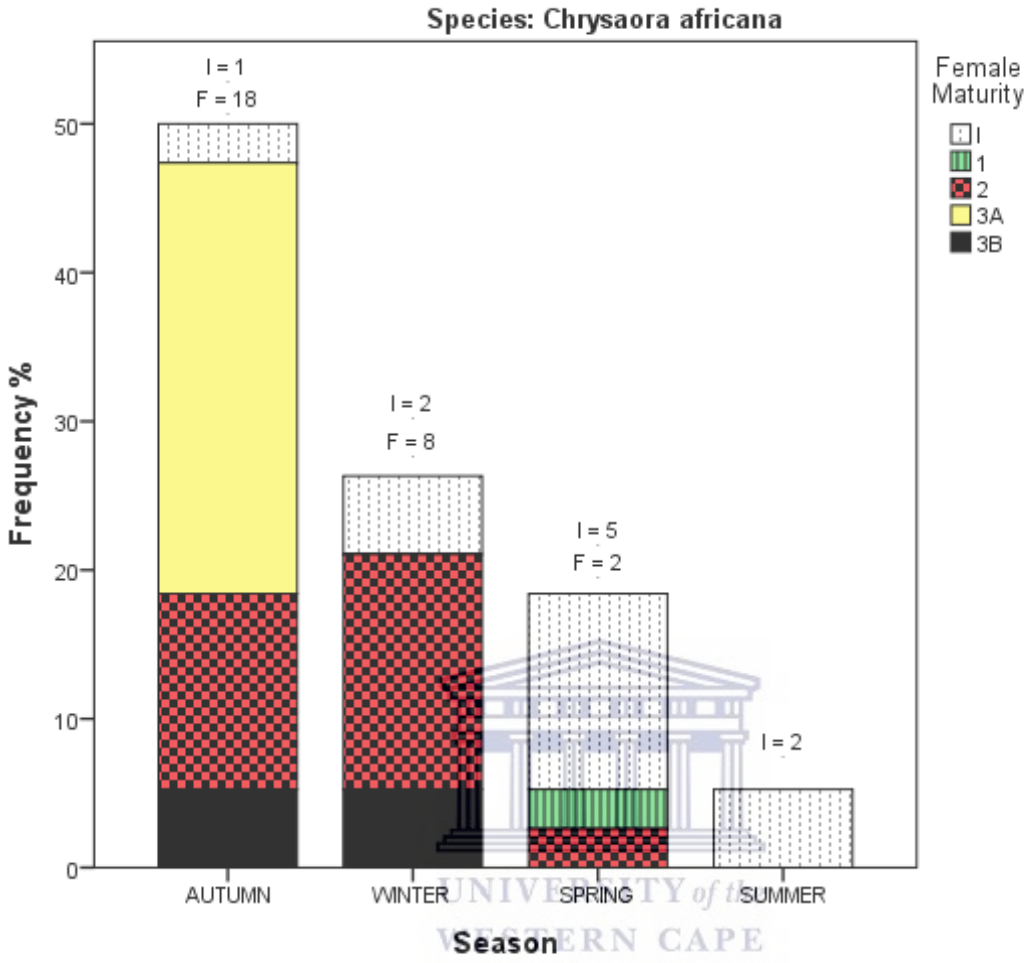


Figure 4.20. The seasonal occurrence of maturity classes (1, 2, 3A and 3B) and sex-indeterminable (I) medusae of *Chrysaora africana* for the period 2012–2013 (pooled years). The numbers on top of each bar is the total number of individuals in the sample.

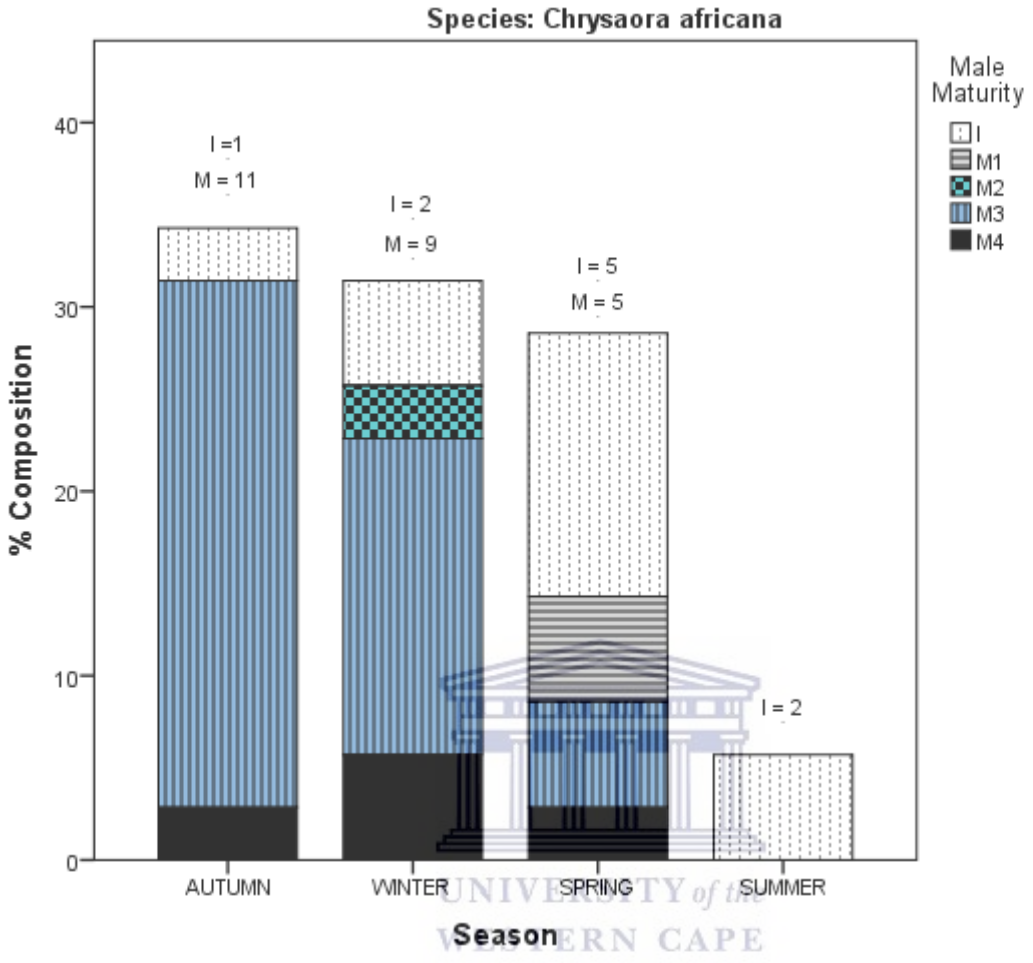


Figure 4.21. The seasonal occurrence of male maturity classes (M1–M4) and sex-indeterminable (I) medusae of *Chrysaora africana* for the period 2012–2013 (pooled years). The numbers on top of each bar is the total number of individuals in the sample.

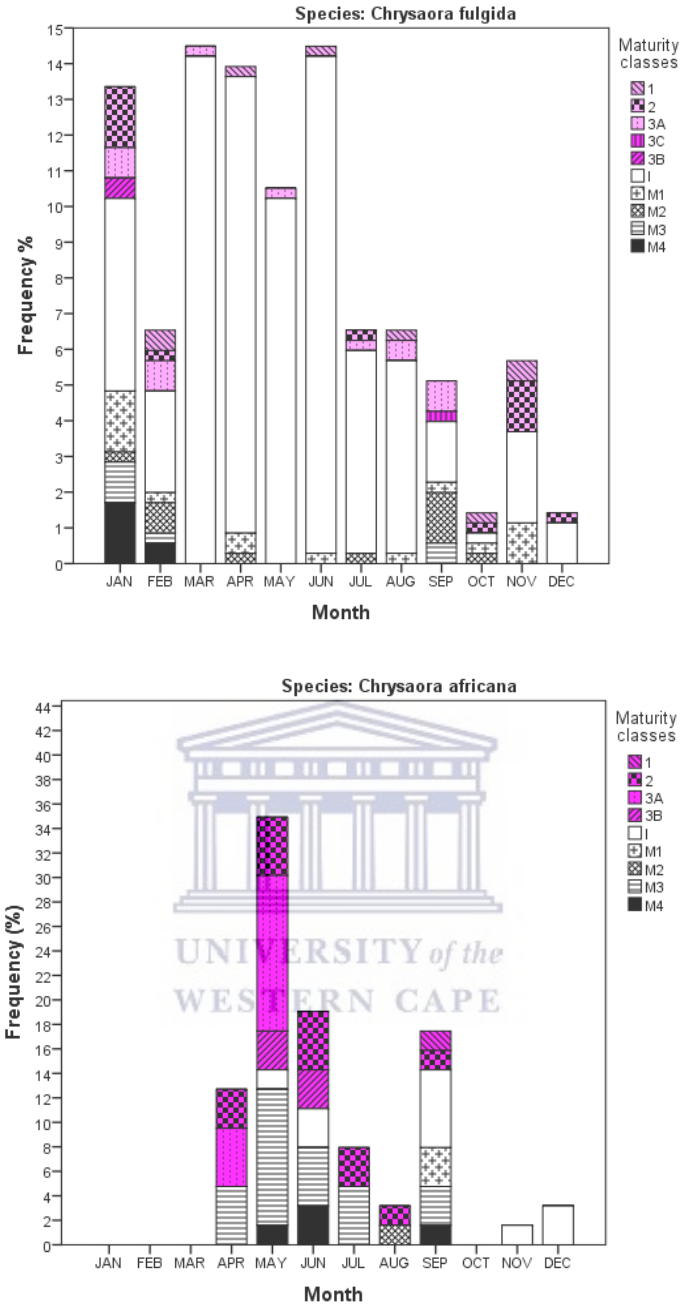


Figure 4.22. The occurrence of maturity classes of female (1–3B), sex-indeterminable (I) and male (M1–M4) *Chrysaora fulgida* and *C. africana* medusae by month (pooled by years).

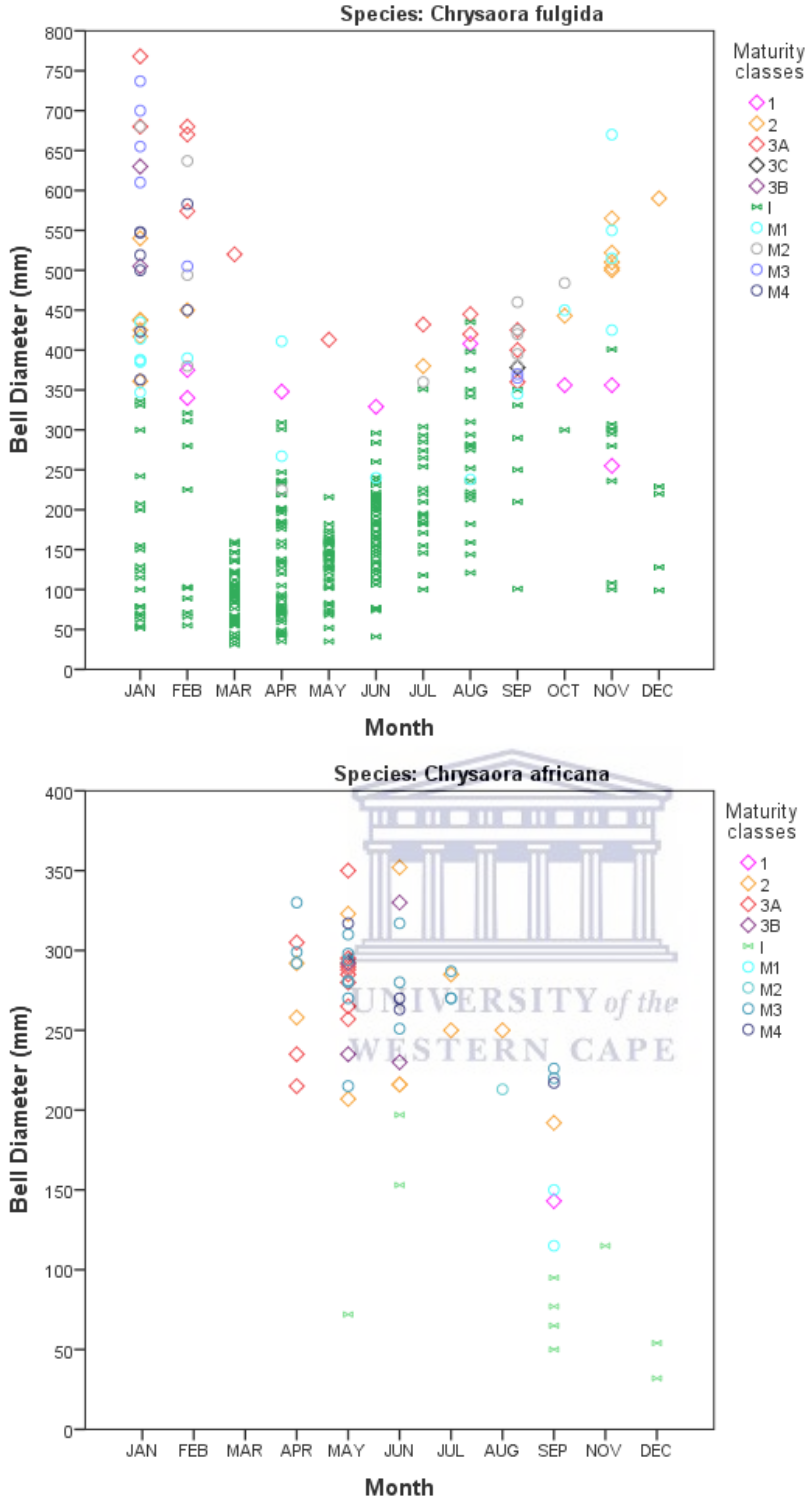


Figure 4.23. The occurrence of individual bell diameters per maturity class of female (1–3B), sex-indeterminable (I) and male (M1–M4) *Chrysaora fulgida* and *C. africana* medusae by month (pooled by years)

TABLES

Table 4.1. The number of *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA) medusae collected per month in the Walvis Bay area during 2012-2015, classed according to sex-indeterminable (I), female (F) and male (M) individuals. *These specimens were selected for their sizes

Year	Month	CF			CA		
		I	F	M	I	F	M
2012	Jan	4	5	6	0	0	0
	Feb	1	3	4	0	0	0
	Mar	23	1	0	0	0	0
	Apr	39	1	3	0	3	2
	May	29	1	0	1	4	2
	Jun	20	0	0	2	3	1
	Jul	15	1	0	0	1	3
	Aug	7	0	0	0	0	1
	Sep	1	1	0	0	1	3
	Oct	0	0	1	0	0	0
	Nov	3	0	0	1	0	0
	Dec	4	0	0	0	0	0
2013	Jan	4	0	0	0	0	0
	Feb	5	0	0	0	0	0
	Mar	27	0	0	0	0	0
	Apr	6	0	0	0	2	1
	May	7	0	0	0	9	6
	Jun	29	1	1	0	2	4
	Jul	5	1	1	0	1	0
	Aug	9	0	1	0	1	0
	Sep	5	2	6	4	1	2
	Nov	6	1	2	0	0	0
	Dec	0	1	0	2	0	0
2014	Jan	11	6	11	0	0	0
	Feb	3	2	1	0	0	0
	Nov*	0	2	0	0	0	0
2015	Feb*	1	1	2	0	0	0
	Aug*	3	3	0	0	0	0
	Sep*	0	1	2	0	0	0
	Oct*	1	2	1	0	0	0
	Nov*	0	4	2	0	0	0
n		268	40	44	10	28	25

Table 4.2. A summary of bell diameters (mm) for *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA), at each medusa maturity (MM) class (described in **Table 4.5**): sex-indeterminable (I), female maturity (1, 2, 3A–3C) and male maturity (M1–M4).

MM	*Chrysaora fulgida*							*Chrysaora africana*						
	Min	Max	n	Mean	Mode	SD	N%	Min	Max	n	Mean	Mode	SD	N%
I	31	435	268	158	236	84	76.1	32	197	10	91	32	51	15.9
1	255	408	8	346	356	44	2.3	143	143	1	143	143		1.6
2	361	590	15	472	361	67	4.3	192	352	12	261	216	49	19.0
3A	360	768	13	522	680	136	4.0	215	350	11	288	215	36	17.5
3C	378	378	1	378	378		0.3							
3B	505	630	2	568	505	88	0.6	230	330	4	272	230	48	6.3
M1	238	670	17	403	238	109	4.8	115	150	2	133	115	25	3.2
M2	225	680	12	445	380	122	3.4	213	213	1	213	213		1.6
M3	365	737	7	563	365	152	2.0	215	330	18	277	270	32	28.6
M4	363	583	8	492	363	74	2.3	217	317	4	267	217	41	6.3

Table 4.3. Results of the Mann-Whitney U test illustrating differences in the median bell diameter of female (F), male (M) and sex-indeterminable (I) medusae between *Chrysaora africana* and *Chrysaora fulgida* collected off Walvis Bay. (Results considered significant at $p \leq 0.05$)

Gender	Mann-Whitney U	Wilcoxon W	Z	Sig. (2-tailed)
F	1068.0	1848.0	6.637	.001
M	1029.0	2019.0	5.981	.001
I	2027.0	38073.0	2.752	.006

Table 4.4. A description of oocyte development stages (FS) for *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA).

FS allocation	Description of female oocyte stage
F1 (pre-vitellogenic stage)	Yolk granules absent in the oocyte; dark staining (blue/purple)
F2 (early vitellogenic stage)	Very little yolk granule development in the oocyte; and cytoplasm has a smooth to patchy granular apprearance; stains blue/purple (not as dark as F1)
F3 (mid vitellogenic stage)	Yolk granules present throughout oocyte but have not accumulated, combination of light pink to red staining with some purple/blue staining
F4 (late vitellogenic stage)	Yolk granules accumulated in oocyte and stains deep pink/red In addition for CF: peripheral area of the oocyte stains deep pink/red
F6 (released stage)	Has the features of an F4 oocyte, however this oocyte is in the process of being released to the subgenital sinus (ovulation) or present in subgenital sinus or present during the disintegration of gastrodermis and subgenital sinus For CF: oocyte elliptical or hourglass shaped, nucleus not clearly visible For CA: oocyte oval shaped

Table 4.5. A description of medusae maturity classes (MM) for *Chrysaora fulgida* and *Chrysaora africana.*

Medusae Maturity (MM) classes			
MM allocation	**Description of MM classes**		
I	No gonads present, sex unidentifiable		
1	Unripe female, predominance of ≥50% pre-vitellogenic oocytes (F1)		
2	Unripe female, predominance of >50% early vitellogenic oocytes (F2) to mid vitellogenic oocytes (F3) and <15% of late vitellogenic oocytes (F4 & F6)		
3	Ripe female, ≥15% of late vitellogenic oocytes (F4 & F6)	3A	Ripe/Ovulating gonad, no visible signs of the disintegration of gonad structures
		3B	Disintegration of gonad structures present
		3C	Partially spent gonad: gonad structures not disintegrating, low ratio of oocytes:specialised gastrodermal cell structures; visible empty "cavities" surrounded by specialised gastrodermal cell structures
M1	Unripe male, <70% of sperm follicles contains spermatozoa		
Mature male	Ripe male, ≥70% of sperm follicles contains spermatozoa	M2	Ripe male with individual sperm follicles visible that contains spermatozoa; pheriphery of follicles may stain darker (blue/purple) than central follicle areas
		M3	Ripe male with with sperm follicles clustered or merged, accompanied by areas of highly condensed spermatozoa; spermatozoa may or may not be released into subgenital sinus
		M4	Ripe male, the disintegration of follicle walls, gastrodermis and subgenital sinus

Table 4.6. A statistical summary of oocyte diameters (µm) from *Chrysaora fulgida* and *Chrysaora africana*, grouped by female medusa maturity (MM) class and illustrating the type of oocyte stage (FS) present per MM class.

Species	MM	FS	n*	Min	Max	n	Mode	Median	Mean	SD	N%
Chrysaora fulgida	1	F1	8	4.52	35.22	329	8.76	12.1	13.2	5.86	82.3
		F2		18.37	44.78	71	18.37	27.3	28.5	6.91	17.8
	2	F1	15	6.4	30.3	82	6.4	16.6	16.7	5.1	10.9
		F2		18.0	73.7	605	22.3	39.7	40.8	12.4	80.7
		F3		61.1	99.8	63	61.1	68.3	71.7	9.9	8.4
	3A, ripe/ ovulating	F1	14	12.9	24.2	4	12.9	16.5	17.5	4.8	0.6
		F2		20.4	73.5	134	39.0	47.6	48.5	14.1	19.1
		F3		61.5	137.4	269	105.0	97.3	97.8	17.4	38.4
		F4		94.4	180.3	290	118.1	129.5	132.0	17.4	41.4
		F6		152.3	174.7	3	152.3	169.8	165.6	11.8	0.4
	3B, disintegration	F2	2	45.1	59.7	4	45.1	56.9	54.6	6.5	4.0
		F3		75.5	97.2	4	75.5	85.7	86.0	9.4	4.0
		F4		91.4	123.9	10	91.4	98.6	102.1	11.0	10.0
		F6		100.4	167.4	82	100.4	132.5	132.2	16.7	82.0
	3C, partially spent	F1	1	17.9	17.9	1	17.9	17.9	17.9		2.0
		F2		22.9	55.8	7	22.9	36.5	37.2	10.7	14.0
		F3		108.7	135.4	6	108.7	124.0	123.0	9.0	12.0
		F4		107.0	154.1	34	107.0	137.2	136.0	14.1	68.0
		F6		111.5	135.5	2	111.5	123.5	123.5	16.9	4.0
	3, combined	F1	17	12.9	24.2	5	12.9	16.9	17.6	4.1	0.6
		F2		20.4	73.5	145	39.0	47.3	48.2	14.0	17.1
		F3		61.5	137.4	279	105.0	68.3	98.2	17.6	32.8
		F4		91.4	180.3	334	118.1	129.5	131.5	17.7	39.3
		F6		100.4	174.7	87	111.5	133.4	133.1	17.6	10.2

Chrysaora africana	1	F1	1	5.7	14.8	40	5.7	11.3	11.0	2.0	80.0
		F2		13.8	29.9	10	13.8	16.2	18.0	5.7	20.0
	2	F1	12	5.4	22.8	51	16.3	16.3	15.8	4.0	8.5
		F2		11.5	61.1	378	23.2	34.7	34.5	9.4	63.0
		F3		39.0	73.9	139	49.6	54.0	54.6	7.8	23.2
		F4		64.8	90.1	27	64.8	70.1	72.3	6.6	4.5
		F6		66.0	100.3	5	66.0	85.4	82.8	15.5	0.8
	3A, ripe/ ovulating	F1	11	6.0	16.9	31	6.0	11.2	11.4	3.4	5.6
		F2		12.0	59.5	250	21.0	36.2	35.9	10.3	45.5
		F3		39.1	73.5	129	39.1	58.8	57.2	8.1	23.5
		F4		62.2	94.4	100	73.4	73.4	73.2	6.2	18.2
		F6		70.3	91.2	40	70.3	79.0	78.7	5.7	7.3
	3B, disintegration	F1	4	6.8	13.7	8	6.8	9.2	9.4	2.1	4.0
		F2		11.4	61.0	94	11.4	31.4	32.4	11.1	47.0
		F3		39.1	72.4	49	39.1	53.3	54.9	9.6	24.5
		F4		70.2	82.0	9	70.2	74.7	76.6	4.1	4.5
		F6		67.2	89.6	40	67.2	79.9	79.2	6.1	20.0
	3, combined	F1	15	6.0	16.9	39	6.0	10.7	11.0	3.3	5.2
		F2		11.4	61.0	344	20.1	35.0	35.0	10.6	45.9
		F3		39.1	73.5	178	51.2	57.9	56.6	8.6	23.7
		F4		62.2	94.4	109	73.4	73.5	73.5	6.1	14.5
		F6		67.2	91.2	80	67.2	79.4	79.0	5.9	10.7

n* = total number of female medusa

Table 4.7. Results of the independent-samples T-test illustrating significant differences in the mean oocyte diameter of each oocyte stage (FS) between *Chrysaora fulgida* and *Chrysaora africana* collected off Walvis Bay. (Results considered significant at $p \leq 0.05$).

Independent Samples T-Test

Mean oocyte diameter		Levene's Test for Equality of Variances		t-test for Equality of Means						
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
									Lower	Upper
F1	Equal variances assumed	22.975	.000	1.960	544	.050	1.08160	.55171	-.00214	2.16534
	Equal variances not assumed			2.374	314.248	**.018**	1.08160	.45566	.18507	1.97813
F2	Equal variances assumed	62.999	.000	10.847	1551	.000	6.53858	.60282	5.35615	7.72101
	Equal variances not assumed			11.009	1517.974	**.000**	6.53858	.59394	5.37355	7.70360
F3	Equal variances assumed	217.570	.000	31.918	657	.000	37.59429	1.17785	35.28148	39.90709
	Equal variances not assumed			32.767	468.941	**.000**	37.59429	1.14731	35.33977	39.84880
F4	Equal variances assumed	124.000	.000	37.400	468	.000	58.28010	1.55829	55.21799	61.34221
	Equal variances not assumed			52.670	460.766	**.000**	58.28010	1.10650	56.10568	60.45452
F6	Equal variances assumed	66.612	.000	26.483	170	.000	53.95302	2.03727	49.93141	57.97463
	Equal variances not assumed			26.716	110.805	**.000**	53.95302	2.01953	49.95110	57.95493

Ghost crabs (*Ocypode cursor*) feeding on an *Aequorea forskalea* medusa in the Skeleton Coast Park.

PICTURE

CHAPTER 5

OBSERVATIONS ON THE TROPHIC ECOLOGY OF *CHRYSAORA FULGIDA* AND *CHRYSAORA AFRICANA* FROM AN EXAMINATION OF STABLE ISOTOPES (δ^{15}N AND δ^{13}C) IN WALVIS BAY, NAMIBIA

CHAPTER 5

OBSERVATIONS ON THE TROPHIC ECOLOGY OF *CHRYSAORA FULGIDA* AND *CHRYSAORA AFRICANA* FROM AN EXAMINATION OF STABLE ISOTOPES (δ^{15}N AND δ^{13}C) OF MEDUSAE IN WALVIS BAY, NAMIBIA

INTRODUCTION

A food web defines "who eats who" in an ecosystem; it predicts how energy and nutrients are transferred between organisms in the natural environment and predicts consumer–resource interactions (Pauly et al. 2009). Modern-day marine trophic transfer models have realised that trophic transfer is more complicated than the simple classical food chain model (phytoplankton → copepod → fish) (Redden et al. 2009), when the "microbial loop" is considered, which gives rise to multiple trohpic enrichment steps in the food chain (Sommer et al. 2002).

In order to understand the role of jellyfish within a food web, ecological models need to incorporate multiple and detailed compartments that represent the true diversity of taxa, their trophic interactions, biomass, growth and biology (Pauly et al. 2009; Purcell 2009). Ideally, an all-inclusive ecological model should also take into account the spatial and temporal variability of individuals (Thompson et al. 2012). Currently, the majority of ecosystem models exclude jellyfish in their food webs, or when they are included the different species are lumped together, and inaccurate model parameters and generalised assumptions are incorporated (Shannon & Jarre-Teichmann 1999; Heymans et al. 2009; Pauly et al. 2009; Purcell 2009). The model output is only as good as the input data, parameters and assumptions, and there is a need for accurate, locally collected data across a wide range of measures. Depending on the underlying model, these include information on biomass, growth and consumption rates, diet, natural mortality (predators etc.), population energetics, and ecotrophic efficiency.

A variety of methods such as stomach content analysis, experimental feeding incubations, animal-borne cameras and molecular biomarkers (stable isotope analysis, fatty acid analysis and DNA-based techniques) have been used (directly or complimentary) to examine trophic relationships in aquatic organisms (Gannes et al. 1997; Gaye-Siessegger et al. 2004a, 2004b; Blankenship & Yayanos 2005; Dunshea 2009; Purcell 2009; Hays et al. 2018). Each of these different methods has its own strengths

and limitations (Gannes et al. 1997; Gaye-Siessegger et al. 2004a, 2004b; Blankenship & Yayanos 2005; Dunshea 2009; Purcell 2009; Hays et al. 2018). Most traditional studies have relied on gut content analysis to investigate diet, predator-prey interactions and define trophic ecology of jellyfish (Purcell & Grover 1990; Purcell & Sturdevant 2001; Pitt et al. 2009a; Purcell 2009). This method gives a "snapshot" on ingested prey at a particular time and place, and falls short when applied to soft-bodied and fragile organisms, or in case of advanced digestion (Hyslop 1980; Pitt et al. 2009a). In the case of jellyfish, this method is challenging due to their aggregated nature of distribution, some being quite large in size, their relatively fast digestion rates, heterogeneous prey fields, diel feeding patterns and when net-caught they are subjected to damage, gut evacuation or net feeding (Purcell 1997; Pitt et al. 2009a; Purcell 2009). Dietary analysis of jellyfish can be further complicated by inter- and intraspecific digestion rates (Båmstedt & Martinussen 2000; Purcell 2009), variability in prey digestion rates (Purcell et al. 1991; Martinussen & Båmstedt 1999) and diel vertical movements of prey and predator (Pitt et al. 2008). Unfortunately, diets estimated from jellyfish gut contents are biased toward shell/carapace bearing prey and the most abundant prey present in the plankton (Pauly et al. 2009). As a result, a true reflection of the complete assimilated diet would not be possible for fractions of undistinguished items such as detritus, microplankton or other jellyfish (Pauly et al. 2009). Assumed diets of jellyfish therefore need to be verified since jellyfish play a crucial role both in trophic models and in real ecosystems (Pauly et al. 2009). Better-quality information on the diet of jellyfish will bring forward the evidence required to improve the resolution currently used for defining these animals in food web models (Pauly et al. 2009).

Stable isotope analysis complements conventional gut-content analysis and represents a technique that determines dietary preferences and trophic positions. The analysis of nitrogen and carbon stable isotope ratios can provide a time-integrated signal of diet, relying as it does on assimilated and not recently ingested food. Through a process of isotopic fractionation, heavier isotopes accrue in the organism's body tissues whereas lighter isotopes are metabolised (faster) and excreted, thus leading to an enrichment of the heavier isotope from diet to consumer (Vander Zanden & Rasmussen 2001; Martínez del Rio et al. 2009). The $^{15}N/^{14}N$ ratio (termed $\delta^{15}N$) has pragmatically been assumed to become enriched by ~3.4‰ per trophic step, and the $^{13}C/^{12}C$ ratio ($\delta^{13}C$) by ≤1‰ per trophic step (Post 2002). $\delta^{15}N$ values identify relative trophic position (Fry 2006), whilst the $\delta^{13}C$ values provides an indication of the

type of primary production at the base of the food web (Fry 2006). Within marine environments, $\delta^{13}C$ has been used as a tool to discriminate between benthic- and pelagic-based productions (Davenport & Bax 2002), and between nearshore and offshore productivity (Miller et al. 2008).

Even though diet and trophic position are the main factors that affect isotopic ratios in animals, fractionation is an intricate process and other sources of variation need to be taken into account to avoid false conclusions (McCutchan et al. 2003; Vanderklift & Ponsard 2003; reviewed by Boecklen et al. 2011). According to Traugott et al. (2013), these include: the type of nitrogen integration and excretion; taxonomic affiliation; habitat type (terrestrial vs. freshwater vs. marine); tissue type; intra-specific variability and seasonal variation in fractionation rates; isotopic baseline variations; omnivory; and movement of organisms and nutrients amongst food webs. Hence, clarifying the sources of variation in the isotopic signatures of species and understanding the magnitudes and causes of the differences among consumer and resource isotopic values are the focal point of stable isotope analysis in trophic ecology (Boecklen et al. 2011).

As briefly described above, the $\delta^{15}N$ and $\delta^{13}C$ properties of stable isotopes effectively allow the temporal-spatial integration of an organism's diet allowing its trophic status to be measured on a continuous scale (Ehleringer et al. 1986; Bearhop et al. 2004; Fry 2006; Boecklen et al. 2011). This can then be applied at the individual level (Traugott et al. 2013), and it can be used to develop models of food web structure (Layman et al. 2012). It can also detect dietary shifts through ontogeny, in particular shifts in niche width, niche position and niche overlap (Hammerschlag-Peyer at al. 2011). Studies on the stable isotope ecology of jellyfish are very limited when compared to other taxonomic groups such as fish and crustaceans (Boecklen et al. 2011), which hampers the development of statistically robust predictive models for jellyfish.

In most marine trophic webs, jellyfish are considered as trophic dead ends (Sommer et al. 2002; Heymans et al 2004; Bakun & Weeks 2006; Pauly et al. 2009; Hays et al. 2018), due to their low nutritional value (Doyle et al. 2007a). It is frequently assumed that they die, sink and decompose and energy transfer takes directly place to detritus (Heymans et al. 2004). However, jellyfish are important predators in pelagic marine systems and act as a food source (occasionally or predominately) for a wide range of marine predators such as fish, birds, turtles, sharks and several invertebrates such as octopus,

sea cucumbers, crabs, barnacles and amphipods (Pauly et al. 2009; Hays et al. 2018). In addition, they provide extensive beneficial ecosystem services in their own right as outlined by Doyle et al. (2014). They exhibit some diet selectivity (Purcell 1997), whereas their vast diversity of feeding mechanisms and body sizes ensures that they are capable of feeding on a broad range of prey types and sizes (Doyle et al. 2014). Ontogenic shifts (Graham & Kroutil 2001) in diet, as well as inter-species differences in diet, reflect a broad suite of characteristics including swimming modes and feeding mechanisms, nematocyst structure, venom toxicity and cnidome composition, morphology and prey behaviour (Costello & Colin 1995; Purcell 1997; Peach & Pitt 2005; Boero et al. 2008).

As in many other ecosystems, little attention has been paid to the actual role of jellyfish in the northern Benguela upwelling ecosystem. At present they are generally considered as a black box, and with the exception of biomass, there is scant knowledge about the other model-needed parameters (Brierley et al. 2001; Fearon et al. 1992; Gibbons et al. 1992; Shannon & Jarre-Teichmann 1999; Heymans et al. 2004, 2009). Indeed, most of the parameters that are used for jellyfish in local ecosystem models are imported from other systems. At present in the northern Benguela, only four studies on the diet of *Chrysaora fulgida,* all conducted over short time periods, are available. In the study of Flynn & Gibbons (2007), it was shown that the diet was diverse, and animals ate a wide range of species from dinoflagellates to carideans, including benthic species. The other three studies were based on stable isotope analysis. Van der Bank et al. (2011) revealed that the bearded goby (*Sufflogobius bibarbatus*) acts as a direct link from jellyfish (*Chrysaora fulgida* and *Aequorea forskalea*) to higher users in the food web. Both Koppelmann et al. (2014) and Schukat et al. (2014) illustrated nitrogen (δ^{15}N) and carbon (δ^{13}C) signals and estimated trophic levels (TL) of various jellyfish taxa: *Chrysaora fulgida* exhibited trophic levels of 3.3 to 3.4.

As Boecklen et al. (2011) have stated “a fundamental challenge facing stable isotope ecology is an understanding of how error (variation) in isotopic signatures propagates throughout models and ecological systems, and to what degree this error limits inferences derived from stable isotopes”. This statement is appropriate in the case of jellyfish studies globally, and locally. The present study is aimed at applying stable isotope analysis (δ^{15}N and δ^{13}C) to *Chrysaora fulgida* and *Chrysaora africana* medusae

collected off Walvis Bay, Namibia, to examine the presence of tissue, ontogenetic, seasonal, spatial and interspecific variability in their trophic level and source production.

MATERIALS AND METHODS

Sampling

Samples of *Chrysaora fulgida* and *Chrysaora africana* were collected off Walvis Bay (Table 5.1), during the period 27 May 2012 to 26 January 2016. Dip-nets were used to collect medusae that were at or close to the sea surface, and animals were immediately placed into buckets filled with ambient seawater. Ephyrae were caught from a ski-boat using a weighted plankton-net of 50 cm mouth diameter (180 µm mesh size), fitted with a 1 L plastic cod-end jar, which was manually hauled vertically from just above the seabed to the water surface. All specimens were transported to the laboratory, and kept at 16 °C overnight to evacuate their stomachs.

Within 24 hours of sample collection, individual maximum bell diameters (in mm) were measured. Tissue samples were taken from the bell, oral arms and gonads of individuals.In the case of small medusae and ephyrae, multiple individuals of similar maximum diameter were pooled (by identical sampling dates) to provide sufficient material for analysis (Table 5.1). Ephyrae were separated from the zooplankton sample through a nested series of sieves of 1000, 500 and 250 µm: all were identified to species level (see Chapters 2 and 3), and identified as *Chrysaora fulgida*. Tissue and (whole) ephyrae samples were washed with filtered seawater (0.2 µm filter), then quickly rinsed with distilled fresh water in order to remove surface salt (Brodeur et al. 2002; Tamelander et al. 2006) and dried to constant dry weight at 60 °C. Thorough washing of jellyfish tissue is required to remove water-soluble metabolic components in order to prevent the misinterpretation of bulk isotope data (MacKenzie et al. 2017). Ephyrae samples (250–1000 µm) were allocated a maximum size diameter of 1 mm and were pooled (by identical sampling dates) and dried. Dried tissue was pulverized to a fine powder using a cleaned mortar and pestle. Subsamples of 2.1–2.3 mg were then weighed and sealed in tin cups for later analysis.

To assess the relative trophic position of ephyrae and medusae of *Chrysaora*; this study analysed $\delta^{13}C$ and $\delta^{15}N$ of fish, zooplankton (crustaceans and other jellyfish) and plants/algae collected from

Walvis Bay lagoon (as summerised in Table 5.10). These taxa were identified to the lowest taxonomic level, rinsed with distilled water and their tissue (whole bodies or muscle) dried for isotope analysis.

In order to provide a broad overview of the trophic structure of the northern Benguela ecosystem, two methodological approaches were applied to obtain the baselines needed to calculate trophic levels. (i) The mean δ^{15}N values (6.13‰; trophic level = 1) of suspended particulate organic matter (POM) taken along a transect (all depths combined) off Walvis Bay (23°S; 14–11°30′E) (see Koppelmann et al. 2013), and (ii) the mean δ^{15}N values (11.3‰; trophic level = 2) of two mytilid bivalve species (*Semimytilus algosus* and *Mytilus galloprovincialis*) as primary consumers.

The trophic level values (TL) of the various consumer organisms were then calculated based on the following equation, modified from Post (2002):

$$\text{Trophic level} = [(\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta\delta^{15}N] + \lambda \quad (1)$$

where $\delta^{15}N_{consumer}$ is the value of each consumer, which is measured directly; $\delta^{15}N_{base}$ is the baseline value of the food web; $\Delta\delta^{15}$N is the enrichment in δ^{15}N per trophic level, and λ is the trophic position of the organism used to estimate the $\delta^{15}N_{base}$.

The relative trophic level of consumer organisms was set at 3.4‰ between consecutive trophic levels (Minagawa & Wada 1984; Hobson & Welch 1992; Post 2002). Stable isotope values of field samples from other northern Benguela studies (Teuber 2009; Jung 2010; van der Bank et al. 2011; Iitembu et al. 2012; Huenerlage & Buchholz 2013; Koppelmann et al. 2013; Schukat et al. 2014) were selectively added to the current data set.

Stable isotope analyses

Isotope samples were measured for δ^{13}C and δ^{15}N at the University of Pretoria (UP) and University of Cape Town (UCT). UP used a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany). In-house standards applied were Merck Gel and DL-Valine: calibrated against the international standards of the National Institute of Standards & Technology (NIST) – NIST 1557b (bovine

liver), NIST 2976 (mussel tissue) and NIST 1547 (peach leaves). Measurement error (SD) was ±0.09‰ for $\delta^{13}C$ and ±0.07‰ for $\delta^{15}N$.

UCT used a Flash 2000 organic elemental analyser passed to a Delta V Plus isotope ratio mass spectrometer (IRMS) via a Conflo III gas control unit (all equipment supplied by Thermo Fischer, Bremen, Germany). In-house standards applied were Merck Gel, seal bone and DL-Valine: calibrated against the International Atomic Energy Agency (IAEA) standards. Measurement error (SD) was ±0.102‰ for $\delta^{13}C$ and ±0.034‰ for $\delta^{15}N$.

Nitrogen is expressed in terms of its value relative to atmospheric nitrogen (N_2), whereas carbon is expressed in terms of its value relative to Vienna Pee-Dee Belemnite (VPDB). All stable ratios are expressed in delta notation using a per mille scale using the standard equation:

$$\delta X\ (‰) = [(R\ sample\ /R\ standard) - 1] * 1000 \quad (2)$$

where X = $\delta^{15}N$ or $\delta^{13}C$ and R = $\delta^{15}N/^{14}N$ or $\delta^{13}C/^{12}C$, respectively.

Lipids were not extracted prior to stable isotope analysis in order to prevent any bias of $\delta^{15}N$ (Hobson et al. 2002; Mintenbeck et al. 2008). However, the presence of lipids can cause depletion in $\delta^{13}C$ irrespective of the carbon source (McConnaughey & McRoy 1979). Therefore, the lipid normalization equation of Post et al. (2007) was used for aquatic animals when the C:N ratio of individual samples >3.5 (n = 110, of which 41 were jellyfish samples):

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 * C{:}N \quad (3)$$

STATISTICAL ANALYSIS

All statistical tests were performed using IBM SPSS v23 Statistics software (SPSS Inc., Chicago, USA). Prior to analysis, the normal distribution and homogeneity of variance of the data sets were tested using Shapiro-Wilk's and Levene's tests, respectively. If the data violated either test, the data were $\log_{10}$ transformed and non-parametric tests were used. *Chrysaora africana* was excluded from most of the analysis due to an insufficient sample size collected (Chapter 2, 3 and 4).

Tissue-specific differences in stable isotope composition (δ^{15}N and δ^{13}C), by season and size-class interval (per 10 cm), were explored (when represented by ≥3 samples per category) for each *Chrysaora* species using the Kruskal-Wallis test or Mann-Whitney test. The Kruskal-Wallis test was followed by Dunn's post-hoc test on each pair of groups when significant differences were detected. For these multiple pair tests, SPSS makes a Bonferroni adjustment to the *p*-value: by multiplying each Dunn's p-value by the total number of tests being carried out. **It must be stressed that owing to the unequal distribution of samples across size class, season and tissue, not all comparisons could be made in all instances**.

The overall effect of medusa size (ephyrae included for *C. fulgida*) on isotope ratios of each tissue type between the two *Chrysaora* species was examined by plotting δ^{15}N, δ^{13}C and C:N values against BD and fitting linear regressions when ≥12 data points were available. In addition, the seasonal effect on size within and between tissue types was examined by plotting δ^{15}N, δ^{13}C and C:N values against BD, fitting linear regressions and testing for differences between the regression coefficients (Zar 2014).

Spatial differences in stable isotope composition (δ^{15}N and δ^{13}C) of the oral arms, restricted to autumn and those size classes commonly represented in all data sets, were explored using a Kruskal-Wallis test to compare the effect of station (coastal inshore: this study, mid-shelf: 23°20'S, 14°12'E and offshore: 23°30'S, 13°40'E) on δ^{15}N and δ^{13}C for *Chrysaora fulgida.* These tests were followed by the relevant post-hoc test. Collected samples of this study represented the coastal inshore station, whereas the mid-shelf and offshore stations were represented by the stable isotopes values obtained from van der Bank et al. (2011).

Size-specific differences between species in stable isotope composition (δ^{15}N and δ^{13}C) of the bell tissue were tested using an Independent-samples Mann-Whitney test. Collected samples were appropriately pooled in order for strict comparisons to be made with the limited data for *Chrysaora africana*.

RESULTS

Tissue-specific effects (gonad, bell and oral arm) in stable isotope composition

In the case of *Chrysaora fulgida* (Table 5.2) collected during spring, there were no significant differences in $\delta^{13}C$, $\delta^{15}N$ or C:N ratios between bell -, oral arm – and gonad tissues of (the only consistently represented) size classes 400.2–500.1 mm and 500.2–600.1 mm. The respective results, in each case, were $\delta^{13}C$ ($H(2) = 3.141$; $p = 0.208$; $H(2) = 0.399$; $p = 0.819$), $\delta^{15}N$ ($H(2) = 0.823$; $p = 0.663$; $H(2) = 4.333$; $p = 0.445$) and C:N ratios ($H(2) = 2.650$; $p = 0.266$; $H(2) = 4.818$; $p = 0.090$).

Neither were there any significant differences in the same measures between bell and oral arm tissues during winter (size class 200.2–300.1 mm) and autumn (size classes 20.0–100.1 mm, and 100.2–200.1 mm). The respective results, in each case, were $\delta^{13}C$ ($U_{200.2–300.1\ mm} = 10.0$, $p = 0.686$; $U_{20.0–100.1\ mm} = 8.0$, $p = 0.476$; $U_{100.2–200.1\ mm} = 35.0$, $p = 0.181$), $\delta^{15}N$ ($U_{200.2–\ 300.1\ mm} = 14.0$, $p = 0.114$; $U_{20.0–100.1\ mm} = 20.0$, $p = 0.114$; $U_{100.2–200.1\ mm} = 23.0$, $p = 0.724$). and C:N ratios ($U_{200.2–300.1\ mm} = 11.0$, $p = 0.486$; $U_{20.0–100.1\ mm} = 9.0$, $p = 0.610$; $U_{100.2–200.1\ mm} = 29.0$, $p = 0.573$).

For *Chrysaora africana* (Table 5.2), the C:N ratios ($U_{200.2–300.1\ mm} = 20.0$, $p = 0.016$) were significantly lower in bell (Median (*Mdn*) = 3.290) than oral arm (*Mdn* = 3.762) tissue during autumn, for animals in size classes 200.2–300.1 cm. As they were too for $\delta^{15}N$ value ($U_{200.2–300.1\ mm} = 19.0$, $p = 0.032$: $Mdn_{bell} = 1.052$, $Mdn_{oralarm} = 1.112$). However, no significant differences were detected for $\delta^{13}C$ ($U_{200.2–300.1\ cm} = 14.0$, $p = 0.413$).

Size effects

Overall, there was a significant negative relationship between $\delta^{15}N$ and BD, and a significant positive relationship between $\delta^{13}C$ and BD, for the bell tissue of both species (Table 5.3, Fig. 5.1). Pronounced differences were apparent in the slopes of the relationships by species. There was a clear negative change in the C:N ratio for bell tissue with increasing individual size for *Chrysaora africana*. By contrast, there were no significant relationships between $\delta^{15}N$ and BD, and $\delta^{13}C$ and BD, when using oral arm and gonad tissues of *Chrysaora fulgida*. Interestingly, the C:N ratios were significantly correlated in the case of oral arm tissues (negative) and gonads (positive) (Table 5.3, Fig. 5.1). In general, plots of the residuals were approximately normally distributed, and no clear patterns in the scatter of data were visible. Significant size-related shifts in both stable isotope signatures, largely independent of time, were evident for both *Chrysaora* species. Although there were differences between the species: bell tissue

values of δ^{15}N and δ^{13}C in *Chrysaora fulgida* showed a difference of ~1‰ and ~1.6‰ (respectively) between ephyrae and the largest medusae, whereas in the case of *Chrysaora africana* differences between the largest and smallest medusae varied between ~1.5‰ and ~2.5‰.

Seasonal effect in *Chrysaora fulgida*

Overall, the mean δ^{15}N for bell tissue (Table 5.4) was the highest during winter and the most depleted during summer; δ^{13}C was the highest during spring and the most depleted during autumn and the C:N ratio was the highest during spring and the lowest during winter. However, given that there is a strong correlation between isotope signature and individual size, and the very unequal representation of size classes amongst seasons, species and tissue types (Tables 5.5), it is not easy to make robust conclusions about the data. That said, bell tissue was sampled in all seasons. Significant relationships between size and δ^{15}N of bell tissue were apparent only in summer and spring (Table 5.6, Fig. 5.2), however there were no significant differences between the slopes of these two seasons (t = 0.446; $t_{0.05(2),42}$ = 2.018). Similarly, significant relationships between bell size and δ^{13}C were seen only in winter and spring (Table 5.6, Fig. 5.3), with no significant differences between their slopes (t = -0.485; $t_{0.05(2),42}$ = 2.018). The relationship between bell diameter and the C:N ratio was significant only during summer and winter, being positive in the former and negative in the latter (Table 5.6, Fig. 5.4) – with their slopes being significant different from each other (t = 3.421; $t_{0.05(2),26}$ = 2.056). Inter-tissue comparisons could only be conducted during spring, with significant relationships being observed only in the case of bell tissue (δ^{13}C, positive; δ^{15}N, negative). A positive and significant relationship was also seen for C:N ratio with bell size only for gonadal tissue (Table 5.6, Fig. 5.5).

Spatial effect in oral tissue of *Chrysaora fulgida*

Overall, the offshore station (Table 5.7) had the most depleted δ^{15}N and the largest sized medusae (mean: 270 mm), whereas the coastal inshore station showed the highest δ^{15}N and the smallest sized medusa (mean: 120.4 mm). In case of δ^{13}C, the mid-shelf station had the highest signal whereas the coastal inshore station showed the most depleted values. However, given the apparent influence of seasonality on data, it is perhaps more appropriate to test for spatial variability in isotope signals at a

common time of year. Given that the collections of van der Bank et al. (2011) were made during autumn (31 March–10 April 2008) on oral arm tissue, analysis here are confined to the same seasonal period and tissue type. For the δ^{15}N of the 50.1–100.1 mm class interval, a significant difference between the mean ranks of at least two pairs of station groups was detected for δ^{15}N ($H(2) = 8.342$; $p = 0.015$). The δ^{15}N value for coastal inshore (*Mdn* = 1.084) was significantly higher ($p = 0.014$) than that of the mid-shelf station (*Mdn* = 0.984), whereas no other significant differences were illustrated between the rest of the station combinations (Tables 5.1). No significant differences were observed between any stations for δ^{13}C ($H(2) = 5.606$; $p = 0.061$).

Interspecific effects and relative trophic position of *Chrysaora* species and other jellyfish within the Benguela system

Size-specific comparisons of bell tissue between the two *Chrysaora* species indicated only significant differences in δ^{15}N (Tables 5.8 and 5.9) between the size classes of 60–130 mm: *Chrysaora fulgida* (*Mdn* = 10.5‰) was significantly more depleted ($U = 50.0$, $p = 0.049$) than *Chrysaora africana* (*Mdn* = 12.07‰). For δ^{13}C, size-specific differences were present only between (Table 5.9) the size classes of 250–350 mm: *Chrysaora fulgida* (*Mdn* = -17.31‰) was significantly more depleted ($U = 60.0$, $p = 0.021$) than *Chrysaora africana* (*Mdn* = -15.40‰). The C:N ratios of the different size classes did not exhibit significant differences between two *Chrysaora* species (Table 5.8).

For this study, the carbon stable isotope values (δ^{13}C) of jellyfish ranged from -15.1‰ for *Aequorea forskalea* to -18.6‰ for ephyrae of *Chrysaora fulgida* (Table 5.10; Fig. 5.6). Nitrogen stable isotope values (δ^{15}N) of jellyfish ranged from 9.9‰ for *Aequorea forskalea* to 11.8‰ for both *Chrysaora africana* (size range: 60–130 mm) and *Chirodropus gorilla*.

Stable isotope ratios (δ^{15}N, δ^{13}C) of various taxa of the northern Benguela food web and calculated trophic levels are shown in Table 5.10. Mean δ^{15}N values varied greatly among taxa (4.1–15.4‰). The most depleted δ^{15}N values were observed for the herbivorous *Limacina inflata* and POM whereas the most enriched values were found in fish. In the entire data set of this study, mean δ^{15}N values ranged from 9.6‰ for cumaceans to 13.8‰ for a species of opisthobranch, and mean δ^{13}C values ranged from -26.6‰ for *Sarcocornia species* to -12.30‰ for *Ulva* species.

The application of the two baseline approaches for the calculated trophic levels (TL) produced a maximum difference (between TLi and TLii) of 0.5, with TLi constantly being higher, between the calculated trophic level of a species (Table 5.10). Comparing these trophic levels (TLi and TLii) with those of the reference studies (TLo), differences of 0.1 to 2.2 in TLs were obtained between the calculated trophic level of species while jellyfish differences ranged between 0.6 and 2 TLs.

DISCUSSION

The interpretation of isotope ratios is not simple and is fraught with multiple sources of variation in isotopic signatures and consumer-resource discrimination (Boecklen et al. 2011). Boecklen et al. (2011) summarised 46 sources of variation in the isotopic signatures of organisms by emergent factors (diet and trophic position), principal mechanistic factors (photosynthetic pathways and consumer-resource discrimination) and secondary mechanistic factors (properties of the consumer, properties of the resource, properties of the environment and analytical properties). Moreover, each category of these "properties" can be partitioned further in order to describe the rest of the 42 identified sources of variation (see Boecklen et al. 2011). Naturally, this variation in isotopic signatures makes the identification of one specific source of variation and the comparison across studies problematic since multiple factors could be involved. Especially in the field when ecosystem complexities are considered, such as the assimilation of multiple food sources that vary temporally and spatially in isotopic content or variable growth and turnover rates in relation to a shift in the isotopic baseline (O'Reilly et al. 2002; Schmidt et al. 2003; Perga & Gerdeaux 2005).

Tissue-specific effects

The present study did not investigate differences in stable isotope ratios of whole body tissue of either *Chrysaora* species, owing to their very large bell sizes and fragile oral arms, which effectively prevented them from being dried whole. Nonetheless, some inter-tissue differences were detected for *Chrysaora africana,* but not for *Chrysaora fulgida.* Tissue-specific isotopic differences have been reported in other wild caught medusae such as *Phacellophora camtschatica* (Towanda & Thuesen 2006), *Aurelia* spp. (D'Ambra et al. 2014) and *Stomolophus meleagris* (Ying et al. 2012). The stable isotope signatures

of the different tissue types seemed to vary between species and within individuals of the same species. This is likely to reflect differences in lipid content (Lucas 1994; Arai 1997; Lorrain et al. 2002; Milisenda et al. 2018), amino acid composition (Schmidt et al. 2004), tissue turnover rates and fractionation values (Tieszen et al. 1983; Miller 2006; D'Ambra et al. 2014).

Information about tissue turnover rates for jellyfish is scant: in the case of *Aurelia,* bell tissue and "whole body" reached stable isotopic steady state on a laboratory-fed diet between 18 to 20 days (based on a half-life of ~9–10 days) (D'Ambra et al. 2014). Interestingly, no differences in δ^{15}N and δ^{13}C of bell and whole *Aurelia* tissues were detected between wild-caught and laboratory-fed (after reaching steady state), except for gonadal (for δ^{13}C) and oral arm (δ^{15}N and δ^{13}C) tissues (D'Ambra et al. 2014). Irrespective of the mechanism driving tissue type differences, bell tissue was identified by D'Ambra et al. (2014) as the most suitable body part representative of the stable isotope composition in *Aurelia*.

Studies that also include jellyfish (Frost et al. 2012; Koppelmann et al. 2014; Schukat et al. 2014; Nagata et al. 2015), generally apply stable isotopes fractionation values of ~3.4‰ for nitrogen and 0–1‰ for carbon: values that were established from animal muscle or whole-body samples (Minagawa & Wada 1984; Post 2002; Sweeting et al. 2007). However, the only experimental study of jellyfish trophic fractionation indicated values of ~4‰ for C and ~0.1‰ for N in whole *Aurelia* spp. medusae (D'Ambra et al. 2014). MacKenzie et al. (2014) has suggested that these unusual fractionation values stem from technical problems arising during the preparation and handling of jellyfish samples.

Several studies have indicated how irregularities in δ^{13}C and δ^{15}N values for the same species can stem from the implementation of different pre-analytical protocols (Feuchtmayr & Grey 2003; Sarakinos et al. 2002; Syväranta et al. 2008; Carabel et al. 2009). In the case for jellyfish, a uniform and pre-analytical standardised processing protocol needs to be established for stable isotope analysis. Data from several studies (Fleming et al. 2011; D'Ambra et al. 2014; Kogovšek et al. 2014; MacKenzie et al. 2014) have shown highly variable effects due to different sampling protocols that lead to biases in the estimation of the trophic levels of jellyfish, especially when attempting to compare trophic relationships among studies (Boecklen et al. 2011). Significant errors can be introduced into diet estimates when inaccurate fractionations are utilised, especially when the isotopic separation among prey sources is small (Vander Zanden & Rasmussen 2001). Hence, as isotopic studies become more universally applied

across a broader range of jellyfish tissue types, it is essential to have robust and valid measures of fractionation available for species-specific tissue types.

Size effects

Stable isotope values of δ^{13}C and δ^{15}N in ephyrae of *Chrysaora fulgida* reflect a diet enriched in δ^{15}N and depleted in δ^{13}C, relative to the largest medusae in this dataset. This indicates that polyps might feed potentially at a higher trophic level than the largest medusae, corresponding perhaps to a shift in diet due to a different foraging habit/habitat.

In attempting to interpret the size-dependent changes in δ^{15}N and δ^{13}C, it is necessary to consider the environment occupied by individuals of different sizes. Ephyrae (and presumably polyps) are located in shallow waters (Chapter 2), whilst larger animals are distributed further offshore (Fearon et al. 1992; Pagès 1992; Brierley et al. 2005), being returned onshore under appropriate winds.

^{15}N: Since the polyp is benthic and releases ephyrae, the newly released latter would be expected to carry the stable isotope signature of the former. Benthic polyps are likely to be exposed to significantly greater amounts of detritus than pelagic animals and, in general, organic matter that sinks and settles on the sea bottom undergoes degradation that results in increased δ^{15}N values (Saino & Hattori 1980, 1987; Altabet & McCarthy 1985). Such could account, in part, for the comparatively high values for δ^{15}N in ephyrae of *Chrysaora fulgida*, and small medusae of both species. Further, the small size of ephyrae limits what can be eaten (Costello & Collin 1994; Sullivan et al. 1994, 1997; Gordoa et al. 2013; Lilley et al. 2014a), and there will be a tendency for the diet to be dominated by microplankton, components of the microbial loop and hydrozoans (Sullivan et al. 1994; Båmstedt et al. 2001; Costello & Colin 2002; Parsons & Lalli 2002; Boero et al. 2007; Zheng et al. 2015; Zoccarato et al. 2016). In addition, the ephyrae in the Bay area will most likely encounter and utilize larvae of benthic and intertidal organisms, such as those of bivalves and decapods (Flynn & Gibbons 2007), more frequently than offshore medusae.

Båmstedt et al. (2001) concluded that the ephyrae of *Aurelia aurita* can catch and feed on phytoflagellates, large copepods and suspended particulate organic matter. Zoccarato et al. (2016) have shown that the ephyrae of *Aurelia aurita* can influence the microplankton community by causing large

declines in the abundances of the more motile microplankton groups (tintinnids, Dinophyceae and aloricate ciliates), with smaller reductions in Bacillariophyceae and Mediophyceae. Olesen et al. (1994) have demonstrated that rotifers such as *Brachionus plicatilis* can be an important prey source for ephyrae of *Aurelia aurita* (4 mm in size) in Kertinge Nor, Denmark. Culturing experiments have verified that ciliates serve as a food source for the ephyra stage of *Aurelia coerulea,* however, the importance of this food source diminished at the meta-ephyra stage (Kamiyama 2018). Sullivan et al. (1994) have found that small (<12 mm diameter) *Aurelia aurita* medusae prey mostly on hydromedusae whereas larger medusae (up to 30 mm diameter) consumed higher copepod quantities in Narragansett Bay, Rhode Island, USA. Matsakis & Conover (1991) have shown that large quantities of the *Rathkea octopunctata* (hydromedusa) were ingested by *Aurelia aurita* medusae (ranging from 10 to 100 mm diameter) in the Bedford Basin (Nova Scotia, Canada). Towanda & Thuesen (2006) have shown, in southern Puget Sound (Washington, USA), that small hydromedusae were generally more enriched in δ^{15}N than the scyphozoan *Phacellophora camtschatica.* Further, some hydromedusae can prey on ciliates (Colin et al. 2005; Morais et al. 2015; Sutherland et al. 2016), and newly released *Obelia dichotoma* medusae (from the Ionian coasts of Apulia, Italy) can concentrate bacteria (*Escherichia coli*) in their gastric system via active filter feeding (Boero et al. 2007). Personal observations confirm that ephyrae of both *Chrysaora* species can prey on hydrozoans. Thus small size, *per se*, is not a pre-requisite for a low δ^{15}N.

Gutiérrez-Rodríguez et al. (2014) verified through experiments that δ^{15}N trophic discrimination within the microbial part of the food web cannot always be adequately tracked, indicating that an individual's actual trophic position may be higher than that estimated from stable isotope analysis. In marine ecosystems, microzooplankton are considered to be the main grazers of small phytoplankton; they can serve as an energy link between pico- and nano-sized particles, and mesozooplankton; they are bacterivores; and they can represent a significant portion of the mesozooplankton diet (Fileman et al. 2011). Nanozooplankton are key elements of the microbial food web as they can consume bacteria and picoplankton (Fileman et al. 2011), whereas nano- and picoplankton (<5 µm in size) are important consumers of bacteria in the temperate Atlantic Ocean (Zubkov & Tarran 2008).

The negative relationship between δ^{15}N and body size observed here is in contrast to the results of almost all previous studies. In the case of medusae, a positive ontogenetic shift in δ^{15}N enrichment with

body size has been reported for *Lychnorhiza lucerna,* but this was not observed for *Chrysaora lactea*, *Mnemiopsis leidyi* and *Olindias sambaquiensis* off the Cananéia Lagoon Estuarine System (Nagata et al. 2015). Similar positive ontogenic patterns for δ^{15}N have been described for *Aurelia aurita* and *Cyanea capillata*, but was not for *Cyanea lamarckii,* off Strangford Lough, North Ireland (Fleming et al. 2015). *Cyanea capillata*, sampled across the North Sea (limited to one summer season), exhibited a significantly positive but weak relationship between δ^{15}N values and weight (MacKenzie et al. 2014). In marine communities, it is expected for the δ^{15}N of marine animals of the same species to increase with body size (Lindsay et al. 1998; Graham et al. 2007; Polito et al. 2013), in part because of possible changes in habitat and prey field (Lindsay et al. 1998; Tanaka et al. 2010; Iitembu et al. 2012; van der Lingen & Miller 2014; Turner Tomaszewicz et al. 2017) as well as behaviour (Mendes et al. 2007; van der Lingen & Miller 2014; Turner Tomaszewicz et al. 2017) and physiology (Lindsay et al. 1998; Jennings et al. 2002; Mendes et al. 2007; Polito et al. 2013) – as such emanates from the nature of "big-eats-small" characteristic of marine food webs (Cohen et al. 1993; Fry & Quinones 1994; France et al. 1998; Jennings et al. 2001, 2002).

Exceptions do exist, however, albeit not yet demonstrated for medusae. Bode et al. (2003) showed a significant negative relationship between δ^{15}N and size for *Sardina pilchardus* (total length ≥180 mm) in the upwelling ecosystem of Galicia (NW Spain), and interpreted such a relationship as the consequence of the increasing consumption of phytoplankton less enriched in ^{15}N than zooplankton prey. However, in a follow-up paper, Bode et al. (2007) reported that the previous significant negative relationship became insignificant due to the large variability in diet when a broader spatial-temporal resolution of the dataset were considered. Carlisle et al. (2012) reported a negative relationship between individual length and δ^{15}N of muscle tissue in the white shark (*Carcharodon carcharias*), from the NE Pacific. This was suggested to reflect the ontogenetic changes in habitat use related to the onset of maturity, because it is widely understood that white sharks are primarily piscivorous at lengths <2 m, whilst animals >3 m feed on marine mammals (Tricas & McCosker 1984; Klimley 1985; Compagno 2001). In this particular case, however, Carlisle et al. (2012) argued that the smallest sharks resided within the coastal waters of the California Current and foraged mainly in the productive coastal food webs that are enriched in δ^{13}C and δ^{15}N and on attaining maturity moved offshore and consumed offshore prey (Carlisle

et al. 2012). Satellite tagging data has shown that juvenile white sharks are found in nearshore waters, while adults are wide-ranging, with extensive periods of oceanic travel and distinct oceanic and coastal visits (Boustany et al. 2002; Dewar et al. 2004; Bonfil et al. 2005). Li et al. (2016) described a negative relationship between δ^{15}N and age in the silky shark *Carcharhinus falciformis* in the NE central Pacific, which was argued to reflect changes in habitat use and preference by different life stages and genders. After birth, juvenile silky sharks switched from coastal waters to offshore and pelagic habitats (Dagorn et al. 2007; Bonfil 2008), and their diets changed from being dominated by jumbo squid (*Dosidicus gigas*) to chub mackeral (*Scomber japonicus*), with female sharks feeding on cephalopods (Cabrera-Chávez-Costa et al. 2010).

Similar arguments can be advanced here. After the release of ephyrae from the benthic polyp, the former is moved from coastal inshore waters via Ekman transport offshore to the outer shelf. As animals increase in size they typically move further offshore and into deeper water, and detrital inputs to the diet likely decrease – at least at the surface. Further, their food entrapment surfaces (tentacles and oral arms) become progressively larger and more widely spaced (Chapter 3), and although not tested, it is likely that in the presence of an otherwise abundant food, only larger prey items will be ingested. Larger medusae thus occur in areas where mesozooplankton dominate communities (Purcell 1989, 2003; Behrends & Schneider 1995; Brodeur et al. 2008b, 2014; Suchman et al. 2008; Shoji et al. 2009). Although the majority of copepods are likely to be omnivorous (Schukat et al. 2014; Ekau et al. 2018), communities in the northern Benguela upwelling region are dominated by herbivores (Table 13 in Mauchline 1998), such as species of *Calanoides, Rhincalanus, Pseudocalanus* and *Calanus* (Jarre et al. 2015; Verheye et al. 2016). As a consequence, the food chains leading to jellyfish will be shorter offshore than inshore, and hence it is expected that δ^{15}N will decline with body size.

^{13}C: Within an ecosystem, δ^{15}N reflects consumption of one species by another – there is a predictable enrichment with increasing trophic level (DeNiro & Epstein 1981; Minagawa & Wada 1984; Peterson & Fry 1987). Whilst δ^{13}C changes little across the food chain (typically <1‰; McCutchan et al. 2003), the actual values are largely driven by the original (autotrophic) source of carbon and therefore do not depend on the direct consumption of autotrophic material by the study organism (DeNiro & Epstein 1978; Fry & Sherr 1984; Hobson et al. 1995; France & Peters 1997). In marine systems, δ^{13}C values are

used to determine an individual's benthic as opposed to pelagic habitat utilisation due to differences in $\delta^{13}C$ fractionation during photosynthesis between benthic macro-algae and pelagic phytoplankton (France 1995; Cherel & Hobson 2007). Factors such as temperature and the rate of primary production can also effect $\delta^{13}C$ values in marine food webs - independent of trophic or habitat shifts (Hinga et al. 1994; Schell 2000; Jaeger & Cherel 2011). Different autotrophs have different amounts of $\delta^{13}C$ and this reflects a very complex array of those factors that influence the processes of photosynthesis and primary production (Hinga et al. 1994; France 1995; Leboulanger et al. 1995; Rau et al. 1997; Bouillon et al. 2011).

In general, C_3 terrestrial plants (-25‰ to -29‰) have very low $\delta^{13}C$ values (O'Leary 1988; Bouillon et al. 2011); marine phytoplankton (-24‰ to -18‰) have slightly higher values (Fry & Sherr 1984) and intertidal benthic macro-algae (-20‰ to -12‰) have slightly higher values still (France 1995; Bouillon et al. 2011). Diatoms have higher $\delta^{13}C$ values than dinoflagellates (Fry & Wainright 1991), and detritus is rarely more enriched or depleted than its source material (Schlacher & Woolridge 1996; Yang et al. 2014). As implied above, $\delta^{13}C$ values will vary with latitude (and hence temperature), being higher at the tropics than at the poles (Rau et al. 1982).

Both *Chrysaora* species show an enrichment of $\delta^{13}C$ with increasing bell diameter, suggesting that sources of production change with animal size. If we extend the arguments cited earlier regarding the likely cross-shelf distribution of different sized animals, then it is possible to explain the patterns observed by reference to changes in the cross-shelf environment. It could then be suggested that the less enriched $\delta^{13}C$ noted inshore reflects differences in temperature, periodic red-tides, as well as allochthonous inputs from the terrestrial environment. Terrestrially-derived organic matter has been described as a carbon source for the hydromedusa *Blackfordia virginica* in two estuaries located in southern Portugal (Morais et al. 2017). The Kuiseb River is a westward flowing ephemeral river that mouths into the Walvis Bay lagoon. It flows for a short period following heavy rainfall but rarely reaches the sea, and ends in the sandy riverbed of a large delta (Huntley 1985). The input of potential seepage of freshwater and brackish water should be considered, these water sources are likely to have depleted dissolved inorganic carbon $\delta^{13}C$ values relative to those in seawater (Peterson 1999). The Walvis Bay lagoon is shallow (<16.5 m) and sheltered (see Chapter 2; Delta Marine Consultants & CSIR 2009), water has a residence time period of half to one week in the Bay that is highly dependent on the winds (DANIDA 2003) and it supports a

surrounding vegetation dominated by *Sarcocornia,* in parts. The δ^{13}C values of *Sarcocornia* off South Africa have been documented as ~-25‰ (Froneman 2001) and in this study -26.6‰ (Table 5.10). The lagoon is subject to periods of very low water temperature associated with coastal upwelling (Hutchings et al. 2009), as well as periodic red-tides dominated by dinoflagellates (Pitcher et al. 2010; Chikwililwa 2014). By contrast further offshore, water temperatures are warmer and the water column is more stratified (Boyer et al. 2000; Cole & Villacastin 2000; Louw et al. 2016), allochthonous inputs will be reduced and phytoplankton communities are those of ageing upwelled waters (Hansen et al. 2014; Ekau et al. 2018).

These results are in contrast to many others, the results of which suggest that the δ^{13}C signature of particulate organic matter decrease with distance offshore, largely as a result of higher production inshore (Hill et al. 2006). Since benthic organisms are more ^{13}C-enriched than pelagic ones (France 1995; Kaehler et al. 2000), δ^{13}C values are expected to be higher in benthic than in pelagic species. That said, a positive correlation has been reported between δ^{13}C and size, and between δ^{13}C and respiration rates for *Pelagia noctiluca* off the Gulf of Trieste (Malej et al. 1993). A positive ontogenetic shift in δ^{13}C has also been shown for *Aurelia aurita* and *Cyanea capillata*, but not for *Cyanea lamarckii,* off Strangford Lough, North Ireland (Fleming et al. 2015).

Shifts in δ^{13}C enrichment are associated with a possible change in diet with size. Larger animals may become more enriched in heavy isotopes as a result of the selective respiration of lighter isotopes (Checkley & Entzeroth 1985); as a result of a diet shift due to a change in habitat use (Iitembu et al. 2012; van der Lingen & Miller 2014; Li et al. 2016) or because of differences in the turnover of organic matter associated with maintenance metabolism (Fry & Arnold 1982). Biochemical analysis has shown a declining size-related trend in *Aurelia* species for both protein and lipids (Lucas 1994). In the case of *Cyanea capillata*, sampled across the North Sea (albeit only from one summer), there was a strong, positive relationship between δ^{13}C and weight (MacKenzie et al. 2014). This relationship is believed to reflect the presence of a higher portion of glycine-rich collagen in the mesoglea tissue of smaller than larger medusae, since glycine is depleted in δ^{13}C comparatively to most other amino acids, and comprises almost 30% of the amino acid content of collagen (MacKenzie et al. 2014).

Seasonal effects

Seasonality does not seem to influence the relationship between size and either δ^{15}N or δ^{13}C of bell tissue in *Chrysaora fulgida* (Table 5.6; Fig. 5.2, 5.3). This is in contrast to the results of others. Temporal differences have been observed in δ^{13}C and δ^{15}N of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata*, from Strangford Lough, Northern Ireland, and this was interpreted to reflect seasonal changes in jellyfish diet rather than baseline shifts in the food web (Fleming et al. 2015). A seasonal shift in diet from a diatom-based food chain (April to June) to a detritus-based food chain (August to September) was reported for *Aurelia aurita* of the same size class (13–18 cm) off Seto Inland Sea, Japan (Fukuda & Naganuma 2001). Javidpour et al. (2016) reported temporal shifts of ~3‰ in δ^{13}C and ~4‰ in δ^{15}N for *Aurelia aurita* over a 4-month period in the W Baltic Sea, and these authors linked this to a dietary switch from pelagic mesozooplankton to benthic microplankton, and/or re-suspended organic particles from the benthos. Milisenda et al. (2018) showed, by way of stomach content and biomarker analyses, that *Pelagia noctiluca* shifted cyclically between carnivory and omnivory which was governed by the seasonal availability of prey, off the Strait of Messina (Sicily, Italy). The absence of a strong seasonal signal in either δ^{15}N or δ^{13}C off central Namibia can be explained by the considerable temporal heterogeneity in the environment observed (Hutchings et al. 2009).

Spatial variability

Medusa size changes with time of year (see Chapter 3 and 4) and with distance offshore. The overall size of animals sampled at the different stations (Table 5.7) indicates that smallest medusae (120.4 mm) occur in the coastal inshore area, bigger medusae (196.3 mm) are found in the mid-shelf station and the largest medusae (270.0 mm) occur offshore (Fearon et al. 1992; Pagès 1992; Brierley et al. 2005). Overall, the coastal inshore station had the highest δ^{15}N and most depleted δ^{13}C values when compared to the other stations. Although significant spatial differences in both stable isotope signatures were noted for similar sized animals in the same season, caution should be exercised in their interpretation owing to differences in methodology (Sweeting et al. 2006; D'Ambra et al. 2014). The samples of van der Bank et al. (2011) collected from the mid- and outer shelf were frozen after sampling and pre-treated by lipid extraction prior to stable isotope analysis. Both Fleming et al. (2011) and

MacKenzie et al. (2017) have shown that freezing jellyfish tissue can lead to an enrichment in δ^{15}N values. D'Ambra et al. (2014) showed that lipid extracted tissue of *Aurelia* spp. significantly affected the C:N ratio and isotope values of δ^{13}C and δ^{15}N. As such, Post et al. (2007) recommended the use of mathematical normalization for δ^{13}C to preserve the integrity of samples for δ^{15}N analysis, since lipid extraction methods cause fractionation in δ^{15}N (Pinnegar & Polunin 1999; Sotiropoulos et al. 2004).

Despite this, spatial variation in δ^{15}N of *Chrysaora fulgida* could reflect partitioning linked to spatially different isotopic baselines or food webs arising from different oceanographic features and environmental conditions in Benguela upwelling system. Ephyrae and juvenile medusae of *Chrysaora fulgida* appear have a strict nearshore distribution, whereas larger sized specimens are spread more widely across the shelf off Namibia (Fearon et al. 1992; Pagès 1992; Brierley et al. 2005). Thus, the animal would consume the sources and types of nitrogen available in its immediate location, which will be influenced by oceanographic features and environmental conditions. Given that medusae offshore are larger than those inshore, the spatial patterns simply reflect changes in size, as articulated above.

C:N ratios

C:N ratios are of interest as they reflect the lipid content (Post et al. 2007) of jellyfish. The low C:N ratios of *Chrysaora fulgida* and *C. africana* (bell tissue) are in broad agreement with data from other systems: 4.0:1 for *Pelagia noctiluca* (Faganeli et al. 1988); 3.1:1 to 4.2:1 for *Aurelia aurita*, *Stomolophus meleagris* and *Cyanea nozakii* (Ying et al. 2012); and 3.9:1 for *Crambione mastigophora* (Keesing et al. 2015). The study of Ying et al. (2012), off the Yellow Sea, demonstrated a positive relationship between size and C:N ratio for *Aurelia aurita,* but no relationship in the case of *Stomolophus meleagris*.

In this study, size related shifts were evident during summer and winter only for *Chrysaora fulgida*; positive during summer and negative during winter. Unambiguous interpretation of these data is difficult, but they imply that lipid content was higher in large medusae during summer than winter. The lipid content of different tissues is linked to their C:N ratios (DeNiro & Epstein 1977; Post et al. 2007), with gonadal tissues having slightly higher C:N ratios than somatic tissue. Milisenda et al. (2018) found significant biochemical differences between somatic and gonadal tissues of *Pelagia noctiluca*, where the total fatty acid concentration in the gonads was up to ten times higher than in the somatic tissues. *Pelagia*

noctiluca appears to be able to selectively assimilate and store fatty acids, which might be a vital reproductive strategy, especially when a part of the fatty acid energy is used for the gonad investment and the development of future ephyra stages. Taken together then this could imply that lipids are moved from one tissue type to another at different times of the year, though given that reproduction in this species occurs year-round, it is more likely to be an artefact of the sample size. More work is clearly needed in this area.

Interspecific differences

The results of this study reveal isotopic size-specific differences between the two *Chrysaora* species in terms of δ^{15}N and δ^{13}C, with post-hoc comparisons highlighting the differences between the size classes 6-13 cm for δ^{15}N, and 25-35 cm for δ^{13}C. The average trophic levels of *Chrysaora africana* were consistently higher than those of *Chrysaora fulgida* (Table 5.10; Fig. 5.6), and this can be interpreted in terms of interspecific differences in their diet (smaller medusae) and geographic distribution (larger medusae). C*hrysaora africana* appears to be a strictly nearshore species, with very few specimens caught offshore, whereas *Chrysaora fulgida* is spread more widely across the shelf (Uanivi et al. 2012, 2016; Uanivi & van der Plas 2013, 2014). These results suggest possible interspecific differences in predatory behaviour and/or life history strategies.

Typically, scyphomedusae capture prey using both 'passive ambush' and 'feeding current' strategies (Kiørboe 2011). Pulsation of the bell, which varies in shape and size between both *Chrysaora* species (see Neethling 2009; Ras 2016), generates feeding currents, with slower velocities normally associated with smaller individuals (Costello & Colin 1994,1995; Kiørboe 2011). Hence, species-specific differences might contribute to different prey being caught and ingested, depending on the escape velocities of putative prey. From personal observations, *Chrysaora fulgida* have much shorter tentacles and a less painful sting than *Chrysaora africana*, and its oral arms are much more folded and spiralled basally than those of *C. africana* (Ras 2016). The latter authors has also shown differences in the cnidome of *C. fulgida* and *C. africana,* suggesting possible feeding differences between the species. That said, the compliment of nematocysts present can potentially be modified due to growth or between

environments as the food preference or availability changes (Mariscal 1974; Peach & Pitt 2005; Wiebring et al. 2010).

Other factors that may account for the different trophic positions of the two species are the size of the capture surface area of the animal (Heeger & Möller 1987) and/or intra-guild predation (e.g. Hansson 1997a; Purcell 2003; Titelman et al. 2007). Larger specimens of *Chrysaora africana* inshore may not be feeding directly on zooplankton but may also be consuming other jellyfish (see Chapter 2). Personal observations reveal that ephyrae of *Chrysaora africana* can eat ephyrae of *Chrysaora fulgida*. Clearly, further experimental research is required to link trophic position with morphological characteristics, metabolism and reproductive status of each *Chrysaora* species.

The overall jellyfish values for δ^{15}N and δ^{13}C in this study ranged from 9.9 to 13.1‰ and -18.8 to -15.1‰, respectively. These values compare well with the results of other studies conducted in the northern Benguela ecosystem (Table 5.10), and fall within the broader range of published stable isotope values (Table 5.11; see also Logan & Dodge 2013) from other ecosystems.

Relative trophic position

While the δ^{15}N values reported here can be used to estimate the relative trophic levels of both *Chrysaora* species, caution should be taken when considering "suitable" baseline indicators. A key obstacle when estimating trophic positions of marine plankton is the identification of the baseline (Tamelander et al. 2009). Due to the matching size resemblance of phytoplankton and heterotrophic microzooplankton, it is currently impossible to separate each other in order to obtain a pure phytoplankton sample in order to characterize the δ^{15}N of primary producers (TL = 1). It is also problematic to classify a primary consumer, since most marine zooplankton are in fact omnivores (Calbet & Saiz 2005; Schukat et al. 2014; Bode et al. 2015).

Many uncertainties are introduced during the establishment of a baseline and its derived trophic levels when a food web is sustained by multiple sources of primary production, such as occurs in coastal environments (e.g. Moore & Semmens 2008; Layman et al. 2012). Species with short life cycles (phytoplankton and small zooplankton consumers) can show large temporal variation in δ^{15}N, which limits their use as reliable baseline indicators (Rolff 2000). In turn, longer-lived species (mussels and fish) have

tissue turnover rates ranging from months to years (Hesslein et al. 1993), and are more suitable baseline indicators as they reflect the integration of signals over longer time scales (Sweeting et al. 2005; Jennings et al. 2008). This is particularly so when accounting for seasonality in δ^{15}N, while being propagated through different food web pathways, are increasingly weakened and delayed with slow turnover rates of the consumer (Jennings et al. 2008). Sessile, filter-feeding bivalves that have a slow turnover rate are becoming increasingly used as a δ^{15}N baseline in food web studies (O'Reilly et al. 2002; Gustafson et al. 2007), following the suggestion of Cabana & Rasmussen (1996). These animals have protracted isotopic turnover rates that can integrate seasonal variability and high frequency - and small-scale variation in the isotopic signals of their diets (Lorrain et al. 2002; Fukumori et al. 2008).

Here, the δ^{15}N of bivalves ranged 10.3 to 12.7‰, while they varied between 8.85 to 9.6‰ off the West coast areas of southern Africa (Hill et al. 2006) and between 9.2 to 10.2‰ in Lüderitz (Namibia) (Kohler et al. 2011). Mussels are effective, non-selective filter-feeders that can filter large volumes of seawater and retain a wide size particle range (ca. 5–35 µm diameter) such as detritus, phytoplankton, bacteria and uneaten aquaculture fish feeds (Seiderer et al. 1984; Neori et al. 2004; Voudanta et al. 2016; Galimany et al. 2017). The mussel *Choromytilus meridionalis*, inhabiting the West Coast of South Africa, showed estimated filtration rates of 6.6 x 10^{10} bacterial cells day^{-1} during upwelling conditions and 2.79 x 10^{10} cells day^{-1} during downwelling conditions (Muir et al. 1986). During upwelling, when the phytoplankton and the detritus content of the water are low, the mussels become nutritionally stressed and produce a lytic style protein enzyme to lyse bacteria and ensure efficient absorption of ingested bacterial biomass through the digestive gland stomach and gut tissues. The production of this lytic substance is temperature-dependent (Seiderer 1983). However, during downwelling conditions, phytoplankton is introduced, bacterial lysis does not happen and bacteria filtered from the water are passed through the gut and voided by faeces (Muir et al. 1986). Therefore, bacteria may indeed contribute significantly to the nutrition of mussels and suggest that bivalves may be an appropriate vehicle to monitor the microbial loop in the northern Benguela.

The trophic positions calculated for jellyfish varied widely, depending on the baseline used: littoral mussels (this study) or POM (Koppelmann et al. 2013). Of the two baseline estimates, the use of bivalves resulted in lower estimates of trophic position than POM for both species of *Chrysaora* (Table 5.10). A

similar finding was noted by Tyler et al. (2016), who used intertidal mussels *Mytilus galloprovincialis* (from the southern Benguela) and phytoplankton (from the northern Benguela) as baselines. These results indicate that literature derived baselines cannot be used with any certainty to estimate trophic position.

In the northern Benguela ecosystem, most trophic levels have been estimated using POM, phytoplankton, primary consumers (copepods) (Bohata & Koppelmann 2013; Koppelmann et al. 2013, 2014; Schukat et al. 2014), or bivalves (Kohler et al. 2011; Iitembu et al. 2012), as δ^{15}N baselines. The type of baseline selected reflects the locality of the studied consumer, relative to the baseline species. The isotopic signatures of primary producers are subjected to greater variation than other trophic levels in an upwelling system because of constantly changing nutrient sources and concentrations (e.g. O'Reilly et al. 2002), and this can affect assessment of relative trophic level. The observations made here are in agreement with others that call for a more careful representation of isotopic baselines (Post 2002; O'Reilly et al. 2002; Gustafson et al. 2007; Layman et al. 2012), and literature-derived baselines should always be used with caution.

In conclusion, this study highlights some important trophic interactions of the different life stages of *Chrysaora fulgida*, and potential interspecies differences. There is still much unexplained variability. To properly reconstruct marine food webs and determine precise trophic levels of consumers of each life stage, it is important to use appropriate food web baselines (Post 2002). A sound knowledge of trophic discrimination factors, isotopic routing and tissue turnover rates is also needed (Gannes et al.1997). In addition, the growth rates of jellyfish of different life-stages need to be determined since both growth and metabolism can influence tissue turnover differentiation, as well as the relative ordering of turnover rates among tissues types (Xia et al. 2013a, 2013b; Busst & Britton 2018). However, stable isotope analysis is a complementary application; with its own limitations that can be overcome by combining it with other methods (e.g. stomach content- and fatty acid analysis: Milisenda et al. 2018; Tilves et al. 2018) in order to obtain more accurate information.

FIGURES

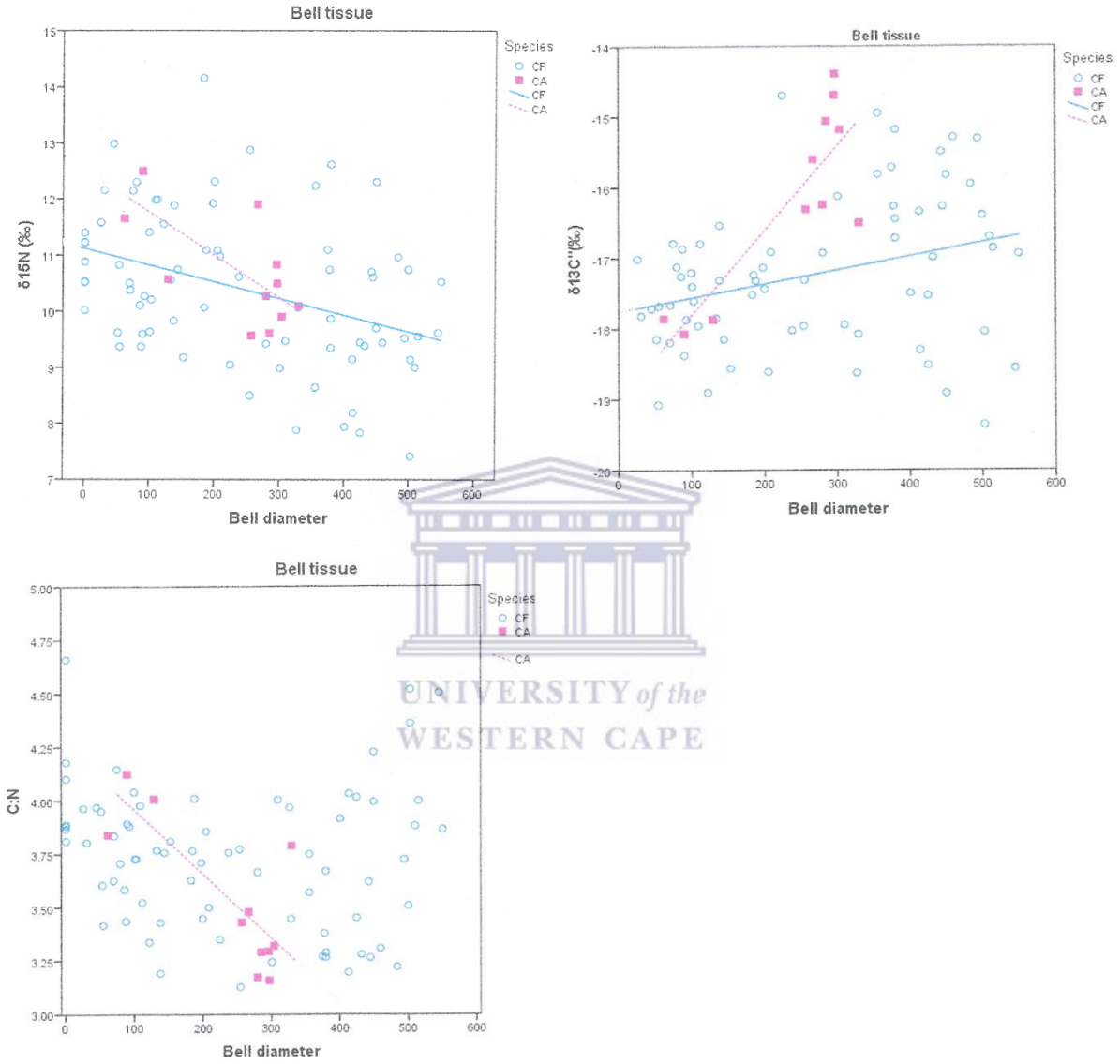


Figure 5.1. Scatterplots of $\delta^{15}N$ (‰), $\delta^{13}C$" (‰) and C:N ratio each respectively, for bell tissue by bell diameter (in mm) of *Chrysaora fulgida* (circles) and *Chrysaora africana* (squares). Fitted linear regressions shown (- - - - -, *C. africana*; ——, *C. fulgida*), and their descriptive parameters are given in **Table 5.3**.

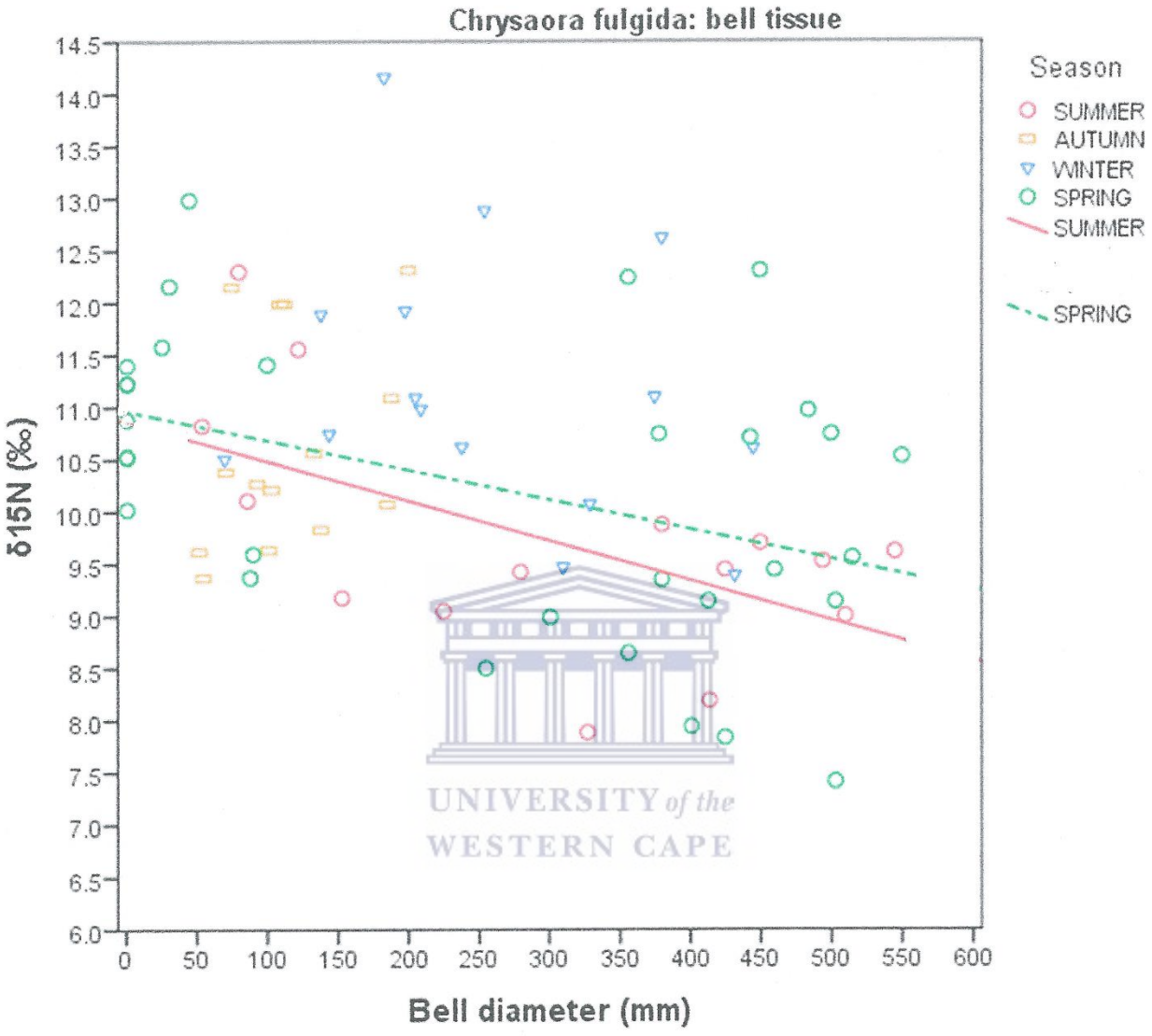


Figure 5.2. Scatterplots of individual isotope values of $\delta^{15}N$ (‰) by bell size, between seasons, for bell tissue for *Chrysaora fulgida*. Descriptive parameters are given in **Table 5.6**.

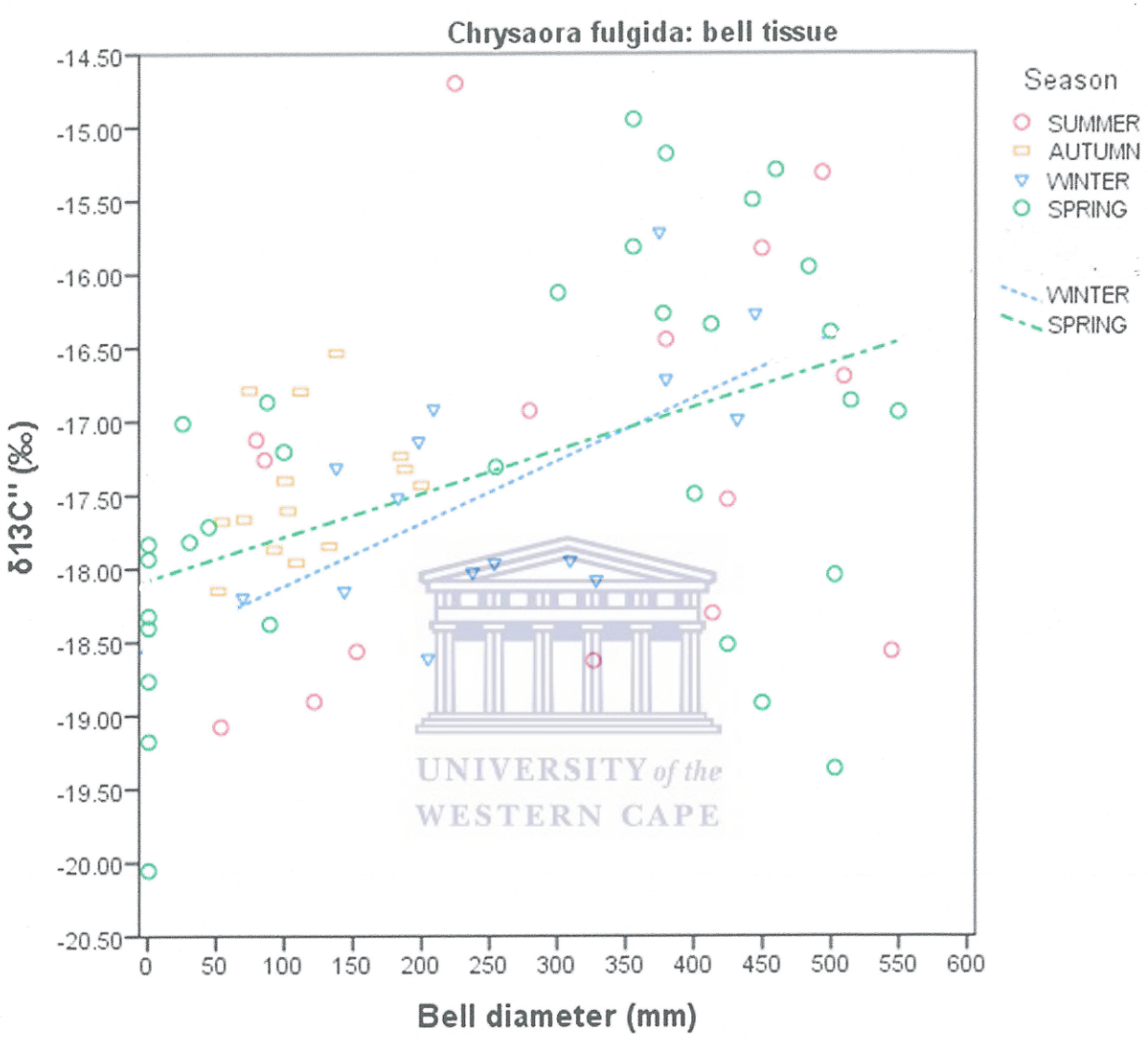


Figure 5.3. Scatterplots of individual isotope values of $\delta^{13}C$" (‰) by bell size, between seasons, for bell tissue for *Chrysaora fulgida*. Descriptive parameters are given in **Table 5.6**.

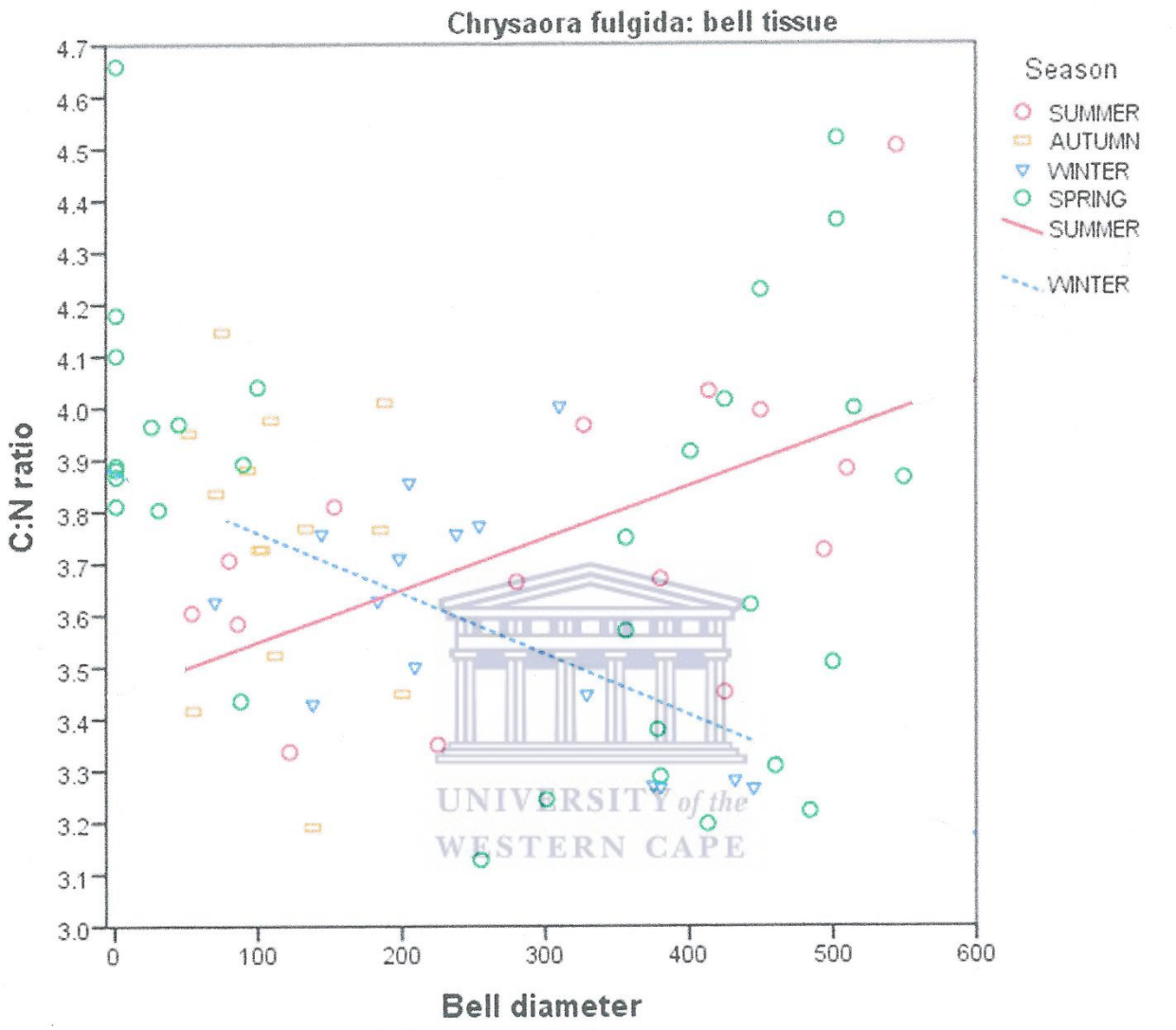


Figure 5.4. Scatterplots of individual isotope values of C:N ratio by bell size, between seasons, for bell tissue for *Chrysaora fulgida*. Descriptive parameters are given in **Table 5.6**.

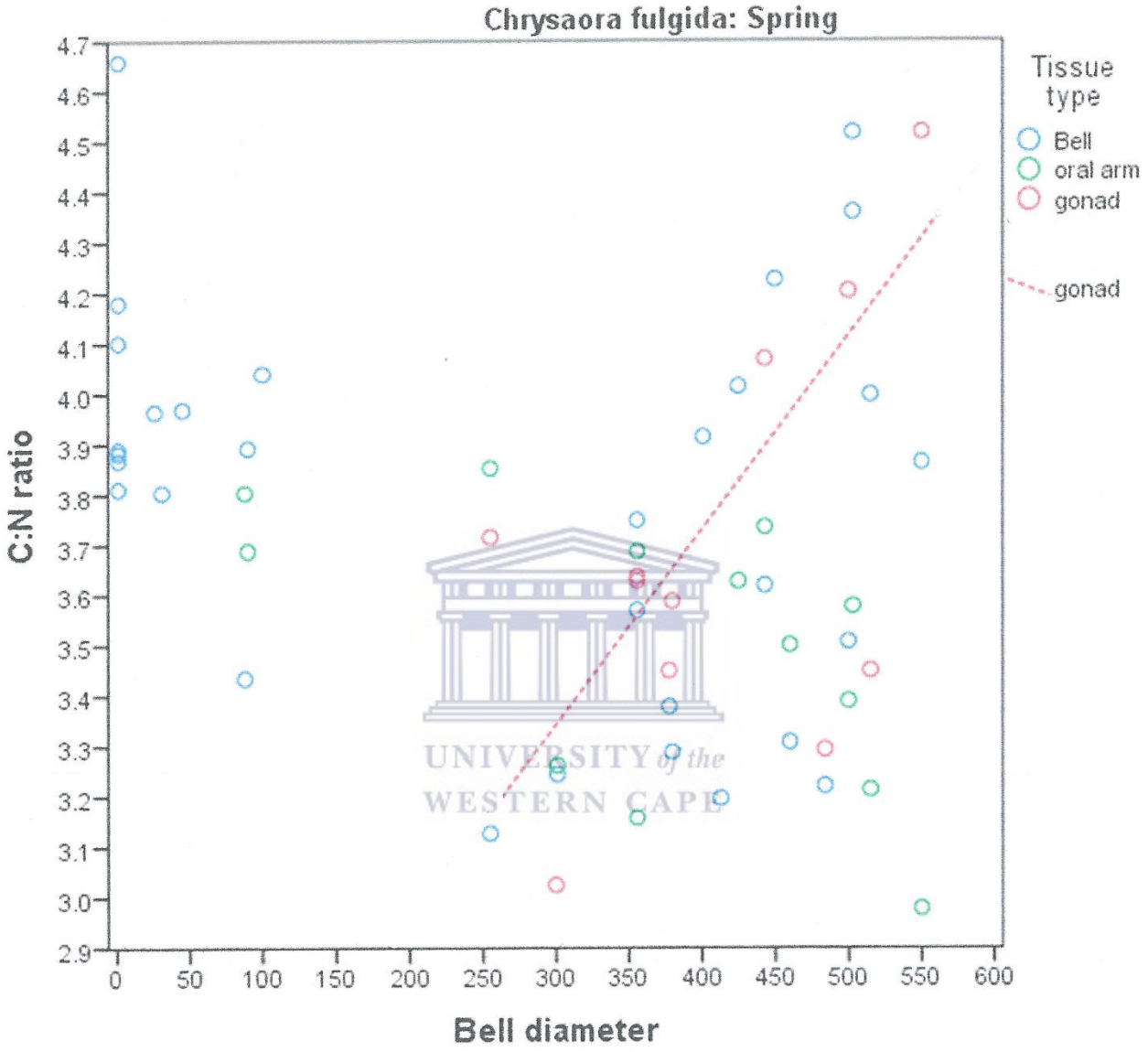


Figure 5.5. Scatterplots of individual isotope values of C:N ratio by bell size, between tissue types, during spring for *Chrysaora fulgida*. Descriptive parameters are given in **Table 5.6.**

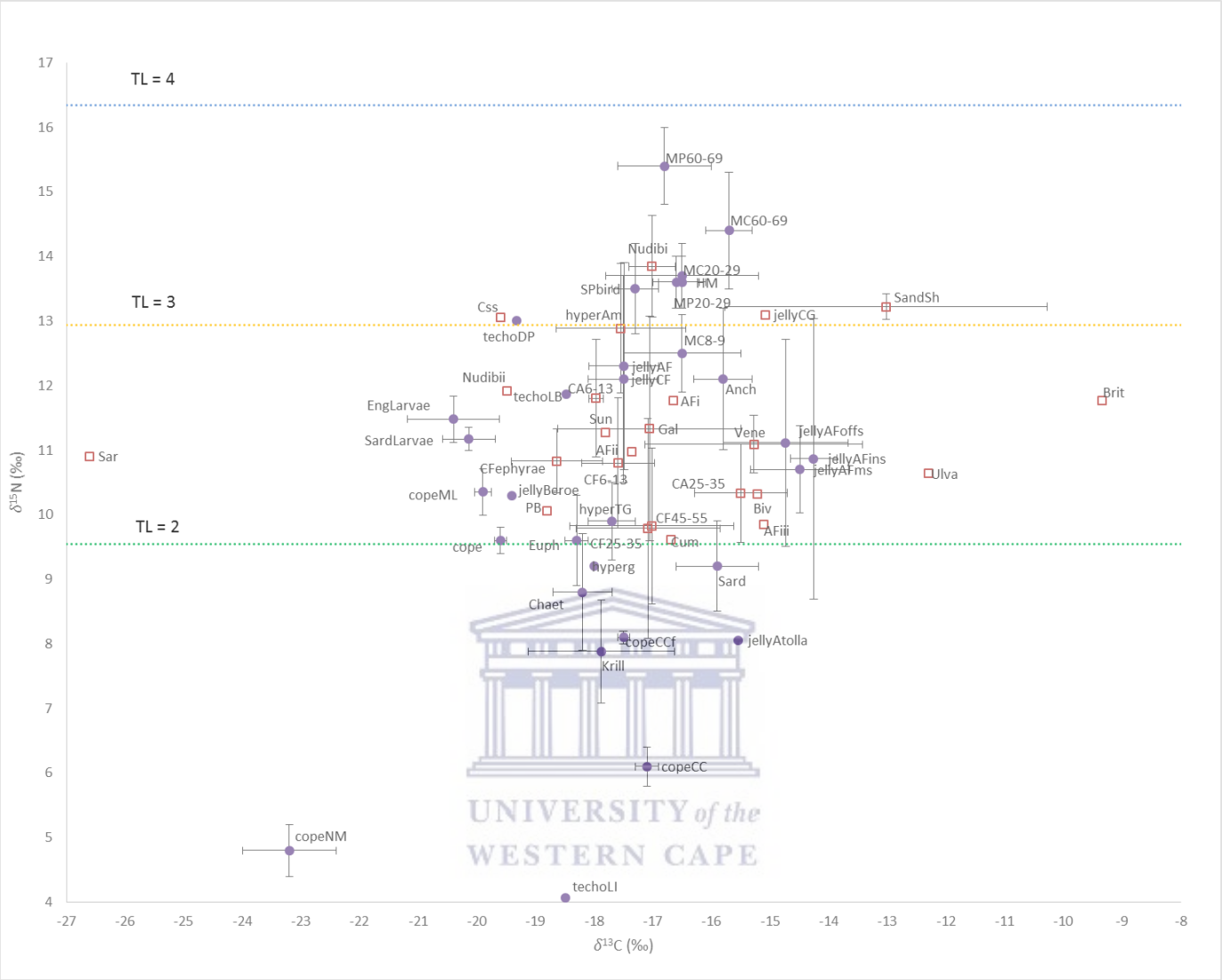


Figure 5.6. Mean (±SD) $\delta^{15}N$ and $\delta^{13}C$" by relative trophic level (TLi) (dashed lines) for jellyfish and various taxa sampled in this study (red squares) and from other northern Benguela studies (solid purple circles). Species abbreviations described in Table 5.10. Trophic levels (TLi) were calculated by applying a trophic enrichment value of 3.4‰ and using mean $\delta^{15}N$ of POM as baseline

TABLES

Table 5.1. Summary of individual and pooled samples per tissue type of wild-caught *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA) collected off Walvis Bay during the period 27 May 2012 to 26 January 2016. $\delta^{13}C$" represents the final isotope values after adjustment for lipid-normalization.

Tissue type	Sample type	Statistic	*Chrysaora fulgida*				*Chrysaora africana*			
			$\delta^{15}N$ (‰)	$\delta^{13}C$" (‰)	C:N	BD (mm)	$\delta^{15}N$ (‰)	$\delta^{13}C$" (‰)	C:N	BD (mm)
Bell	Individuals	n	38	38	38	38	5	5	5	5
		Mean	10.38	-16.89	3.67	350	10.85	-16.80	3.75	210
		Median	10.07	-16.94	3.67	380	10.10	-16.50	3.79	257
		SD	1.55	1.04	0.344	140	1.51	1.28	0.386	113
		Minimum	7.41	-19.36	3.13	26	9.57	-18.07	3.29	90
		Maximum	14.16	-14.95	4.52	550	12.49	-15.06	4.12	330
	Pooled	n	30	30	30	30	7	7	7	7
		Mean	10.33	-17.67	3.73	161	10.80	-15.98	3.47	234
		Median	10.32	-17.83	3.76	111	10.57	-15.61	3.32	280
		SD	1.21	0.92	0.286	125	0.73	1.42	0.332	97
		Minimum	7.88	-19.08	3.20	31	9.91	-17.87	3.16	62
		Maximum	12.30	-14.70	4.50	545	11.90	-14.40	4.01	304
Oral arm	Individuals	n	19	19	19	19	3	3	3	3
		Mean	11.07	-18.06	3.49	371	10.90	-16.51	3.70	302
		Median	11.17	-17.93	3.58	356	10.71	-16.56	3.70	292
		SD	1.36	0.99	0.276	125	0.91	0.64	0.004	24
		Minimum	8.71	-19.46	2.98	138	10.10	-17.12	3.70	285
		Maximum	13.86	-16.18	3.85	550	11.88	-15.84	3.70	330
	Pooled	n	15	16	16	16	3	3	3	3
		Mean	11.22	-18.07	3.84	164	12.53	-15.93	3.81	299
		Median	11.19	-17.74	3.77	111	12.54	-15.99	3.82	297
		SD	1.01	1.10	0.349	108	0.51	0.23	0.147	4
		Minimum	9.99	-19.86	3.26	55	12.02	-16.12	3.66	296
		Maximum	13.45	-16.56	4.66	428	13.04	-15.68	3.96	304
Gonads	Individuals	n	19	19	19	19				
		Mean	10.3861	-17.4813	3.79	416				
		Median	10.2892	-17.8977	3.72	380				
		SD	0.781	0.979	0.485	90				
		Minimum	8.54	-18.73	3.03	255				
		Maximum	11.89	-15.68	5.26	565				
	Pooled	n	3	3	3	3	3	3	3	3
		Mean	10.09	-19.87	4.32	435	11.25	-16.52	3.69	300
		Median	9.93	-19.54	4.35	414	11.03	-16.39	3.67	304
		SD	0.57	0.58	0.202	101	0.99	0.29	0.112	10
		Minimum	9.62	-20.55	4.10	347	10.39	-16.85	3.59	289
		Maximum	10.73	-19.53	4.50	545	12.33	-16.31	3.81	308

Table 5.2. Seasonal changes in $\delta^{13}C$", $\delta^{15}N$ and C:N by tissue type and bell diameter for *Chrysaora fulgida* and *Chrysaora africana* collected off Walvis Bay during the period 27 May 2012 to 26 January 2016. Season: Spr, spring; Sum, summer; Aut, autumn; Win, winter. Size classes 1-7, as (respectively, mm), 20.0-100.1; 50.1-100.1; 100.2-200.1; 200.2-300.1; 300.2-400.1; 400.2-500.1; 500.2-600.1. Tissue type: OA, oral arm; Gon, gonads. Station: *, coastal inshore; **, mid-shelf; ***offshore.

Species	Season	Tissue	Size Class	N	log ($\delta^{15}N$ +1)			log ($\delta^{13}C$" * (-1))			C:N ratio		
					Mean	Median	SD	Mean	Median	SD	Mean	Median	SD
Chrysaora fulgida	Spr	Bell	6	7	1.044	1.068	0.058	1.221	1.213	0.036	3.584	3.507	0.400
	Spr	Bell	7	4	1.004	1.015	1.250	0.058	1.243	0.028	4.185	4.179	0.305
	Spr	OA	6	4	1.066	1.069	0.037	1.268	1.268	0.018	3.563	3.564	0.150
	Spr	OA	7	3	1.038	1.004	0.069	1.256	1.270	0.025	3.257	3.214	0.302
	Spr	Gon	6	3	1.066	1.060	0.020	1.236	1.255	0.035	3.855	4.069	0.491
	Spr	Gon	7	3	1.069	1.053	0.036	1.263	1.264	0.010	4.409	4.518	0.909
	Win	Bell	4	4	1.092	1.080	0.034	1.252	1.255	0.017	3.720	3.764	0.153
	Win	OA	4	4	1.139	1.144	0.031	1.265	1.264	0.033	3.988	3.822	0.459
	Aut	Bell	1	6	1.049	1.039	0.038	1.245	1.247	0.012	3.826	3.857	0.244
	Aut	OA	1	4	1.087	1.084	0.009	1.239	1.243	0.015	3.803	3.746	0.156
	Aut	Bell	3	8	1.078	1.073	0.035	1.239	1.240	0.012	3.675	3.745	0.275
	Aut	OA	3	6	1.098	1.101	0.043	1.259	1.271	0.026	3.852	3.746	0.377
	Aut*	OA	2	4	1.087	1.084	0.009	1.239	1.243	0.015			
	Aut**	OA	2	8	0.988	0.984	0.046	1.182	1.167	0.045			
	Aut***	OA	2	3	0.996	0.982	0.064	1.199	1.201	0.010			
Chrysaora africana	Aut	Bell	4	5	1.047	1.052	0.022	1.185	1.178	0.025	3.269	3.290	0.110
	Aut	OA	4	4	1.110	1.112	0.032	1.209	1.204	0.017	3.794	3.762	0.122

Table 5.3. Statistical parameters for the linear regressions between $\delta^{13}C$", $\delta^{15}N$ and C:N each respectively, with bell diameter (BD) for *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA), where *a* is the slope and *b* the intercept parameter (± *S.E.).*

Signal	Species	Tissue type	*a*	*b*	r^2	*n*	*F*	*P*
$\delta^{15}N$	CF	Bell*	-0.003 ± 0.001	-11.123 ± 0.249	0.148	75	12.631	0.001
		Oral arm	-0.002 ± 0.001	11.755 ± 0.420	0.086	35	2.993	0.093
		Gonad	0.003 ± 0.002	9.290 ± 0.770	0.089	22	1.963	0.177
	CA	Bell	-0.008 ± 0.002	12.531 ± 0.571	0.514	12	10.565	0.009
$\delta^{13}C$"	CF	Bell*	0.003 ± 0.001	-18.003 ± 0.202	0.169	75	14.871	<0.001
		Oral arm	-0.001 ± 0.001	-17.811 ± 0.358	0.020	35	0.659	0.423
		Gonad	-0.002 ± 0.003	-16.894 ± 1.324	0.024	22	0.496	0.490
	CA	Bell	0.012 ± 0.002	-19.005 ± 0.522	0.757	12	31.226	<0.001
C:N	CF	Bell*	0.000 ± 0.000	3.777 ± 0.066	0.010	75	0.768	0.384
		Oral arm	-0.001 ± 0.000	4.014 ± 0.102	0.314	35	16.553	<0.001
		Gonad	0.003 ± 0.001	2.734 ± 0.459	0.239	22	6.266	0.021
	CA	Bell	-0.003 ± 0.001	4.258 ± 0.166	0.660	12	19.452	0.001

*Ephyrae included

Table 5.4 Statistical summary of the overall mean of $\delta^{15}N$ (‰), $\delta^{13}C$" (‰) and C:N ratio by tissue type per season for each *Chrysaora* species.

Species	Tissue type	Season	n	$\delta^{15}N$ (‰)		$\delta^{13}C$" (‰)		C:N ratio	
				Mean	SD	Mean	SD	Mean	SD
Chrysaora fulgida	bell*	SUMMER	15	9.71	1.15	-17.33	1.36	3.75	0.30
		AUTUMN	14	10.67	1.04	-17.45	0.48	3.74	0.26
		WINTER	15	11.20	1.30	-17.44	0.81	3.57	0.24
		SPRING	31	10.23	1.41	-17.32	1.33	3.79	0.39
	oral arm	SUMMER	6	11.03	0.69	-18.28	1.53	3.58	0.33
		AUTUMN	10	11.42	0.92	-17.84	0.96	3.83	0.30
		WINTER	6	12.40	1.03	-18.14	1.18	3.75	0.52
		SPRING	13	10.40	1.17	-18.10	0.80	3.50	0.27
	gonad	SUMMER	8	10.17	0.67	-18.54	1.32	4.00	0.29
		WINTER	2	10.86	0.09	-16.64	0.81	3.54	0.02
		SPRING	12	10.38	0.85	-17.51	1.03	3.82	0.61
Chrysaora africana	bell	SUMMER	2	12.49	0.00	-18.07	0.00	4.12	0.00
		AUTUMN	7	10.11	0.46	-15.49	0.85	3.35	0.21
		WINTER	1	11.90		-15.61		3.48	
		SPRING	2	11.11	0.77	-17.86	0.01	3.92	0.12
	oral arm	AUTUMN	5	11.55	1.16	-16.27	0.59	3.77	0.11
		WINTER	1	12.54		-15.99		3.66	
	gonad	AUTUMN	2	10.71	0.45	-16.62	0.32	3.74	0.10
		WINTER	1	12.33		-16.31		3.59	

*Ephyrae included

Table 5.5. Statistical summary for $\delta^{15}N$ (‰), $\delta^{13}C$" (‰) and C:N ratio by season and tissue type for each *Chrysaora* species. Season: Spr, spring; Sum, summer; Aut, autumn; Win, winter. Tissue type: OA, oral arms; Gon, gonads.

Species	Season	Tissue type	N	$\delta^{15}N$ (‰)		$\delta^{13}C$" (‰)		C:N ratio (‰)		Bell diameter (mm)	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD
Chrysaora fulgida	Sum	Bell	15	9.709	1.153	-17.325	1.359	3.751	0.3	303.0	171.9
		OA	6	11.031	0.69	-18.284	1.532	3.583	0.325	346.8	152.8
		Gon	8	10.172	0.668	-18.541	1.324	3.997	0.29	413.3	86.5
	Aut	Bell	14	10.674	1.036	-17.449	0.478	3.74	0.264	115.4	48.3
		OA	9	11.421	0.918	-17.843	0.963	3.832	0.296	120.4	46.0
	Win	Bell	15	11.201	1.298	-17.437	0.809	3.57	0.239	260.7	113.1
		OA	6	12.401	1.026	-18.145	1.182	3.747	0.517	257.5	51.7
		Gon	2	10.862	0.093	-16.642	0.813	3.543	0.017	410.0	49.5
	Spr	Bell*	31	10.227	1.41	-17.316	1.327	3.793	0.395	260.0	209.0
		OA	13	10.404	1.166	-18.098	0.801	3.498	0.274	372.5	152.9
		Gon	12	10.376	0.85	-17.513	1.034	3.819	0.609	423.5	100.5
Chrysaora africana	Sum	Bell	2	12.494	0	-18.073	0	4.124	0	90.0	0.0
	Aut	Bell	7	10.111	0.463	-15.485	0.853	3.35	0.214	292.7	22.5
		OA	5	11.551	1.159	-16.267	0.585	3.775	0.114	300.0	17.4
		Gon	2	10.711	0.455	-16.622	0.325	3.737	0.102	298.5	13.4
	Win	Bell	1	11.904		-15.608		3.478		267.0	
		OA	1	12.537		-15.986		3.661		304.0	
		Gon	1	12.335		-16.309		3.59		304.0	
	Spr	Bell	2	11.111	0.765	-17.864	0.011	3.922	0.119	95.5	47.4

*Ephyrae included

Table 5.6. Statistical parameters for the linear regressions between $\delta^{13}C$, $\delta^{13}C$ and C:N each respectively, with bell diameter (BD) by season and tissue type for *Chrysaora fulgida*, where *a* is the slope and *b* the intercept parameter (± *S.E.)*

Signal	Season	Tissue type	*a*	*b*	r^2	*n*	*F*	*P*
$\delta^{15}N$	Summer	Bell*	-0.004 ± 0.002	10.863 ± 0.529	0.323	15	6.193	0.027
	Autumn	Bell*	0.007 ± 0.006	9.830 ± 0.725	0.116	14	1.579	0.233
	Winter	Bell*	-0.003 ± 0.003	12.043 ± 0.863	0.079	15	1.118	0.310
	Spring	Bell*	-0.003 ± 0.001	10.966 ± 0.376	0.178	31	6.272	0.018
	Spring	Oral arm	0.000 ± 0.002	10.459 ± 0.921	0.000	13	0.004	0.950
	Spring	Gonads	0.003 ± 0.002	9.053 ± 1.080	0.136	12	1.576	0.238
$\delta^{13}C$	Summer	Bell*	0.002 ± 0.002	-18.036 ± 0.723	0.088	15	1.253	0.283
	Autumn	Bell*	-0.001 ± 0.001	-17.799 ± 0.338	0.94	14	1.245	0.286
	Winter	Bell*	0.004 ± 0.002	-18.543 ± 0.452	0.351	15	7.038	0.020
	Spring	Bell*	0.003 ± 0.003	-18.079 ± 0.346	0.214	31	7.892	0.009
	Spring	Oral arm	-0.002 ± 0.001	-17.378 ± 0.587	0.137	13	0.496	0.490
	Spring	Gonads	-0.003 ± 0.003	-16.304 ± 1.359	0.077	12	0.496	0.490
C:N	Summer	Bell*	0.001 ± 0.000	3.448 ± 0.137	0.33	15	6.417	0.025
	Autumn	Bell*	- 0.001 ± 0.002	3.867 ± 0.192	0.041	14	0.507	0.490
	Winter	Bell*	-0.001 ± 0.000	3.875 ± 0.138	0.305	15	5.718	0.033
	Spring	Bell*	0.000 ± 0.000	3.912 ± 0.113	0.059	31	1.807	0.189
	Spring	Oral arm	-0.001 ± 0.000	3.862 ± 0.181	0.298	13	4.674	0.054
	Spring	Gonads	0.004 ± 0.001	2.185 ± 0.643	0.405	12	6.806	0.026

*Ephyrae included

Table 5.7. Station summary of the overall mean of $\delta^{15}N$ (‰), $\delta^{13}C$” (‰) and bell diameter (mm) of *Chrysaora fulgida*.

Station	N	$\delta^{15}N$ (‰)		$\delta^{13}C$ (‰)		Bell diameter (mm)	
		Mean	SD	Mean	SD	Mean	SD
Coastal inshore	10	11.42	0.92	-17.84	0.96	120.4	46.0
Mid-shelf	25	9.40	0.82	-15.06	1.04	196.3	145.1
Offshore	11	8.53	0.99	-16.20	0.43	270.0	226.9

Table 5.8. Results of the Mann-Whitney U test illustrating size-specific differences of bell tissue in the median $\delta^{15}N$, $\delta^{13}C$" and C:N values between *Chrysaora africana* and *Chrysaora fulgida* collected off Walvis Bay. (Results considered significant at $p \leq 0.05$)

Value (size range, mm)	Mann-Whitney U	Wilcoxon W	Z	Sig. (2-tailed)
$\delta^{15}N$ (60-130)	50.0	60.0	2.002	0.049
$\delta^{15}N$ (250-350)	53.0	89.0	1.636	0.114
$\delta^{13}C$" (60-130)	15.5	25.5	-1.451	0.152
$\delta^{13}C$" (250-350)	60.0	96.0	2.309	0.021
C:N (60-130)	34.0	44.0	0.751	0.736
C:N (250-350)	16.5	52.5	-2.197	0.59

Table 5.9. Statistical summary of size-specific differences of bell tissue for $\delta^{15}N$, $\delta^{13}C$" and C:N ratio values for *Chrysaora fulgida* (CF) and *Chrysaora africana* (CA)

Species	Size range (mm)	$\delta^{15}N$				$\delta^{13}C$"				C:N ratio			
		Mean	n	Median	SD	Mean	n	Median	SD	Mean	n	Median	SD
CF	Ephyrae	10.830	7	10.880	0.498	-18.640	7	-18.400	0.776	4.143	7	4	0.378
	60-130	10.801	15	10.500	1.005	-17.592	15	-17.610	0.615	3.867	15	4	0.352
	250-350	9.788	9	9.420	1.701	-17.084	9	-17.310	1.227	3.667	9	4	0.500
	450-550	9.825	12	9.580	1.210	-17.016	12	-16.785	1.398	4.000	12	4	0.603
CA	60-130	11.800	4	12.070	0.911	-17.968	4	-17.970	0.118	4.000	4	4	0.000
	250-350	10.335	8	10.185	0.762	-15.500	8	-15.395	0.789	3.125	8	3	0.350

Table 5.10. Summary of mean $\delta^{15}N$, $\delta^{13}C$ and C:N ratio with standard deviations (SD) for jellyfish and other taxa in the northern Benguela ecosystem. Mean sizes were measured as total length (cm). $\delta^{13}C'$ represents lipid normalized values. n = number of samples (total number of individuals). Trophic values are calculated via (TLi) mean $\delta^{15}N$ of POM (calculated from Koppelmann et al. 2013) and (TLii) mean $\delta^{15}N$ of two mytilid bivalve species (11.3‰) collected during this study. TLo refers to the trophic level as per reference study.

Taxa	code	$Part sampled	Size	n	$\delta^{15}N$‰	SD ($\delta^{15}N$‰)	C:N	SD (C:N)	$\delta^{13}C$‰	SD ($\delta^{13}C$‰)	$\delta^{13}C$ ‰	SD ($\delta^{13}C''$)	TLi	TLii	TLo	Source
POM				48	6.1	0.1										Koppelmann et al. 2013
Molluscs (length = total length, cm)																
Mytilus galloprovincialis	MG	f		1(4)	12.7		3.5		-18.38		-18.4		2.9			This study
Semimytilus algosus	Biv	f		1(4)	10.3		4.1		-15.9		-15.2		2.2			This study
Venerupis corrugates	Vene	f			11.1	0.4	4.1	0.1	-16.0	1.7	-15.3	1.9	2.5	1.9		This study
Limacina inflata	techoLI	w			4.1		7.3		-22.4		-18.5		0.4	-0.1	1.0	*Koppelmann et al. 2013
Desmopterus papilio	techoDP	w			13.0		7.4		-23.3		-19.3		3.0	2.5	2.7	*Koppelmann et al. 2013
Limacina bulimoides	techoLB	w			11.9		6.3		-21.4		-18.5		2.7	2.2	2.0	*Koppelmann et al. 2013
Brown coloured nudibranch (Opisthobrachia	Brach	w		2(6)	13.8	0.8	4.1	0.1	-17.8	0.5	-17.0	0.4	3.3	2.7		This study
Nudibranch (*Polycera capensis*)	Poly	w		1	11.9		4.1		-20.3		-19.5		2.7	2.2		This study
Crustaceans																
Copepoda	cope	w	<1	3	9.6	0.2	4.2	0.2	-20.4	1.2	-19.6	0.1	2.0	1.5	2.1	Iitembu et al. 2012
Nannocalanus minor	copeNM	w		3(35)	4.8	0.4	3.6		-22.7	0.8	-23.2	0.8	0.6	0.1	2.1	Schukat et al. 2014
Calanoides carinatus (C5 stgae)	copeCC	w		4(58)	6.1	0.3	10.4		-19.9	0.2	-17.1	0.2	1.0	0.5	2.4	Schukat et al. 2014
Calanoides carinatus (female)	copeCC	w		3(56)	8.1	0.1	4.3		-17.8	0.1	-17.5	0.1	1.6	1.1	3.0	Schukat et al. 2014
Metridia lucens	copeML	w		2(100)	10.4	0.4	3.8		-19.7	0.2	-19.9	0.1	2.2	1.7	3.7	Schukat et al. 2014
Cumacea sp.	Cum	w		1(>100)	9.6		5.7		-19.0		-16.7		2.0	1.5		This study
Sand shrimp (*Palaemon peringueyi*)	SandSh	w		3(150)	13.2	0.2	3.7	0.2	-13.3	2.5	-13.0	2.7	3.1	2.6		This study
Krill (*Euphausia hanseni*)	Krill	w		6	7.9	0.8	3.6		-17.9	1.3			1.5	1.0		Huenerlage &

															Buchholz 2013
Euphausiids (Nematoscelis sp.)	Euph	w		3	9.6	0.7	3.8		-18.2	0.2	-18.3	0.2	2.0	1.5	3.5	Schukat et al. 2014
Chaetognaths (*Sagitta* sp.)	Chaet	w		4(5)	8.8	0.9	4.8		-18.2	0.5			1.8	1.3	3.2	Schukat et al. 2014
Hyperia galba	hyperg	w		1	9.2		4.1		-18.1		-18.0		1.9	1.4	3.3	Schukat et al. 2014
Themisto gaudichaudi	hyperTG	w		3	9.9	0.6	4.1		-17.8	0.5	-17.7	0.4	2.1	1.6	3.6	Schukat et al. 2014
hyperiid amphipods	hyperAm	w		11(>1000)	12.9	1.0	4.4	0.1	-18.6	1.1	-17.5	1.1	3.0	2.5		This study
Echninoderms Brittle stars (*Ophioderma wahlbergii*)	Star	w		1(14)	11.8		6.7		-12.7		-9.3		2.7	2.1		This sudy
Cnidarians (length = bell diameter, cm)																
Aequorea forskalea	AFi	b	9	1(28)	11.8		3.1		-16.7		-16.7		2.7	2.1		This study
Aequorea forskalea	AFii	b	7	1	11.0		3.2		-17.4		-17.4		2.4	1.9		This study
Aequorea forskalea	AFiii	b	22	1	9.9		3.4		-15.1		-15.1		2.1	1.6		This study
Aequorea forskalea	jellyAF	b	12	6	12.3	1.6	4.0	1.3	-17.9	1.1	-17.5	0.6	2.8	2.3		*Teuber 2009
Aequorea forskalea (offshore)	jellyAFoffs	b		11	11.1	1.6			-14.7	1.1			2.5	1.9		van der Bank et al. 2011
Aequorea forskalea (mid-shelf)	jellyAFms	b	9	11	10.7	0.7			-14.5	0.8			2.3	1.8		van der Bank et al. 2011
Aequorea forskalea (inshore)	jellyAFins	b	8	4	10.9	2.2			-14.3	0.4			2.4	1.9		van der Bank et al. 2011
Atolla sp.	jellyAtolla				8.1		4.1		-16.3		-15.5		1.6	1.0		*Jung 2010
Beroe sp.	jellyBeroe			1	10.3		4.0		-19.4		-19.4		2.2	1.7	3.7	Schukat et al. 2014
Chirodropus gorilla	jellyCG	b	26	1	13.1		3.5		-15.1		-15.1		3.0	2.5		This study
Chrysaora africana	CA_{6-13}	b	6-13	4(7)	11.8	0.9	4.0	0.6	-19.3	0.3	-18.0	0.1	2.7	2.1		This study
Chrysaora africana	CA_{25-35}	b	25-35	8(21)	10.3	0.8	3.1	0.4	-15.6	0.9	-15.5	0.8	2.2	1.7		This study
Chrysaora fulgida	jellyCF			1	12.1	1.6	3.9		-17.5	0.6			2.8	2.2	3.4	*Schukat et al. 2014
Chrysaora fulgida	CFephyrae	b	<1	7(>100)	10.8	0.5	4.1	0.4	-20.0	0.9	-18.6	0.8	2.4	1.9		This study
Chrysaora fulgida	CF6-13	b	6-13	15(84)	10.8	1.0	3.9	0.4	-18.2	0.6	-17.6	0.6	2.4	1.9		This study
Chrysaora fulgida	CF_{25-35}	b	25-35	9(14)	9.8	1.7	3.7	0.5	-17.6	1.1	-17.1	1.2	2.1	1.6		This study
Chrysaora fulgida	CF_{45-55}	b	45-55	12(14)	9.8	1.2	4.0	0.6	-18.1	1.8	-17.0	1.4	2.1	1.6		This study
Pleurobrachia sp.	PB	w		1	10.1		4.7		-20.1		-18.8		2.2	1.6		This study
Fishes (length = total length, cm)																
Sunfish (*Mola mola*)	Sun	m	53	1	11.3		3.6		-17.8				2.5	2.0		This study

Cape silver side (*Atherina breviceps*)	Css	m		1(2)	13.1		4.4		-20.7		-19.6		3.0	2.5		This study
Galjoen (*Dichistius capensis*)	Gal	m	35		11.3	1.7	5.1	1.8	-18.8	0.3	-17.1	1.6	2.5	2.0		This study
Horse mackeral (*Trachurus capensis*)	HM		41	11	13.6	0.4	3.4	0.2	-16.5	0.4			3.2	2.7	3.3	Iitembu et al. 2012
Cape Anchovy (*Engraulis capensis*)	Anch		9	105	12.1	1.1	3.7	0.3	-16.2	0.6	-15.8	0.5	2.8	2.2	2.7	Iitembu et al. 2012
Sardine (*Sardinops sagax*)	Sard		18	23	9.2	0.7	3.4	0.2	-15.9	0.7			1.9	1.4	2.0	Iitembu et al. 2012
Shallow water Cape hake (*Merluccius capensis)*	MC_{8-9}		14	19	12.5	0.6	3.2	0.1	-16.5	1.0	-16.5	1.0	2.9	2.4	3.0	Iitembu et al. 2012
Shallow water Cape hake (*Merluccius capensis*)	MC_{20-29}		25	22	13.7	0.5	3.2	<0.1	-16.5	1.3			3.2	2.7	3.3	Iitembu et al. 2012
Shallow water Cape hake (*Merluccius capensis*)	MC_{60-69}		64	13	14.4	0.9	3.1	<0.1	-15.7	0.4			3.4	2.9	3.5	Iitembu et al. 2012
Deep-water Cape Hake (*Merluccius paradoxus*)	MP_{20-29}		26	19	13.6	0.4	3.1	<0.1	-16.6	0.4			3.2	2.7	3.3	Iitembu et al. 2012
Deep-water Cape Hake (*Merluccius paradoxus*)	MP_{60-69}		62	16	15.4	0.6	3.4	<0.1	-16.8	0.8			3.7	3.2	3.8	Iitembu et al. 2012
Sardine larvae (*Sardinops sagax*)	SardLarvae		1	10	11.2	0.2			-20.1	0.5			2.5	2.0		Geist 2013
European Anchovy (*Engraulis encrasicolus*)	EngLarvae		2	6	11.5	0.4			-20.4	0.8			2.6	2.1		Geist 2013
Plants																
ulva species	Ulva				10.6		8.7		-12.3		-12.3		2.3	1.8		This study
Sarcocornia species	Sar				10.9		12.1		-26.6		-26.6		2.4	1.9		This study
Birds																
Storm petrel (Hydrobatidae)	SPbird	fe		4	13.50	0.70	2.9		-17.3	0.4			3.2	2.6	4.6	Schukat et al. 2014

Note. *This study applied the lipid normalization equation of Post et al. (2007). $ f = flesh, w = whole, m = muscle, b = bell, fe = feathers

Table 5.11. Summary of $\delta^{15}N$, $\delta^{13}C$ and C:N ratios with standard deviations (SD) for jellyfish in other marine ecosystems. m = medusa, e = ephyrae.

Species	$\delta^{15}N‰ \pm SD$	$\delta^{13}C‰ \pm SD$ [$]	C:N	n, [#]pooled samples	stage (size mm)	Tissue type	Location	Reference
Pelagia noctiluca		-18.8 ± 0.9	4 ± 0.2	14	m (<3 to >5)		Gulf of Trieste	Malej et al. 1993
Phacellophora camtschatica	15.0 ± 0.2	-25.7 ± 1.2		4	m	whole	southern Puget Sound, Washington, USA	Towanda & Thuesen 2006
	14.9 ± 0.2	-27.6 ± 0.7		2	m	gonad		
	13.6 ± 0.9	-24.4 ± 1.1		2	m	oral arms		
	16.5 ± 0.1	-10.1 ± 0.9		2	m	mesolgea		
Polyorchis penicillatus	15.8	-26.4		1[#]2	m	whole		
Muggiaea atlantica	15.2	-30.0		1[#]200	m	whole		
Phialidium lomae	15.8	-29.2		1[#]75	m	whole		
Aequorea victoria		-16.79(0.44)		33	m		northern California Current	Miller et al. 2008
Aurelia aurtia		-16.97(0.82)		15	m			
Beroe		-18.54(0.19)		9	m			
Chrysaora fuscescens		-14.87(0.15)		23	m			
Phacellophora camtschatica		-16.86(0.62)		11	m			
Catostylus mosaicus		-22.2 to -20.9			m		Smiths Lake, New South Wales, Australia	Pitt et al. 2008
Jellyfish (AS 512)	8.9	-24.0	3.3	1	m	tentacle	Dumont d'Urville Sea (East Antarctica)	Giraldo et al. 2011
Jellyfish (AS 509)	9.3	-24.0	3.0	1	m			
Jellyfish (AS 508)	5.3	-24.4	3.0	1	m			
Siphonophores	6.6 ± 0.9	-23.9 ± 0.4	3.1	3	m	whole		
Pelagia noctiluca	5.6 ± 0.5	-17.8 ± 0.6		5	m	whole	Western Mediterranean Sea	Cardona et al. 2012
Cotylorhiza tuberculata	1.6 ± 0.3	-17.4 ± 0.2		5	m	whole		
Aurelia aurita	4.8 to 10.6	-22.0 to -17.4	3.1 to 4.2	6	m (140-200		Yellow Sea, China	Ying et al. 2012
Stomolophus meleagris				4	m (450-750)			
Cyanea nozakii				2	m (560-600)			

Aurelia spp.	11.5 ± 0.5	-18.3 ± 0.4	3.5 ± 0.2	31	m (280.2 ± 30.6)	bell	northern Gulf of Mexico	D'Ambra et al. 2014
	12.0 ± 0.7	-18.8 ± 0.9	3.5 ± 0.3	31	m (280.2 ± 30.6)	oral arms		
	11.6 ± 0.9	-19.6 ± 0.7	3.7 ± 0.3	31	m (280.2 ± 30.6)	gonads		
	11.8 ± 0.7	-18.7 ± 0.7	3.6 ± 0.2	31	m (280.2 ± 30.6)	whole		
Aurelia aurita	9.7 ± 1.6	-19.0 ± 1.2	3.6 ± 0.2	43	m (~60-360)	bell	Strangford Lough, Northern Ireland	Fleming et al. 2015
Cyanea lamarckii	11.0 ± 1.8	-19.8 ± 1.0	3.7 ± 0.3	36	m (~40-200)	bell		
Cyanea capillata	12.4 ± 1.8	-19.7 ± 1.3	3.6 ± 0.1	43	m (~60-850)	bell		
Mnemiopsis leidyi	10.1 to 11.38	-19.62 to -18.64	2.86 to 4.00	21	m	ectoderm of the lobes	Cananéia Lagoon Estuarine System, Sao Paulo, Brazil	Nagata et al. 2015
Chrysaora lactea	10.55 to 11.23	-19.55 to -17.38	2.62 to 3.24	17	m	bell		
Lychnorhiza lucerna	9.91 to 11.01	-18.70 to -17.11	2.54 to 3.34	37	m	bell		
Olindias sambaquiensis	11.95 to 12.28	-17.72 to -16.24	1.62 to 2.97	7	me	bell		
Rhacostoma atlanticum	12.71 ± 0.08	-15.88 ± 1.01	1.55	2	m	bell		
Pelagia noctiluca	3.7 ± 0.1 to 5.0 ± 0.2	-20.5 ± 0.1 to -18.2 ± 0.1		40	m	somatic	Strait of Messina (Sicily, Italy)	Milisenda et al. 2018
Pelagia noctiluca	4.5 ± 0.5	-20.87 ± 0.2		20	e (3-10)	whole	Catalan coast in the NW Mediterranean	Tilves et al. 2018
Pelagia noctiluca	5.5 ± 0.5	-20.55 ± 0.4		15	m (40-97)	whole		

[$](Standard error)

Jellyfish beach stranding in Walvis Bay.

PICTURE

CHAPTER 6

CONCLUSIONS

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CONCLUSIONS

This thesis has examined aspects of the ecology and life history of both species of *Chrysaora*, using samples of zooplankton and medusae collected from a shallow lagoon and bay off central Namibia during the period February 2012 to January 2016. This is a unique time series and there are no comprehensive long-term data on the abundance and distribution of jellyfish in the northern Benguela system. Most studies that have been conducted in the northern Benguela have tended to focus on short periods of sporadic sampling and they have often implemented different sampling methods and equipment (Pagès & Gili 1991; Fearon et al. 1992; Gibbons et al. 1992; Pagès 1992; Jung 2010; van der Bank et al. 2011; Koppelmann et al. 2014).

1) Is there any seasonality changes in the abundance of ephyrae of each Chrysaora species off Walvis Bay?

All of the taxa recovered from the zooplankton net (Chapter 2) were characteristically neritic, and included meroplanktonic Hydrozoa and Scyphozoa, as well as cydippid ctenophores and shallow water siphonophores. In general, the same assemblage of jellyfish taxa (*Bougainvillia*, *Obelia*, *Clytia*, *Chrysaora fulgida* and *Muggiaea atlantica*) was present across seasons and years. However, the community composition and densities varied seasonally and inter annually. Taxa exhibited differences in the scale of their maximum abundances (Chapter 2): 1) extremely high density taxa such as *Chrysaora fulgida*; 2) high density taxa *Muggiaea atlantica*, *Obelia* sp., *Proboscidatyla* sp. and *Bougainvillia* sp.; 3) low density taxa such as *Clytia* sp. and 4) taxa such as *Chrysaora africana*, *Pleurobrachia* sp. and *Mitrocomella* sp. that occurred infrequently and rarely. No clear seasonal succession of species was observed, except for the developing stages of ephyrae. Both *Chrysaora* species showed a restricted period of liberating ephyrae: *Chrysaora fulgida*, during mid-winter to mid-summer, over a six month period; and *Chrysaora africana*, during early winter to mid-spring, over a five month period. Consequently, recruitment of ephyrae of both *Chrysaora* species to the plankton off Walvis Bay was not continuous throughout the year and their abundance differed beween years and species.

Chapter 2 established that water temperature, day length and wind speed were the main variables that explained seasonal changes in the composition and structure of gelatinous zooplankton in Walvis Bay. The active upwelling phase was linked with blooms of the ephyrae of *Chrysaora fulgida,* but not hydromedusae. This suggests that these factors may be important in strobilation of polyps and studies to examine in the laboratory are suggested. At this stage, no polyp beds of *C. fulgida* have been detected *in situ*, but emphasis should be placed on this so that it becomes possible to mirror the work of Di Camillo et al. (2010), Toyokawa et al. (2011) and Makabe et al. (2014), and additionally determine the influence of Benguela Niño and Niña anomalies, and other climate-linked variables, on ephyra production and polyp growth and development. If nothing else, this study has at least narrowed the search field for the polyps in the wild!

Chapter 2 supports the findings of Berrill (1949), Lucas (2001), Lucas et al. (2012) and Kogovšek et al. (2012). That is, more than one environmental factor appears to activate asexual reproduction of the polyp (e.g. decreasing water temperature associated with upwelling, low prey abundance, and the commencement of longer day length), and these likely work in synergy and in the correct sequence at critical periods. However, the specific environmental factors might be particular to individual populations (Walvis Bay versus Lüderitz) and species (different eco-physiological requirements *of Chrysaora fulgida* versus *Chrysaora africana*), and that the response of the benthic stage might partly be governed by its genotype. It is clear that there may be substantial genetic structure within populations of the same species in the same ecosystem (Dawson et al. 2015) that may span a multitude of spatial scales. The Benguella upwelling cell in the vicinity of Lüdertiz (Namibia) forms a semi-permanent barrier towards the interchange of biota between the northern and southern parts of the system (van der Bank & Holtzhausen 1998) – due to a combined effect of changes in circulation and turbulence/stratification – near 24°30‘S in the vicinity of Meob Bay (Agenbag & Shannon 1988). It would therefore be necessary to expand future studies across the spatial-temporal continuum. In the case of Namibia, this should extend from the Orange to the Cunene Rivers.

The densities of ephyrae of *C. fulgida* that were recorded in the waters off Walvis Bay are higher than have been reported for any other species of Scyphozoa. A very large number of ephyrae released over a relatively short period of time suggests either that the number of ephyrae produced by each

strobila is high, that polyps strobilate repeatedly and/or that the polyp population itself is enormous. Polyps of *Chrysaora quinquecirrha* may produce up to 16 ephyrae each, though between 3–6 is more common (Calder 1974), and restrobilate 1–4 times in a given season; and there is evidence to suggest that some polyps may strobilate in a given season up to four successive years (Littleford 1939; Truit 1939). Adult populations of *C. fulgida* off Namibia are enormous (Lynam et al. 2006), which implies either that (1) the survival rate of ephyrae may be high, which, it could be argued, reflects the presently small population of pelagic fishes (Roux et al. 2013); and/ or (2) that the polyp population is large, that ephyra production rates are high and/ or (3) recruitment of new benthic populations of polyps are high. As recently reported by Ziegler & Gibbons (2018), the polyps of this species have an ability to reproduce asexually at a rate that also appears to be unparalleled, reinforcing the idea that the benthic stage of *C. fulgid*a may play a very important role in influencing medusa population sizes: an argument proposed also by Hernroth & Gröndahl (1985) for *Aurelia aurita* in the Gullmar Fjord. Regardless, it implies that the polyp phase of this species is deserving of more attention – *in situ*.

2) Can different morphological features be decerned between the ephyrae of each Chrysaora species and what are their growth rates?

Now that it is understood that there are two species of *Chrysaora* off Namibia (Neethling 2009; Ras 2016), comprehensive monitoring of the populations of the two species requires that they be distinguishable *in situ*, at the ephyra stage as well as the adult. Concrete morphological dissimilarities were documented to distinguish *C. africana* from *C. fulgida* in Chapter 3, despite the limited sample size of *Chrysaora africana.* That is, despite differences in colour, the presence/absence of branched canals on the periphery of velar and rhopalial canal tips is diagnostic. In the case of *C. fulgida* the morphological development from an ephyra (Stage 0) to a juvenile medusa could be described successfully in six stages (Chapter 3), whilst missing stages were noted for *C. africana*. In general, the development of ephyrae described here agrees with patterns described for other species in the genus from elsewhere.

Three growth periods are typically reported for populations of *Aurelia aurita* and *Chrysaora quinquecirrha* in the wild: slow growth during the winter and early spring; exponential growth once temperature and food availability have increased in spring; and finally, shrinkage in the summer and

autumn following sexual reproduction (Möller 1980; Schneider 1989; Lucas & Williams 1994; Olesen et al. 1996; Riisgård et al. 2010). The first growth period of *Chrysaora fulgida* (Stage 0–5), namely slow growth and morphological development, corresponds with that for *Aurelia aurita.* The growth rate (4.33 and 3.45% d^{-1} for 2012 and 2013, respectively) and ontogenic development period (~164 days) of ephyrae of *C. fulgida* appear slower and longer (respectively) than most other species. They are likely to be influenced by the low water temperatures observed close to the coast, coupled with prey availability (abundance/quality).

The prolonged duration of the ephyra stage poses interesting problems for the species involved, as it will be linked to an increased risk of predation from, e.g. pelagic fishes. Ephyrae can be eaten by a variety of fish species (Lamb et al. 2017), and it is not unlikely that anchovies and sardines would have preyed upon them when the latter populations were large (Roux et al. 2013). However, now that these fish are effectively absent from off Namibia (at least in population sizes that warrant a commercial fishery), the survival of the ephyrae is enhanced, meaning that large numbers are now in a position to recruit to adult populations. Clearly more work of a laboratory nature is needed to unravel this mystery further, but the arguments presented by Roux et al. (2013), appear to be supported by the data presented here.

3) Is there any seasonality patterns with regard to the sexual reproduction of each Chrysaora species?

Differences in gonad maturity between the two *Chrysaora* species were evident – medusae of *Chrysaora fulgida* displayed aseasonal, reproductive heterogeneity (maturing at ~300 mm diameter) and individuals were semelparous, whilst *C. africana* appeared strongly seasonal and the females were iteroparous. Both species were non-brooding, gonochoristic and exhibited no clear sexual dimorphism. Whilst gametogenesis in both species was similar to that displayed by other Discomedusae, synchronous and group-synchronous oocyte development was observed in *C. fulgida* and *C. africana*, respectively.

In Chapter 4, the maturity status of the gonad could not be determined macroscopically but histological analysis could provide precise information on oocyte and gonad development. Unlike the findings of Schiarit et al. (2012) for *Lychnorhiza lucerna*, the gametogenic status and the categories of individual medusa maturity status adapted from Pitt & Kingsford (2000) were appropriate to distinguish

between sex–indeterminable (I) and mature (MAT) medusae. However, in order to explore gonad development of ripe medusae in more detail (e.g. partially spent, disintegration, ripe) other histological features in the gonad should be considered to obtain a "whole picture" such as the position of the F6 oocytes/spermatozoa, the presence of empty "cavities" and the disintegration of certain structures. The combined use of oocyte diameters, gametogenic status and maturity status assisted in highlighting the differences between the two *Chrysaora* species and to establish their reproduction strategies.

Ripe *Chrysaora fulgida* medusae were present throughout the year, which suggested the continuous production of planulae by the population, and by implication polyps. Individuals could become reproductively active from any size above ~300 mm bell diameter, though some individuals as large as 590 mm were not reproductively mature. Medusae are generally considered to be semelparous and to die after reproduction. The evidence from *C. fulgida* supports this, though it is possible that some female individuals may be iteroparous (see below). Reproductive heterogeneity is poorly understood within animal populations, but has been the subject of some theoretical and field studies in semelparous plants (Acker et al. 2014). In collaboration with colleagues from Norway, this is currently under investigation from a modelling perspective by an MSc student at UWC, but essentially it would appear to allow a clonal organism (the polyp) to spread its risks. And will vary with the degree of environmental variability. Given that length of time in the plankton is linked to survival in an upwelling ecosystem (advection, predation), an individual medusa may postpone the onset of sexual maturity under unfavourable environmental conditions (very low or high temperatures, poor food etc.), only to reproduce (and then die) when conditions become favourable for it to do so. Hence, if an individual is capable of reproducing at a small size, it should do so given that subsequent mortality rates are high. Such at least, has been demonstrated in semelparous plants (Acker et al. 2014). As noted earlier, this will vary with the degree of environmental variability, and populations in temperate waters, which show pronounced seasonality and environmental synchronicity (time and space), would be expected to show lesser reproductive heterogeneity.

Clearly, however, there are advantages to reproduction at a large size, as individual fecundity would be increased, relative to that of smaller individuals. The presence of a partially spent ovary in an individual specimen of *Chrysaora fulgida* having a relatively small bell size (BD = 378 mm) at maturity suggested that some individual female medusae may not die after spawning. Not only would these

individuals continue to grow in body size, but their ovary sizes and folds would increase, ensuring an increase in fecundity and a greater likelihood of reproductive success (Lucas & Dawson 2014). There was a positive 30-fold difference in fecundity between the minimum and maximum bell diameters of *Rhopilema esculenta* (Huang et al. 1985), whereas *Linuche unguiculata* demonstrated a positive 13-fold difference in daily egg production rates between the minimum and maximum bell diameters over a 90 mm size interval (Kremer 1976). Additionally, positive exponential/linear relationships between medusa diameters (*Aurelia aurita*, *Lychnorhiza lucerna*) and the number of eggs and/or larvae per female have been reported (Schiariti 2008; Chiaverano et al. 2015; Goldstein & Riisgård 2016). Considering these characteristics collectively, the potential fecundity of *Chrysaora fulgida* might be very high and the sexual reproduction phase of *Chrysaora fulgida* might contribute greatly towards the population explosions and geographical dispersion off Namibia.

Another intriguing question is: would offshore medusa populations of *C. fulgida* also sexually reproduce throughout the year? If they do, what would happen to those planulae? Scyphozoan planulae require appropriate types of substrate for settlement and metamorphoses into polyps, in order to complete the metagenetic life cycle (Lucas et al. 2012). Recent experiments by Gambill et al. (2016) demonstrated that planulae of *Cyanea lamarckii* settled within five days with access to substrate, and that settlement was more successful and faster at warmer temperatures. However, when access to the substrate was denied and they were maintained within the water column, the planulae could remain viable for settlement for a longer time period at colder temperatures than warmer temperatures (21, 21 and 14 days at 11.3, 13.4 and 19.4 °C, respectively). Based on these maximum times of viability, the local hydrodynamic model predicted dispersal distances for planulae of *C. lamarckii* up to 100 km before settlement (Gambill et al. 2016). In addition, semelparity is associated with larger egg sizes with associated higher juvenile survivorship than iteroparous species (Crespi & Teo 2002), would this be a possible fitness trait for *C. fulgida* (offshore presence) exhibiting bigger egg size (than *C. africana*) to enhance the survival of their planulae? Future studies should expand across the spatial-temporal continuum to investigate medusa reproduction while the success of settlement and metamorphosis of planulae should be investigated similar to the study of Gambill et al. (2016).

The life span of a scyphozoan medusa is assumed to be concomitant to the time period, equal or less, of the medusae population being present in the field with their usually disappearance after reproduction (Arai 1997). For example, the disappearance of *Cyanea capillata* medusae from the water column was associated with reproduction mortality and the subsequent appearance of planulocysts (Brewer 1991). In the case of *Chrysaora africana* in Walvis Bay, medusae with eggs and sperm appeared during April (Chapter 4). This generation of medusae disappeared by the end of September of the same year. However, this cohort was "born" (time period of occurrence of ephyrae stages) during the previous year during late-autumn till mid-spring (May till October; Chapter 3). Thus, the next cohort of ephyrae overlapped with the adult medusa generation over a 5-month period. Therefore, suggesting that the life span for *Chrysaora africana* medusae are estimated to be roughly 16 months, the time duration of one cohort developing through their ephyra to medusa stages and completing their sexual reproductive part of life cycle.

The literature indicates that *C. fulgida* are found off Namibia all year around (Flynn et al. 2012). This is in contrast to the situation in most temperate ecosystems (and the Benguela upwelling ecosystem is a temperate one), where populations of medusa are found during spring, summer and autumn but are generally absent during winter (Lucas & Dawson 2014). It was originally suspected, given that ephyra release is usually stimulated by a (often sudden) decline in water temperature, and that ephyra release would occur on a trickle basis throughout the year since upwelling occurs pretty much throughout the year. This was not the case, however, which suggests that the build-up of populations is facilitated by a lifespan, of at least some individuals, of greater than one year which might be enabled by reproductive heterogeneity and some individuals that may be iteroparous. In the laboratory, *C. fulgid*a could survive for >20 months (Flynn et al. 2012). The theoretical lifespan (t_{max}) of *C. fulgida* was estimated from the values supplied by Palomares & Pauly (2009) – an inverse of the von Bertalanffy growth equation, considering maximum bell diameter as 95% of the asymptotic length (see Taylor 1958) – which amounted to 0.44–1.67 years at L_{∞} = 68.2–68.8 cm. However, Palomares & Pauly (2009) did not include the goodness-of-fit estimator of ELEFAN to illustrate the uncertainty of model fit for *K*. This study attempted to estimate t_{max}

of *C. fulgida* via bell diameter frequency data[2] at L_∞ = 84.55 cm, and obtained a highly uncertainty for *K* and the parameter estimates were not biologically sensible implicating an inadequate representation of the true population derived from sampling only at Walvis Bay.

Different adaptive strategies were evident between the two *Chrysaora* species, which might reflect their adaptive phenotypic plasticity towards different environmental conditions and habitat occupation. Hutchings et al. (2007) reported differences in larval growth, survival and their plastic responses to variation in food and temperature between four populations of Atlantic cod (*Gadus morhua).* These traits, and their plastic responses towards food and temperature, illustrated that populations differed genetically in their responses to the environment across spatial scales at which microsatellite DNA failed to detect the population structure (Hutchings et al. 2007). The different survival reaction norms showed that warm-water populations were more sensitive to changes in food, whereas cold-water populations were more sensitive to changes in temperature (Hutchings et al. 2007). Hence, indicating that neither the direction nor the magnitude of demographic responses to environmental change is required to be the same between populations (Hutchings et al. 2007). Adaptive phenotypic plasticity, might explain the reason for *C. africana* being "less fit" in the northern Benguela ecosystem since Namibia represents the southern limit of its species distribution, which otherwise appears to be most common along the west coast of Africa and the Gulf of Guinea (Ranson 1949; Kramp 1961).

The present study should be viewed as preliminary since information of gonad maturity for the population of *Chrysaora fulgida* and *Chrysaora africana* medusae were only studied in the vicinity of Walvis Bay. Considering that population genetic structures of scyphomedusae may span various spatial scales of hundreds-of-meters to hundreds-of-kilometers and the influence of spatial-temporal variability in environments (Pitt & Kingsford 2000; Lucas 2001; Dawson et al. 2015; Chiaverano et al. 2016). Hence, it would be advantageous to expand future studies across the spatial-temporal continuum in order to obtain

[2] The ELEFAN I routine of the FISAT II package (Gayanilo et al. 2005; available at http://www.fao.org/fishery/topic/16072/en), was used to fit the length frequency data to the von Bertalanffy growth function (VBGF). In total, 5508 and 114 specimens of *Chrysaora fulgida* and *Chrysaora africana* were measured, respectively in Walvis Bay. Almost 70% of the *C. fulgida* population was between 0.1 and 10 cm in diameter, although individuals ranged overall in size from 0.118 to 85 cm. Fifty percent of the *C. africana* population had a BD between 20.1 and 30 cm whereas individuals ranged in overall size from 0.267 to 37.5 cm.

a clear picture with regard to the existence of separate local populations, stock or metapopulation (Kingsford 1998; Kingsford & Mooney 2014); possible environmental drivers for reproduction; and the state of reproduction for these *Chrysaora* species off Namibia. It has become clear that much of the success of Scyphozoa can be related to the reproductive flexibility of the group, in addition to their bipartite life cycle. Much work remains to be done and the data collected here will lead to much debate around this.

4) What are the inshore trophic relationships of Chrysaora species?

The present results of Chapter 5 should be viewed as preliminary, since samples were collected from a relatively small number of specimens, with poor supporting baseline data. However, this study has not only illustrated size-associated shifts in trophic ecology, but also revealed spatial, inter-species and some tissue differences in the northern Benguela upwelling system. Size would appear to be the over-riding factor that influences the isotope signatures of *Chrysaora fulgida*; size being linked in turn to space. It has been shown for the first time that small animals have higher $\delta^{15}N$ than adults, implying that they feed at a higher trophic level. Such would agree with animals feeding on components of the microbial loop, whilst adults eat from the more traditional plankton food web. This reflects differences in space, but must almost certainly be linked to changes in cnidome, morphology and behavior and more work is needed to elucidate this. That *C. africana* feeds at a higher trophic level that *C. fulgida* can be explained by the fact that the former is known to eat the latter – something that in turn may influence the distribution of the latter. More work is certainly needed in this regard. Thus, these findings arise a question about who eats whom, in natural conditions, and which factors (e.g. predator/prey size ratio) determine this predatory interaction.

The wide range of individual variability in stable isotope signatures (within the same size class and season) infers multiple sources of variation. These could include, but are not limited to, water temperature and nutrient status, geographical/regional movement, maturity status, etc. I must agree with Fleming et al. (2015), that caution must clearly be exercised to prevent the oversimplification of jellyfish in ecosystem models. In a broader perspective, the inclusion of a “generalised” jellyfish in ecological models is expected to underestimate the collective effect in terms of energy flow or their role in large-fisheries-

based ecosystems (Pauly et al. 2009). An attempt must be made to integrate life cycles and life histories with their energy pathways into food web models.

As with all tools, there are limitations to the use of stable isotope analysis. In line with the observations of Boecklen et al. (2011), this must include a balanced taxonomic and ecosystem coverage, general dependence on literature values for key parameters such as isotopic fractioning values, untested or unrealistic assumptions such as lipid corrections, low predictive power of the trophic levels for comparative studies, and a lack of experimental studies. This study reiterates the fundamental need, in line with the various reviewed topics of different taxa (e.g. Vander Zanden & Rasmussen 2001; Vanderklift & Ponsard 2003; Bearhop et al. 2004; Post et al. 2007; Boecklen et al. 2011; Layman et al. 2012), of species-specific information that are inevitably relevant in interpreting isotope data sets of jellyfish such as trophic discrimination factors, isotopic routing, tissue turnover rates and lipid extraction.

Growth rates of jellyfish need to be explored. Both growth and metabolism can influence tissue turnover differentiation, as well as the relative ordering of turnover rates among tissues following a diet-switch, hence their relative contributions to isotopic turnover rates per tissue type need to be estimated (Xia et al. 2013a, 2013b; Busst & Britton 2018). In the context of this study wild populations of juvenile (2.9–29.5 mm in diameter) medusae (see above footnote[2]) of *Chrysaora fulgida* exhibited slow growth (~4% d^{-1}) (Chapter 3), which contrasted with the high growth coefficients (K = 1.10–4.30 $year^{-1}$) reported by Palomares & Pauly (2009) for larger medusae (70.5–620.5 mm in bell diameter). Thus, implicating relatively slow isotopic turnover rates for juvenile medusa tissue whereas elevated turnover rates seemed to be facilitated by the faster growth rates of larger, potential reproducing medusae.

There is a clear need for the calibration of key isotopic parameters with laboratory and field data (Boecklen et al. 2011). Especially emphasis on the experimentation part via experimental diet-switch studies completed in controlled conditions by resolving species-specific tissue turnover rates and trophic fractionation factors to determine the trophic ecology of jellyfish. Further work will be required to investigate the influence of the microbial loop to improve confidence when interpreting stable isotope data and trophic positions of both *Chrysaora* species in the northern Benguela system. As such novel methods such as molecular biology should be used in combination with stable isotope analysis, biomass size spectra of plankton, fatty acid analysis and stomach content analysis.

In summary, this thesis has added greatly to our knowledge of the biology of *Chrysaora fulgida*, and to a lesser extend *C. africana*, off central Namibia. However, it has just scratched the surface, and has generated a large number of hypotheses that should be followed up if we are to understand the ecology better and the demographic rates involved in the complex life cycles of bloom-forming jellyfish. It is clear that *C. fulgida* has the potential to have benefited greatly following the loss of anchovies and sardines from the ecosystem, as it has a number of attributes that enable it to capitalise on opportunities presented to it. It is inconceivable, at this stage, that the northern Benguela ecosystem will ever revert to one dominated by fish given the nature of one of the species that has come to the fore subsequent to overfishing.

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ANNEXURE 1

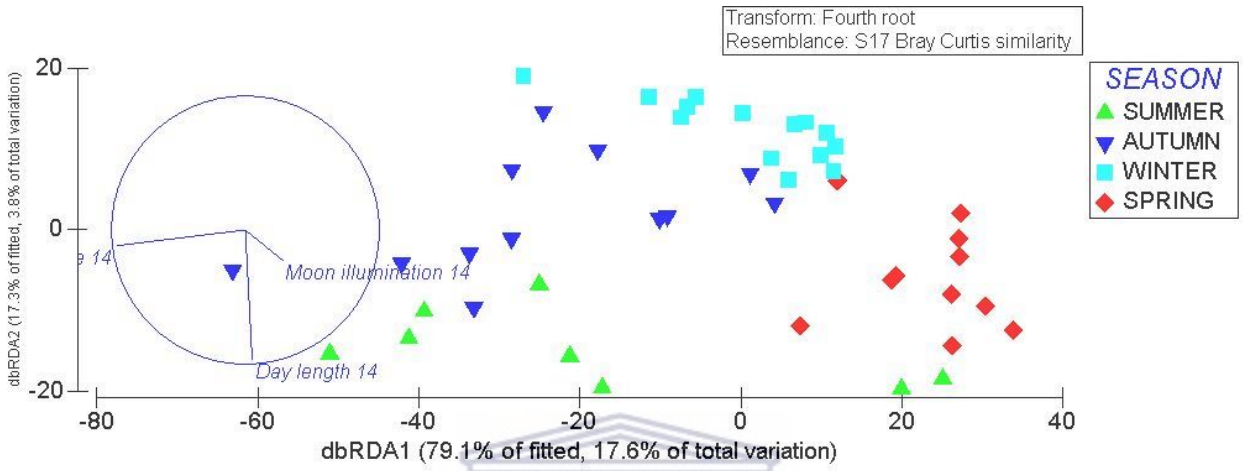

Figure S1. Two-dimensional visualisation of the multivariate multiple regression dbRDA performed on the gelatinous community and environmental predictors (with a 14-day lag): vectors show the direction and strength of the environmental gradients. The seasonal presence of the samples is indicated in symbols.

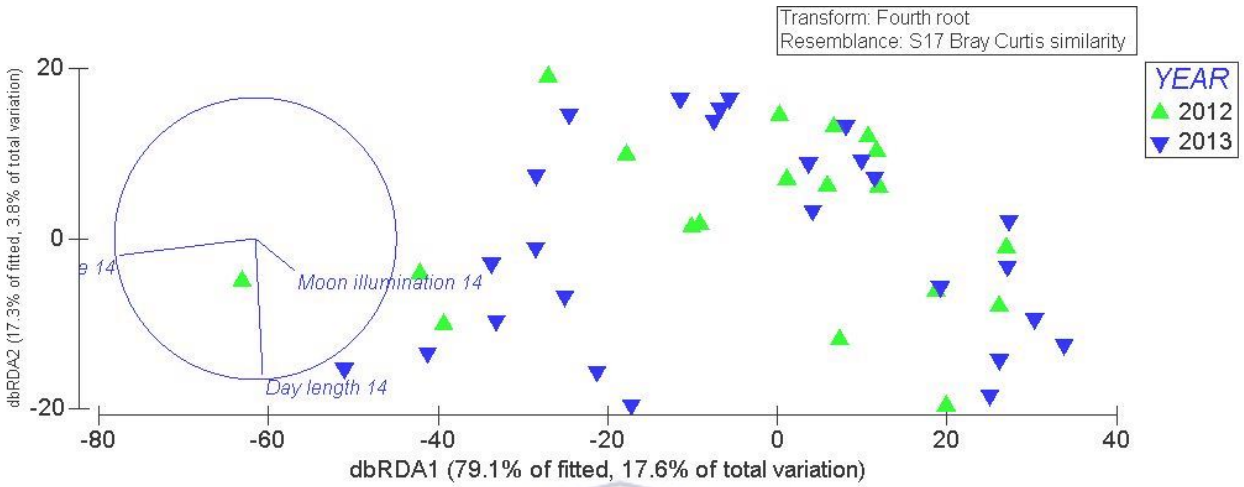

Figure S2. Two-dimensional visualisation of the multivariate multiple regression dbRDA performed on the gelatinous community and environmental predictors (with a 14-day lag): vectors show the direction and strength of the environmental gradients. The annual presence of the samples is indicated in symbols.

Table S1. Coefficient of determination (R^2) of linear regressions between measured environmental parameters.

Environmental parameters	Sea temperature (°C)	Day length (in minutes)	Moon illumination	Wind speed ($m.s^{-1}$)
Sea temperature	1	0.179	0.001	0.076
Day length	721	1	0.006	0.008
Moon illumination	722	721	1	0.012
Wind speed	640	639	640	1

The lower part of the table reports sample sizes.

Table S2. Coefficient of determination (R^2) of linear regressions between mean abundances of main medusa species and measured environmental parameters (contemporary and preceding).

Environmental parameters	Lag in days	Main species					
		CF All Stages	CF Stages 0&1	*Obelia* sp.	*Proboscidactyla* sp.	*Bougainvillia* sp.	*Muggiaea atlantica*
Bottom sea temperature	0	0.089	0.089	0.172	0.111	0.020	0.003
	1	0.030	0.030	0.205	0.106	0.008	0.007
	2	0.027	0.028	0.127	0.071	0.009	0.003
	3	0.032	0.033	0.048	0.067	0.014	0.004
	4	0.047	0.047	0.015	0.072	0.008	0.004
	5	0.071	0.071	0.035	0.077	0.002	0.010
	6	0.066	0.067	0.172	0.076	0.007	0.005
	7	0.064	0.064	0.181	0.068	0.020	0.003
	14	0.080	0.080	0.389	0.082	0.001	0.004
Day length	0	0.020	0.020	0.044	0.000	0.032	0.000
	1	0.019	0.018	0.046	0.000	0.031	0.000
	2	0.017	0.016	0.050	0.000	0.029	0.000
	3	0.015	0.014	0.053	0.001	0.028	0.000
	4	0.014	0.014	0.090	0.001	0.028	0.000
	5	0.012	0.011	0.058	0.001	0.026	0.000
	6	0.011	0.010	0.061	0.002	0.024	0.000
	7	0.009	0.009	0.065	0.003	0.023	0.000
	14	0.002	0.002	0.088	0.010	0.014	0.000
Wind speed	0	0.080	0.081	0.023	0.029	0.014	0.022
	1	0.116	0.117	0.046	0.106	0.018	0.045
	2	0.029	0.029	0.047	0.091	0.001	0.129
	3	0.081	0.081	0.005	0.006	0.002	0.063
	4	0.025	0.024	0.034	0.002	0.004	0.000
	5	0.031	0.031	0.026	0.003	0.002	0.001
	6	0.075	0.075	0.060	0.000	0.004	0.085
	7	0.214	0.213	0.046	0.112	0.018	0.097
	14	0.078	0.079	0.000	0.105	0.043	0.040

Table S3. Results of the DistLM marginal and sequential tests for the abundance of gelatinous fauna collected at Walvis Bay during 2012-2013, with a 14-day lag for day length, moon illumination and sea temperature as predictors.

Marginal Tests*							
Variable		**SS(trace)**	**Pseudo-F**	**p**	**Proportion**		
Day length of 14-day lag		20844	6.6911	0.002	0.03920		
Moon illumination of 14-day lag		11479	3.6187	0.004	0.02159		
Sea temperature of 14-day lag		83077	30.368	0.001	0.15624		
Sequential Tests							
Variable	**AICc**	**SS(trace)**	**Pseudo-F**	**p**	**Proportion**	**Cumulative**	**res.df**
+ Sea temperature of 14-day lag	1315.8	83077	30.368	0.001	0.1562	0.15624	164
+ Day length of 14-day lag	1309.2	22840	8.743	0.001	0.0430	0.19919	163
+ Moon illumination of 14-day lag	1306.4	12533	4.9128	0.001	0.0236	0.22276	162

Sequential tests were conducted using the 'step-wise' procedure and AICc criteria. All variables were log(x+1) transformed, prior to analysis.

* Residual DF = 164

ANNEXURE 2

Protocol for dehydrating and embedding jellyfish tissue [obtained from Dr. Cathy H. Lucas, Associate Professor in Marine Biology, Ocean and Earth Science, National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton, SO14 3ZH, UK, Tel: +44 (0)23 8059 6617, cathy.lucas@noc.soton.ac.uk].

Dehydration:

30%	alcohol	1 hour
50%	alcohol	1 hour
70%	alcohol	1 hour
80%	alcohol	1 hour
90%	alcohol	1 hour
100%	alcohol	1 hour
100%	alcohol	1 hour

- 1 gonad per pot
- Label Carefully

(marker pen may dissolve in alcohol or histoclear)

10% alcohol stages may be split over two days

Embedding:

- Put tissue in Histoclear (Xylene) and overnight → 24hrs

- Can do a 50% Histoclear / 50% Wax stage in the oven overnight

WARNING: Histoclear is quite volatile: do a few pots at a time or cover pots in oven

- Put tissue in melted wax and overnight in oven at 60 °C.

- Embed in clean wax

- Place gonad in tray and fill each of the wells with wax
- Pour over with molten wax to the rim
- Gently push down a mounting block on top
- Top up the back of the mounting block with more wax
- Insert a thin label with the sample ID
- Once wax is completely set, push the wax block out of the mould.

ANNEXURE 3

Protocol for staining with Haematoxylin and Eosin [obtained from Dr. Cathy H. Lucas, Associate Professor in Marine Biology, Ocean and Earth Science, National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton, SO14 3ZH, UK, Tel: +44 (0)23 8059 6617, cathy.lucas@noc.soton.ac.uk].

Staining:

Dewax in Histoclear/Xylene	5 min
Rinse in 100% alcohol	1 min
Rinse in 70% alcohol	1 min
Stain in Haematoxylin	4 min
Wash in running tap water	15-20 min
Counterstain in Eosin	2 min
Rinse in tap water	1 min
Dehydrate in 100% alcohol	2 min
Dehydrate in 100% alcohol	2 min
Clear in Histoclear/Xylene	2 min

Mounting in DPX:

- Place thin line of DPX mountant across middle of the slide
- Put on cover slip and wait for DPX to spread out
- Push down on coverslip so DPX reaches all edges
- Once set can peel off any excess from around the coverslip