Dedicated dads: A study on the nesting behaviour of *Spondyliosoma emarginatum* (Telostei: Sparidae)

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Dissertation presented for the degree of Master of Science in the Department of Biological Sciences, University of Cape Town

October 2020

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Declaration

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Abstract

Fish display the most diverse parental care behaviours within the animal kingdom. These behaviours are important from evolutionary and conservation perspectives as parental care is critical for the development and survival of the young.

This study used video monitoring to uncover the nesting behaviour of an endemic southern African species of the Sparidae family, *Spondyliosoma emarginatum* (steentjie). *S. emarginatum* has evolved a nesting strategy by which males create nests on the seafloor for females to lay their eggs in. The eggs are fertilised and guarded by the male until they hatch. This species is particularly interesting as it has evolved a life-history strategy unique to the Sparidae, a combination of protogyny (female to male sex change) and male parental care.

A compound nesting site with over 50 nests was discovered in 9 to 14 m depth in False Bay, South Africa. A large diversity in nest size and habitat was uncovered. The first nest with eggs appeared on the 3rd of September and this number gradually increased to a maximum of 26 nests on the 3rd of October. Eggs took from seven to nine days to hatch. During nesting, males were affected by stochastic weather events in the form of south-easterly gales. Nesting sites are likely limited to sheltered bays along South Africa's mostly exposed coast, and the optimal depth is probably a trade-off between storm exposure and temperature. Deeper nests are expected in the east where the water is warmer.

Nests were filmed daily to reveal how male behaviour changes before egg deposition and during egg development. After egg deposition, males increased their time on the nest from 30 to 52 minutes per hour. Nest defence included the regular clearing of invertebrate invaders (brittle stars, hermit crabs, sea cucumbers, and sea stars), and chasing away other fish species (sand gobies, Roman, and hottentot) and neighbouring male steentjies. Energy intensive behaviours such as clearing the nest and fanning the eggs remained constant irrespective of egg presence. In addition, males do not feed when guarding eggs, which explains the drop in male condition during spring. The revelation of this nesting site is useful for conservation and fishery management as the nests and nesting males are vulnerable to both fishing and seabed disturbances.

Spondyliosoma spp. fulfil the requirements of the size-advantage model of protogyny. Their short life-span, in particular, their even shorter egg-laying life-span, classifies this species as an opportunist. This strategy may explain its success and numerical dominance in a wide range of biogeographic zones. The nesting behaviours shares much in common with freshwater opportunistic fish species and set it apart from the bulk of the Sparidae.

Acknowledgments

I would like to thank my supervisor Colin Attwood. Colin was an incredibly attentive supervisor, with a constant eye for detail and a passion for this project. His mentorship was an immense help and source of motivation. Colin also provided me with invaluable support and guidance during my first year as an international student, which was greatly appreciated settling into a new country.

An immense thank you to all the divers who were essential to this project, it would not have been possible without them! A special mention must be given to the buddy team that found the nesting site (Cameron Russell and Michael Daniel), to my incredible diving buddies who helped me regularly on the site: Michael Daniel and Daniel Seldon. The logistics of this project were also greatly facilitated by Andrea Plos who drove the boat and provided crucial surface support. I would also like to thank Matty Carr, who patiently helped me through many coding challenges, his presence and support throughout the writing process also made it one of the most enjoyable parts.

Finally, I can never thank my family enough for their continuous support. My sister has an incredible eye for detail, which was very helpful during writing, especially in figure design! And to my mum, an immense thank you for everything, which extends far beyond this dissertation. She always provides me with a continuous source of motivation and drive by being invested and involved in anything I do.

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Introduction

Parental care, the investment into offspring survival, is widespread throughout the animal kingdom and is an integral part in the reproductive life-histories of animals. Among the different care-giving species, fishes have evolved some of the most diverse forms of parental care in their sex allocation of care, and in the care-giving behaviours themselves. Of these parental care behaviours, the building and guarding of nests is widespread and represents a vulnerable and critical stage of a fishes' life-history. During nesting, fishes are exposed to natural and anthropogenic predation, while also experiencing a decrease in condition associated with the energy expenditure required to guard and maintain a nest for days to weeks at a time. The added widespread occurrence of sequential hermaphroditism in fishes creates complex life-history strategies that need to be taken into account for the successful management of exploited species.

In this dissertation, I report on the first collection of behavioural data on a wild nesting population of Steentjies (*Spondyliosoma emarginatum*). *S. emarginatum* is distributed throughout South Africa and belongs to one of only two genera in the Sparidae family that provides parental care. In addition, the co-occurrence of parental care and protogyny (female to male hermaphrodite) represents a novel evolutionary strategy in the family and only known to also occur in the Labridae and Gobiidae. I describe information on the nesting site habitat, the length of the spawning season, and the behaviour of courting and guarding males. These descriptions and the associated analyses will improve our knowledge of this species' life-history, increase our understanding of parental care in fishes, provide new insights into the effect of co-occurring hermaphroditism and parental care, and help inform local and regional conservation efforts. Because this type of investigation is relatively unusual in the marine ichthyological literature in South Africa, I will preface my dissertation with a review of parental care behaviours in vertebrates, and more specifically in fishes, to put my work into context.

1. Chapter 1 – Literature review

1.1. Parental care

1.1.1. Evolution

Species have evolved through the process of natural selection to maximise lifetime reproductive success (LRS), which is defined as the number of surviving offspring produced (Clutton-Brock, 1988), or as the number of gene copies that an individual leaves to future generations across its entire lifespan (Gross, 2005). Heritable traits and behaviours that increase LRS will increase in frequency through this process.

One such trait embedded in reproductive life-history and intrinsically linked to offspring survival is parental care. Parental care was first defined by Trivers in 1972 as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving and hence reproductive success at the cost of the parent's ability to invest in other offspring." (Trivers, 1972). Throughout the animal kingdom, parental care is widespread and characterised by four major strategies: no care, female-only care, male-only care, and bi-parental care. These forms are not mutually exclusive e.g. a species can show a combination of female-only and bi-parental care (Blumer, 1982). Accompanying these differences in the sex-allocation of care are a wide diversity of care-giving behaviours.

To understand the diversity of care-giving strategies across the animal kingdom, it is important to look at the evolutionary forces driving this behaviour (Baylis, 1981). Darwin was the first to comment on parental care in his work on sexual selection. However, he did not focus on the evolution of parental care, but rather on the link between parental care and sexual selection (Darwin, 1875). It was 60 years later that research on the evolution of parental care and its role in life-history theory got underway, but since then numerous hypotheses have been formulated and tested (Baylis, 1981). An exhaustive review of this subject is beyond the scope of this dissertation (readers can refer to Royle et al., 2012), but the major concepts insofar as they impact on my work and helped to build hypotheses are discussed below.

Investment hypothesis

The first models for the evolution of parental care were built on the investment hypothesis, which draws on two important concepts: there is a cost associated with parental care (Trivers, 1972; Williams, 1996), and these costs differ between the sexes (Bateman, 1948). William's Principle, recognised that investment into the present comes at the cost of investment into the future (Williams, 1966), and is defined as:

$$LRS = P(RE) + F(SE)$$

Here, LRS is the sum of the parent brood (P) and the future brood (F), where the total effort that can be expended by an organism over its lifetime (E=1) is distributed between reproductive effort (RE) and growth or somatic effort (SE) (Gross, 2005). William's principle is illustrated graphically by the sum of the reproductive and somatic allocation curves (Figure 1). Trivers used William's principle along with the assumption that a female's gametic investment is larger than that of a male's, to explain why a male was more likely to desert the female post-fertilisation and the female was more likely to provide parental care (Trivers, 1972). A female has less opportunity than a male for future broods, due to the high reproductive effort required to produce each gamete. She is better off ensuring her current brood is cared for and survives (Baylis, 1981). This also explains why males spend more energy on attracting females, and the common occurrence of sexual dimorphism (Baylis, 1981).

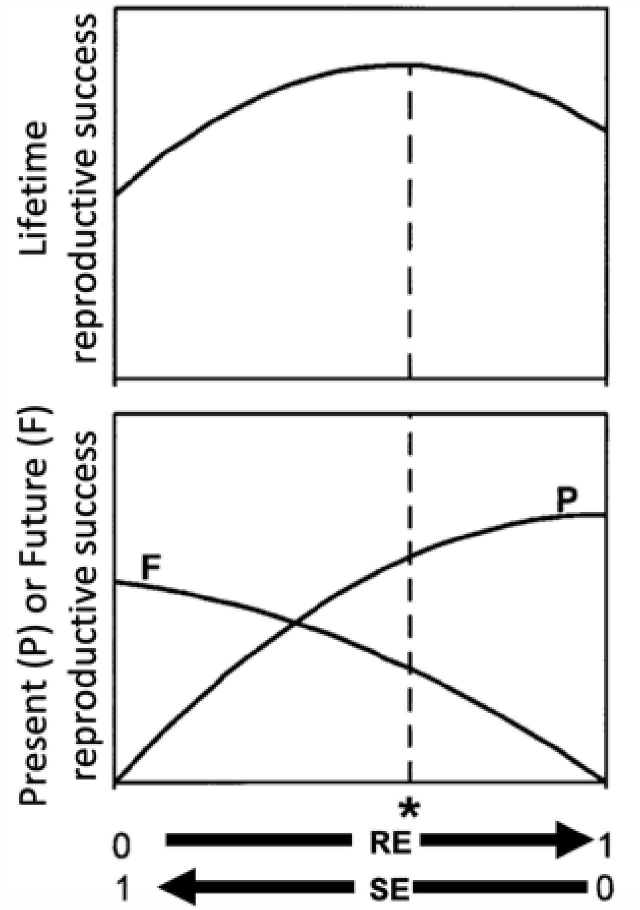

Figure 1. Graphical representation of William's principle. Bottom graph: reproductive success in the present (P) and in the future (F) vary with investment into reproductive effort (RE) and somatic effort (SE), respectively. Energy allocated into RE cannot be allocated into SE. This represents the cost of reproduction and the trade-off in present and future reproductive success. Top graph: an optimal solution is reached through natural selection to maximise lifetime reproductive success at the investments indicated by the asterisk (∗) (Gross, 2005)

Rate – limit hypothesis

While the investment theory describes most parental care patterns in terrestrial vertebrates, it fails to describe the widespread dominance of male-only care in fishes. To resolve this, Baylis put forward the rate-limit hypothesis (Baylis, 1981). He states that environmental stochasticity and varying rates of gametogenesis (gamete production) between the sexes can explain the dominance of paternal care in fishes (Baylis, 1981). Environmental stochasticity caused by the interaction of winds, currents and tides seen in rivers and some coastal zones provide a selection pressure that might favour demersal eggs. Where the risk of eggs being swept away to unfavourable environments is high, there will be an advantage in holding eggs fast. The evolution of territoriality then comes as species spend more time to locate and defend optimal spawning grounds (Baylis, 1981). Some species would then naturally evolve to staying with and guarding their eggs (Figure 2).

The environmental effect on life-history traits was also modelled in detail by Winemiller and Rosen in 1992 (Figure 3). Different environmental conditions lead to trade-offs between life-history traits and result in three main life-history strategies: periodic, opportunistic and equilibrium (Winemiller and Rose, 1992). It is thought that parental care maintains high juvenile survivorship in equilibrium strategy species that are characterised by low fecundity (Winemiller and Rose, 1992). These concepts help explain the effect of the environment on the evolution of parental care in fishes. When addressing why fishes express male-only care, Baylis attributes this to the faster rate of gametogenesis in males (Baylis, 1981). Males produce and release sperm at a faster rate than females produce and release eggs, so males can maximise breeding opportunities by monopolising optimal breeding sites to attract females (Baylis, 1981). Finally, most fishes are external fertilisers, which is strongly associated with paternal care (Mank *et al.*, 2005). The combination of external fertilisation, environmental stochasticity and differential rates of gametogenesis are ultimately what led to the evolution of paternal care in fishes (Baylis, 1981).

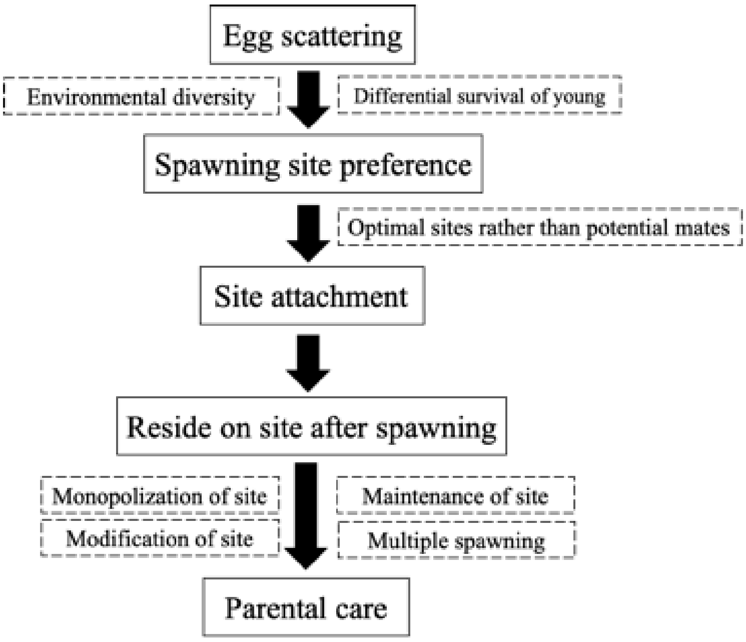

Figure 2. The evolution of parental behaviour from a non-guarding, egg scattering ancestral state. The factors suggested as instrumental in proceeding to the next step are listed under each heading. (Baylis, 1981)

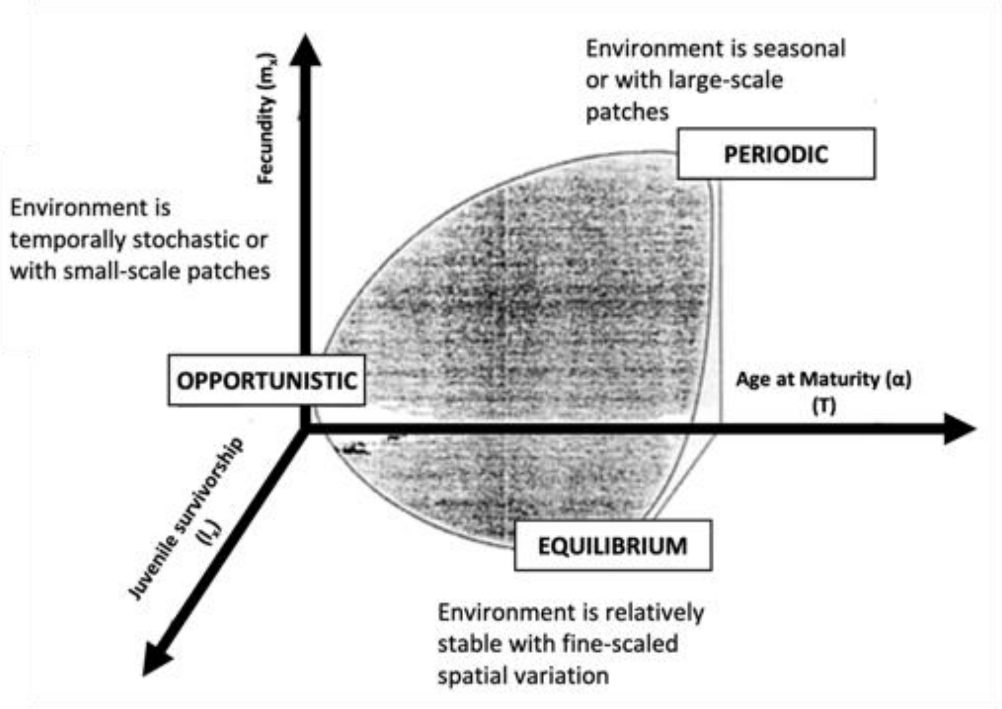

Figure 3. Fish life-history strategies based on trade-offs and selection in response to environmental variation. The opportunistic strategy (small T, small m_x, small I_x) maximizes colonizing capability in environments that change frequently on small spatio-temporal scales. The periodic strategy (large m_x, large T, small I_x) is favoured in environments having large-scale cyclic or spatial variation. The equilibrium strategy (large I_x, large T, small m_x) is favoured in environments with low variation in habitat quality and strong direct and indirect biotic interactions (Winemiller and Rose, 1992)

1.1.2. Distribution across major vertebrate groups

Maternal and bi-parental care: mammals, birds, reptiles and amphibians

All mammal species provide parental care, the dominant form of which is live-bearing followed by maternal care (Reynolds *et al.*, 2002). Live-bearing is absent in two families from the monotreme order, the platypuses (Ornoithorhynchidae) and spiny anteaters (Tachyglossidae), which instead lay single eggs (Reynolds *et al.*, 2002). Bi-parental care occurs in 9% of mammal genera, which include the carnivores, primates and rodents (Reynolds *et al.*, 2002). There are no instances of male-only care in mammals.

All bird species provide parental care. Bi-parental care occurs in 90-95% of species (Reynolds *et al.*, 2002; Benun Sutton and Wilson, 2019). Only 5-10% of species display female-only care and < 1% have male-only care (Reynolds *et al.*, 2002).

Most reptiles lay eggs without parental care. Female-only care in the form of egg guarding occurs in only 3% of genera, and live-bearing occurs in 20% of squamates (snakes and lizards). Finally, bi-parental care occurs in eight species of crocodilians (Reynolds *et al.*, 2002). There are no instances of male-only care in reptiles.

Parental care is rare in amphibians and present in only 8% of genera (Reynolds *et al.*, 2002) and unlike birds, mammals, and reptiles, all four care-giving strategies are present. Male-only care and female-only care each occur in 9% of amphibians. Only 1% of amphibians provide bi-parental care. A diversity of care-giving behaviour is present in amphibian genera, including egg guarding, the transport of tadpoles orally or on the adults' bodies, and live-bearing (Reynolds *et al.*, 2002).

Paternal care: Fishes

As with amphibians, all four major parental care strategies are present in fishes and they provide the largest diversity of parental care behaviours than any other vertebrate group. They are the only vertebrate group where male-only care becomes the dominant form of care. Care is present in 20-30% of teleost families, 10% provide male-only care, 3% bi-parental care and 1% female-only care (Reynolds *et al.*, 2002).

1.1.3. Parental care in fishes

As mentioned above, fishes are unique among vertebrates in the abundance of male care and in the diversity of parental care strategies that have evolved. The range in parental investment strategies for fishes lie along a continuum of increasing investment from oviparity to viviparity with many intermediate stages (Figure 4). Lecithotrophy refers to provisioning solely from the ovum yolk whereas anything further is termed matrotrophic (DeMartini and Sikkel, 2006). This concept is a little misleading in fishes as it represents a continuum of increasing maternal investment: oviparity might only represent a little investment to the female but could require a large investment from the male providing care for the eggs. It is still a useful framework to understand the varying reproductive strategies in fishes.

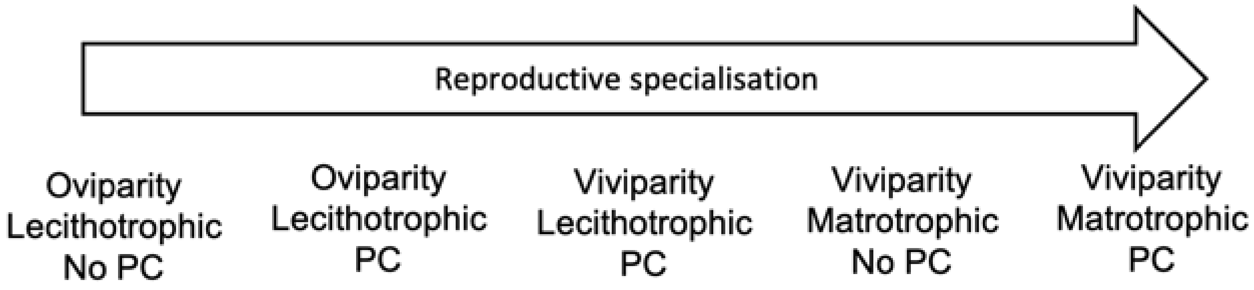

Figure 4. A continuum of increasing reproductive specializations in fishes. Each stage is a different combination of three factors: parity (top), embryo provisioning (middle) and presence or absence of parental care (PC) (bottom)

Chondrychtii

The Chondrychthii (cartilaginous fishes), or sharks and rays, are the oldest living group of jawed vertebrates (Wourms, 1977). They are internal fertilisers with extended embryonic development periods (few months to years) and care-giving is exclusively female (Stehmann, 2002). Egg-laying occurs in 40% of species and is assumed to be the ancestral state (Dulvy and Reynolds, 1997). However, chondrichthyans have evolved a wide variety of care-giving behaviours on a spectrum of increasing maternal input from oviparity to live-bearing (Dulvy and Reynolds, 1997). Live-bearing strategies in chondrichthyans can be broadly described as placental, or aplacental. In aplacental strategies, nutrients are derived from yolk reserves (known as ovovivipary), through embryonic cannibalism, or via placental analogues that secrete "uterine milk" (Wourms, 1977; Dulvy and Reynolds, 1997). It can be argued that parental care in oviparous chondrichthyans is through investment into durable and resistant egg capsules, and site selectivity for egg laying (Koob *et al.*, 1998).

Sarcopterygii

The Sarcopterygii (lobe-finned fishes) include two fish orders that display parental care. The Coelacanthiformes include one family, Latimeriidae, represented by two species known as Coelacanths that provide female-only care in the form of live-bearing (Balon *et al.*, 1988). The Lepidosireniformes include two families, Lepidosirenidae and Protopteridae, known as lungfishes that provide male-only parental care in the form of nest building (Greenwood, 1986).

Actinopterygii

The Actinopterygii make up 96% of living fish species (Nelson *et al.*, 2016). While a definite estimate on the number of families with parental care fluctuates due to unresolved phylogenetic trees (Mank *et al.*, 2005) and the lack of information on breeding habits for most species (Balon, 1975), it is thought to occur in 20-30% of the ~400 known Actinopterygian families (Blumer, 1982; Mank *et al.*, 2005). Recent attempts to summarise the distribution of parental care among the Actinopterygii revealed that parental care has evolved repeatedly and independently about 30 times from a basal ancestral state of no care (e.g. male-only care in the Spariformes), which is why they have often been used to model the evolution of parental care (Figure 5) (Mank *et al.*, 2005; Benun Sutton and Wilson, 2019). Male care has evolved independently ~22 times and female care about seven times (Mank *et al.*, 2005). While many orders appear to be polymorphic in parental care strategies, this is often resolved at the family level (Mank *et al.*, 2005; Benun Sutton and Wilson, 2019). In fishes with parental care, external fertilisation is predominantly linked to paternal care while internal fertilisation is linked to maternal care. This helps explain the dominance of paternal care since 86% of care associated with external fertilisation is male and external fertilisation occurs in 89% of families (Gross and Sargent, 1985). In contrast, 86% of care provided by fish with internal fertilisation (11% of families) is female-only (Gross and Sargent, 1985). Parental care is far more common in freshwater fish compared to marine fish, occurring in 60% of freshwater families (~50 families) compared to only 16% of marine families (~32 families) (Blumer, 1982). This relates to the rate-limit theory and the higher environmental stochasticity of rivers compared to the ocean (Baylis, 1981).

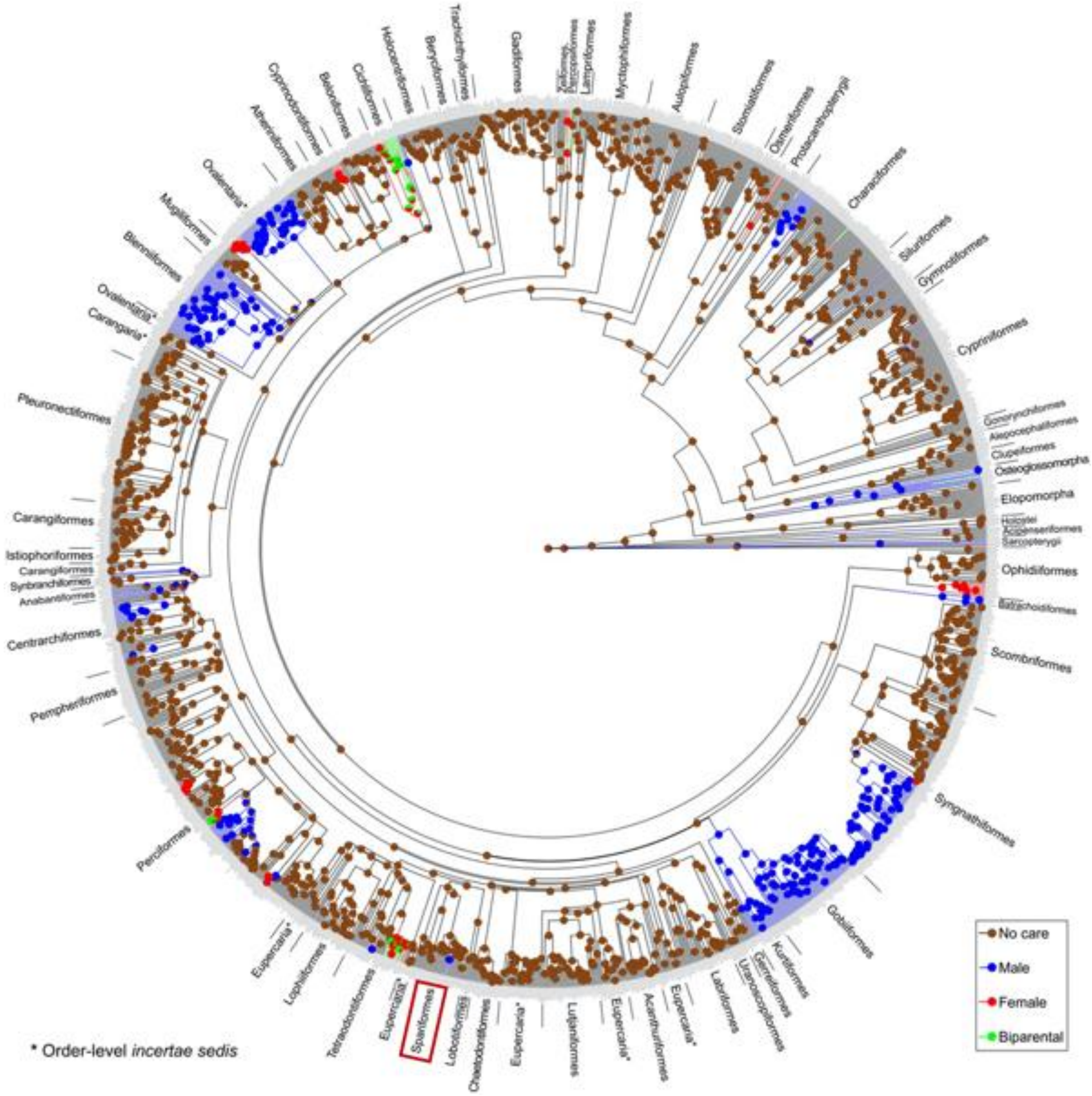

Figure 5. Ancestral state reconstruction of parental care in bony fishes. Tree is based on a summary of 1000 replicates using the symmetrical-rates model. Pie charts at the nodes represent maximum-likelihood support for ancestral state reconstructions (N = 1514 species). The red box highlights the Spariformes in which the Sparidae family lie. (Benun Sutton and Wilson, 2019)

In 1975, Balon grouped fish into 32 guilds according to their different spawning strategies (Table 1) (Balon, 1975). These classifications highlight the incredible diversity in fish reproductive strategies and their associated level of parental care. While there is some overlap between the guilds, there is a clear distinction in the type and amount of investment between the three major strategies: non-guarders, guarders and live-bearers. Non-guarders provide little to no parental care. They spawn pelagic eggs (pelagophils) that are carried by currents in the water column, or they spawn demersal eggs that are deposited on various substrates but not guarded. Similarly to the chondrichthyans, it could be argued that the choice and preparation of a substrate for egg laying is a form of parental investment. Guarders provide parental care of their eggs. Finally, bearers provide some of the most extreme forms of parental care where eggs develop on or in a fishes' body. Within each strategy, the care-giving individual carry out one or multiple behaviours that ensure the survival of the eggs (Table 2). The most common form of parental care activity is guarding, which occurs in 95% of all care-giving species (Blumer, 1979; Gross and Sargent, 1985).

Table 1. A classification of fish reproductive guilds according to chosen spawning substrate. When a definition is blank it means the term has already been defined higher up in the table. (Balon, 1975)

Subsection	Guild	Spawning substrate
Non-guarders		
Open substratum spawners	Pelagophils	in the water column
	Litho-pelagophils	on rock/gravel, the larvae/eggs may float
	Lithophils	on a rock or gravel bottom
	Phyto-lithophils	on submerged plants, rocks, logs or gravel
	Phytophils	within or on live vegetation
	Psammophils	on roots or grass above a sandy bottom or on sand
Brood hiders	Lithophils	-
	Speleophils	within crevices or holes
	Ostracophils	in gill cavities i.e. mussels
	Aero-psammophils	out of water in sand
	Xerophils	in moist sand, sod or mud beneath cracked dry crust
Guarders		
Substratum choosers	Lithophils, Phytophils, Pelagophils	-
	Aerophils	on the underside of broad leaves or rocks that overhang the water
Nest spawners	Lithophils, Phytophils, Psammophils, Speleophils	-
	Aphrophils	in a floating froth nest produced by the parent
	Polyphils	on various substrates (non-specialised)
	Ariadnophils	in a nest held together by sticky secretions from the male's kidneys
	Actinariophils	in anemones
Bearers		
External	Transfer brooders	On the parent's body until a suitable substrate is found
	Forehead brooders	On a hook protruding from the forehead of the parent
	Mouth brooders	In the parent's mouth
	Gill-chamber brooders	In the parent's gills
	Skin brooders	On the surface of the parent's body
	Pouch brooders	On the surface of the parent's skin but covered by a layer of skin to form a pouch
Internal	Ovi-ovoviviparous	Eggs are incubated in the body cavity but may be released at any time during development
	Ovoviviparous	Eggs are incubated in the body cavity
	Viviparous	Embryos are nourished via absorptive organs

Table 2. Range of parental care behaviours in fishes (Blumer, 1982)

Form of care	Definition
Brood pouch egg carrying	Eggs held in a special sac-like external structure during their development
Cleaning eggs	Taking the eggs into the mouth and cleaning them of any debris
Coiling	The parent coils its body around the egg mass while guarding them. This guarding posture reduces the eggs' exposure to air at low tide, when the oviposition site is intertidal
Ectodermal feeding	A specialized mucus produced on the body surface of the parent is used as food by the young fry
Egg burying	Depositing eggs beneath the substrate surface or covering eggs with substrate material
External egg-carrying	Eggs attached to the parent externally and carried until hatching
Fanning	Moving the pectoral, pelvic, anal, or caudal fins over the egg mass or fry, to aerate them and remove sediment
Guarding	Displaying towards and/or actively chasing conspecifics and heterospecifics that approach the eggs or fry, or the site where they are located
Internal gestation	Female retains eggs in her body and their development takes place inside the ovaries or oviducts
Moving	Taking eggs or fry by mouth from one location to another, often from one nest to another
Nest building and maintenance	Digging a depression in the substrate, a burrow, or making an elevated mound with substrate materials. Assembling a cup or tube structure with pieces of vegetation. Blowing mucus-covered bubbles that form a floating mass
Oral brooding	Holding eggs and fry in the mouth or gill cavities during their development, typically ending with the release of well-developed fry
Removal	Dead or diseased eggs removed by mouth from the egg mass
Retrieval	Taking eggs or fry that fall or stray from the nest or school into the mouth, and returning them to the nest or school
Splashing	Splashing water on eggs deposited out of water or eggs exposed at times of low tide
Substrate cleaning	The removal of detritus, algae, and animals from the site where eggs are to be deposited

1.1.4. *Nest guarding*

According to Trivers, “parental investment does not include mate-getting activities”. He excluded nest-building from parental investment since it is often first used as mate-attraction (Trivers, 1972). For the purpose of this work, parental investment is defined using Blumer’s more inclusive definition: "non-gametic contributions that directly or indirectly contribute to the survival and reproductive success of the offspring" (Blumer, 1979).

Nest building occurs across the animal kingdom and is crucial for the survival of the young (Crisp and Carling, 1989).

Whereas the study of nests has mostly focused on birds, over recent years fish have been the topic of an increasing number of studies, focusing mostly on two families: the Gasterosteidae (sticklebacks) and the Gobiidae (gobies) (Crisp and Carling, 1989). The taxonomic diversity of nest building species is therefore still poorly represented in the literature.

The evolution of nests can be explained in light of Baylis' rate-limit theory that demersal eggs select for territoriality. Territoriality arose as a result of males monopolising optimal breeding sites to attract females, but in some cases these optimal breeding sites might have been limited. Fishes able to transform sub-optimal sites into optimal ones such as through the creation of a nest or burrow would be more likely to attract a female (Baylis, 1981). The question remains as to why a male would then stay with and guard the eggs post spawning. Baylis came up with four major factors to explain this:

- Denying access to other conspecifics
- Opportunity for multiple spawnings
- The nest might only be optimal for the eggs through constant work i.e. removing sediment
- Protection from predators

Lastly, it is important to clarify the definition of a nest. In its broadest definition, a nest is any structure used to house eggs (Navarrete-Fernández *et al.*, 2014). At their most basic form, nests include structures already present in the habitat i.e. plants or underhanging rocks (Balon, 1975). Some species slightly modify spawning substrates such as salmonid females that construct small depressions known as "redds" in gravel rivers (Crisp and Carling, 1989). Other species simply clear the bottom substrate to make a clean surface (Navarrete-Fernández *et al.*, 2014). Nests can become far more complex and include the creation of burrows (DeMartini and Sikkel, 2006), foam nests (Andrade and Abe, 1997), and giant complex geometric structures (Kawase *et al.*, 2013). The action of nest building is only one aspect of parental investment and fish continue to carry out multiple post-fertilisation activities on the nest to ensure their eggs remain protected and well ventilated (Green and McCormick, 2005).

1.2. Parental care and hermaphroditism

It is difficult to talk of parental care in fishes without mentioning another key attribute to reproductive life histories: the sexual system. Teleost fishes display the most diverse forms of sexual systems than any other vertebrates (Smith and Wootton, 2016; Kuwamura *et al.*, 2020), ranging from gonochorism (separate sexes) to hermaphroditism, defined as protogynous (female first), protandrous (male first), simultaneous or bi-directional (DeMartini and Sikkel, 2006; De Mitcheson and Liu, 2008). Hermaphroditism has evolved independently in several teleost families (De Mitcheson and

Liu, 2008; Erisman *et al.*, 2013) and is estimated to be present in 461 species, 156 genera, 41 families and 17 orders (Kuwamura *et al.*, 2020). Protogyny is the most abundant type (305 species of 20 families), followed by bi-directional (66 species of seven families), simultaneous (55 species of 13 families), and finally protandry (54 species of 14 families).

Following William's principle, hermaphroditism has evolved to maximise LRS (Warner, 1975; Buxton and Garratt, 1990) and two main models are used to explain the adaptive significance of different types of hermaphrodites. For protogyny and protandry, the size advantage model (SAM) is the most widespread hypothesis, and it states that sex change occurs when one sex reproduces more efficiently when small and young, and the other sex when larger and older (Ghiselin, 1969; Kuwamura *et al.*, 2020; Pla *et al.*, 2020). Bateman's principle states that female reproductive success is limited by egg production and thus increases with body size, while male reproductive success is instead limited by the ability to gain access to eggs and is thus affected by the mating system (Charnov and Hutchinson, 1979). In 1975, Warner set out conditions that would select for protogyny or protandry in teleost fish populations (Warner, 1975). In species where the mating system is characterised by territorial polygamous males and where male experience is required to find a mate, there is a clear selective advantage to being a large male and protogyny is the most adaptative strategy (Warner, 1975; Erisman *et al.*, 2013). In contrast, in species with paired spawnings and a low density of males, male reproductive success is not affected by size and instead the species will benefit from large fecund females, and so protandry is favoured (Erisman *et al.*, 2013). Finally, in species with spawning aggregations and high sperm competition, the predicted sexual system is gonochorism (Kuwamura *et al.*, 2020). Other models include the risk of movement model where bi-directional sex change is favoured in low-density species where individual encounters are scarce (i.e. in deep sea fishes) and the ability to change to either sex is adaptive (Erisman *et al.*, 2013).

An additional benefit to hermaphroditism is that sex reversal occurs in response to demographic conditions, which allow species to adapt locally by choosing when and if to change sex (Buxton and Garratt, 1990). This parallels parental care, as both these traits are evolutionary labile and polymorphic among most genera and families (Erisman *et al.*, 2013). Surprisingly, no studies have examined the link between hermaphroditism and parental care. How does the co-occurrence of parental care and hermaphroditism affect the sex allocation of reproductive effort? The answer is unknown, and answers are scarce in the literature. Some studies remark on the co-occurrence of protogyny and parental care in fishes, which occurs in the Labridae (Alonzo and Warner, 2000; Alonzo and Heckman, 2010), and Caracanthidae (Wong *et al.*, 2005). Bi-directional hermaphroditism was also recorded in the Gobbiidae (Nakashima *et al.*, 1996). Finally protandry and parental care is known in clownfishes of the Pomacentridae (Swagat Ghosh *et al.*, 2012).

The sex allocation of reproductive effort is likely to follow a different dynamic in care-giving hermaphroditic species compared to gonochoristic species. This is due to the potential "safety net" provided by the opportunity to redeem failed reproduction as one sex by successfully reproducing as another. The evolution of parental care with protogyny should be treated as a novel evolutionary strategy that requires further research, and one such family where this relationship can be explored is the Sparidae.

1.3. The Sparidae

1.3.1. Parental care and hermaphroditism

The Sparidae (seabreams and porgies) are a teleost family in the Spariformes order (Betancur *et al.*, 2017) encompassing 38 genera and 150-160 coastal fish species (Pla *et al.*, 2020). While describing the phylogenetic placement of the Sparidae in the Actinopterygii is out of the scope of this study, it is worth knowing that prior to 2013 the Sparidae were placed under the Perciformes (Betancur-R *et al.*, 2013).

They have a widespread geographical range that includes the north east Atlantic and Mediterranean, the western and southern African coast, the western Indian Ocean, the central western Atlantic, the north western and eastern Pacific, New Zealand waters, southern Australia, and the Red Sea (Santini *et al.*, 2014). In these waters they are found in continental-shelf and brackish waters where they can be seen over rocky reefs and sandy bottoms (Santini *et al.*, 2014). The Sparidae range in size from 20-200 cm (Pla *et al.*, 2020) and include many commercially important species (Carpenter, 1999; Attwood *et al.*, 2019).

The Sparidae have been the subject of numerous studies since they display the most complex expression of hermaphroditism in teleost fishes (Buxton and Garratt, 1990). Recent estimates show that 84% of Sparidae species are hermaphrodites, and the same genera often contains species of different sexual systems (e.g. *Diplodus* spp., *Pachymetopon* spp., *Chrysoblephus* spp.)(Figure 6) (Erisman *et al.*, 2013). Of the 28 genera for which the sexual system is known, 20 are gonochoristic, 12 are protogynous and eight are protandrous (Pla *et al.*, 2020). Studying the distribution of sexual systems in the Sparidae has been challenged by difficulties in diagnosing accurately some species and their distribution in deep or offshore habitats (Erisman *et al.*, 2013). Recent studies still disagree on some diagnoses such as on the sexual system of the *Pagrus* and *Diplodus* genera (Kuwamura *et al.*, 2020; Pla *et al.*, 2020). Many Sparidae species still challenge the predictions of the SAM such as *Acanthopagrus berda*, which is a protandrous hermaphrodite with high sperm competition due to spawning aggregations (Erisman *et al.*, 2013).

Parental care is rare in the Sparidae. In 1979, only one species was used to document parental care in the family (Blumer, 1979). Forty years later, when reproductive information was gathered on 18 out of the 38 genera, only two genera showed evidence of parental care, *Spondyliosoma* and *Spicara*, both of which provide male-only care in the form of nest building and guarding of the eggs (Figure 7) (Harmelin and Harmelin-Vivien, 1976; Tunley *et al.*, 2009; Benun Sutton and Wilson, 2019). It is important to note that *Spicara* along with the rest of the Centrarchidae were recently included in the Sparidae family (Day, 2008; Betancur *et al.*, 2017). Based on the assumption of an ancestral state of no care, parental care evolved independently in the Sparidae and could represent an advanced feature in the family. Both genera are also protogynous (Kuwamura *et al.*, 2020) so the evolution of parental care along with protogyny is a novel evolutionary strategy in the family. In addition, *Spondyliosoma* and *Spicara* are in the top ten most wide-ranging Sparidae genera (Table 3). This suggests that this novel evolutionary strategy is just as successful as pelagophilic strategies.

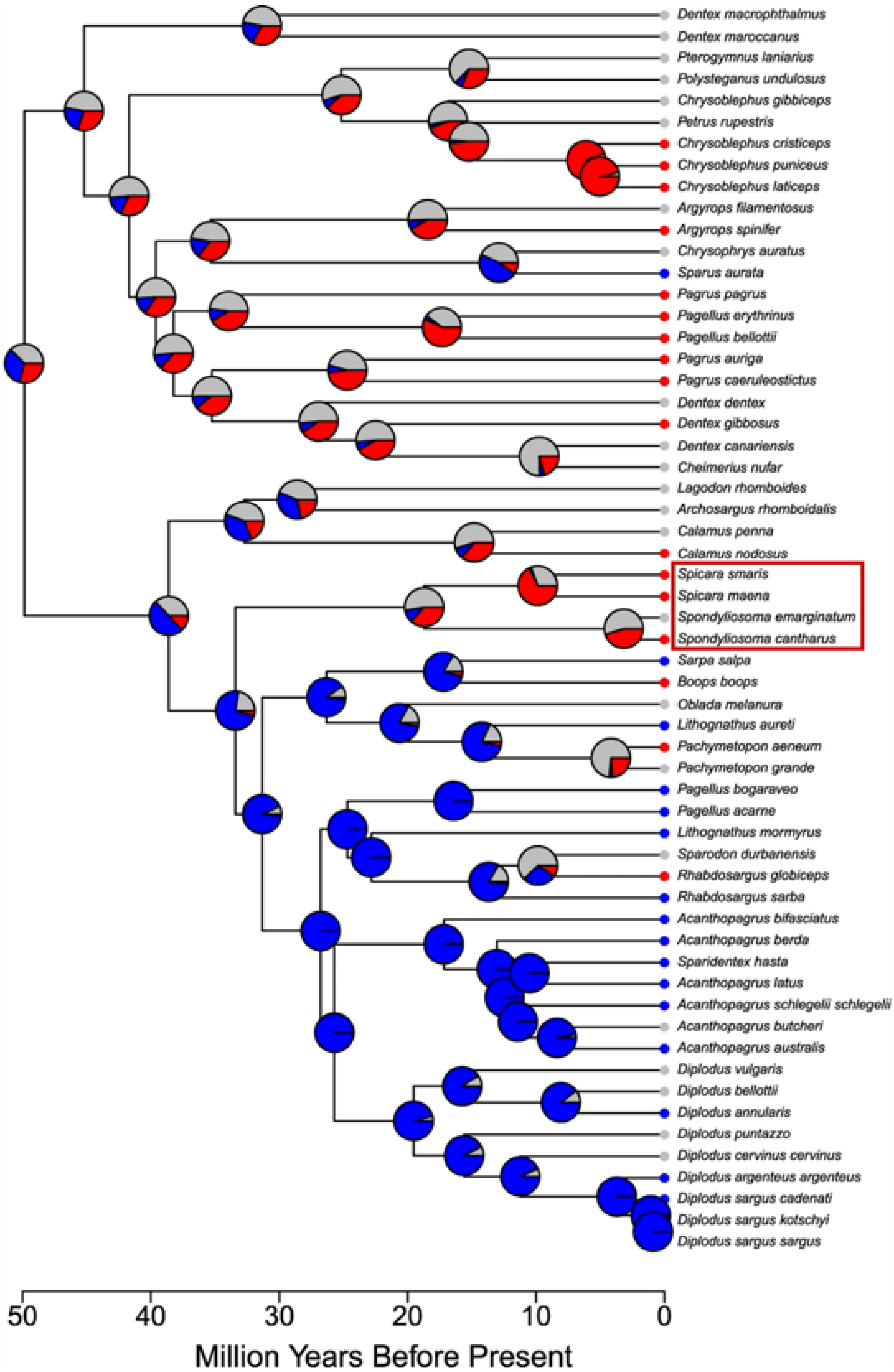

Figure 6. Ancestral state reconstruction in the Sparidae. Sexual system is coded as gonochorism (grey), protandry (blue) and protogyny (red). The pie area indicates the likelihood of character state at each node for the three states. (Pla *et al.*, 2020). The red square outlines the only species that display parental care. NB: *Spondyliosoma emarginatum* was incorrectly described as gonochoristic, it is a protogynous species

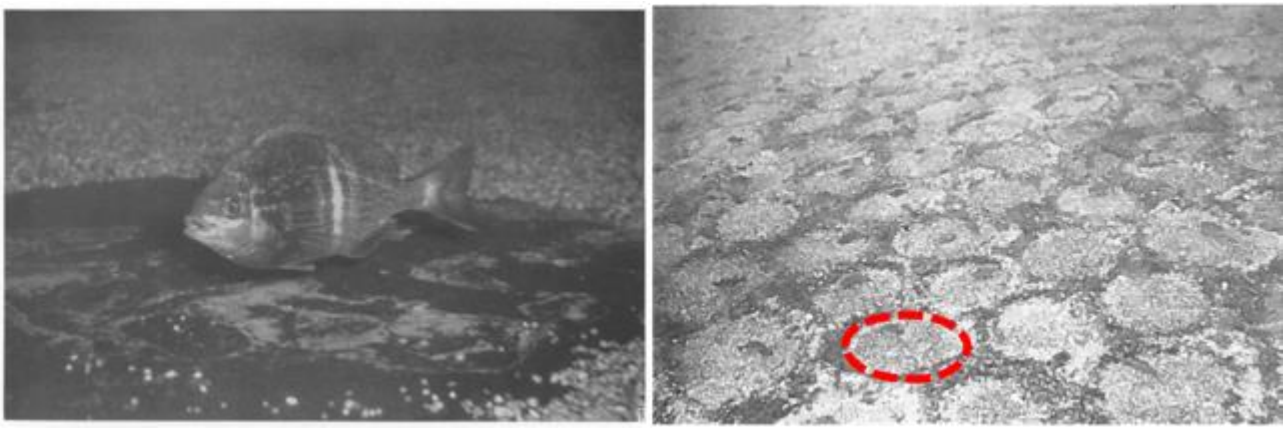

Figure 7. Nesting Sparidae. Left pane: *Spondyliosoma cantharus* male on a nest in the Plymouth aquarium, UK (Wilson, 1958). Right pane: nesting site for *Spicara smaris* in the Port-Cros national park, France. A nest is highlighted by a red circle. (Harmelin and Harmelin-Vivien, 1976)

Table 3. Top ten most wide ranging sparids along with their known sexual systems. Gonochoristic (G), protandry (PA), protogyny (PG). Only *Spondyliosoma* and *Spicara* spawn demersal eggs and provide parental care. Data on sexual systems extracted from Ortiz, 2019 and Pla *et al.*, 2020. Data on FAO areas extracted from FishBase. FAO area codes extracted from FAO, 2015

Genus	Nº Species	FAO marine areas	Sexual systems
Pagrus	6	21, 27, 31, 34, 37, 41, 47, 57, 61, 71, 81	G, PG
Diplodus	23	21, 27, 31, 34, 37, 41, 47, 51	G, PA
Dentex	14	27, 34, 37, 47, 57, 61, 71, 77	G, PG
Acanthopagrus	20	37, 47, 51, 57, 61, 71, 81	G, PA
Rhabdosargus	6	37, 47, 51, 57, 61, 71, 81	PA, PG
Spicara	8	27, 31, 34, 37, 47, 51	PG
Pagellus	6	27, 34, 37, 47, 51	PA, PG
Boops	2	27, 34, 37, 47, 51	PG
Spondyliosoma	2	27, 34, 37, 47, 51	PG
Lithognathus	4	27, 34, 37, 47, 51	PA

1.3.2. Sparidae in South Africa

South Africa is home to 46 Sparidae species, which is more than that of any other. These include seven endemic species (Ortiz, 2019) and nine listed as threatened by the IUCN (IUCN, 2020). All species of South African Sparidae produce pelagic eggs except for the one *Spondyliosoma* species and two *Spicara* species, which produce demersal eggs and provide parental care (Ortiz, 2019). See Table 4 for a breakdown of the sexual systems found in South African Sparidae.

Table 4. Distribution of sexual systems among South African sparids. In number of species, the numbers in bracket represent species for which the sexual system is assumed but not confirmed. In the number of species, the number in brackets includes the total number of known and assumed species of that sexual system (Mann, 2013; Ortiz, 2019)

Sexual system	Number of species	Proportion of species
Gonochoristic	14	30%
Protogyny	6 (8)	13% (30%)
Protandry	6 (10)	13% (15%)
Unknown	11	23%

1.4. Introduction to methods

1.4.1. Study species

S. emarginatum is a member of the Sparidae in the Spariformes order (Betancur *et al.*, 2017). The genus includes one other species, *S. cantharus* (Black bream).

Diet

S. emarginatum is omnivorous and shifts from a predominantly herbivorous diet at smaller sizes (<178 mm) to a more carnivorous one at larger sizes (Fairhurst *et al.*, 2007).

Distribution

The *Spondyliosoma* genera is the fourth most wide-ranging sparid behind *Diplodus*, *Pagrus* and *Boops*. *S. emarginatum* is considered endemic to South Africa and is widely distributed around the southern and eastern coast. It also occurs on the Atlantic coast in the sheltered conditions of Langebaan Lagoon and Saldanha Bay (Fairhurst *et al.*, 2007; Tunley *et al.*, 2009). While some divers have said to have spotted *S. emarginatum* to the west of the Cape Peninsula (Zsilavecz, 2005), the next accepted northernmost limit is to the east of the Cape Peninsula in False Bay. *S. emarginatum* is widely distributed throughout False Bay (De Vos *et al.*, 2015) and along the eastern coast throughout the shallow waters of the Aghulas Bank (Attwood and Ensair, 2020). While the GBIF database also maps *S. emarginatum* across Namibia (n=3), Mozambique (n=1) and Mauritius (n=1), these records have limited information and no accompanying photographs. The Namibian records date from a 60ft otter trawl deployed during a historical research survey near the border between South Africa and Namibia in 1947 (GBIF, 2017). The trawl might have travelled from South African waters into Namibian waters before being brought up. We have since received photographic evidence of *S. emarginatum* individuals in Namibia (Attwood, Pers. Comm.). They might reach their range limit around the Namibian and South African border at the Benguela upwelling system, which is a known natural species barrier (Barange *et al.*, 1992). The only sighting available in Mozambique is from three individuals caught in a gillnet in 2015. The Mauritius record comes from a 1984 fisheries guidebook based on catches from local markets around the island (Bauchot and Bianchi, 1984). There is no information on the catch location and there have been no sightings in Mauritius since. It is likely that the species is mostly concentrated around South Africa. Recently, the genus has received attention in terms of its phylogeographic distribution (McKeown *et al.*, 2020; Neves *et al.*, 2020). These studies have confirmed the genetic basis of classifying *S. cantharus* and *S. emarginatum* as separate species as well as revealing distinct monophyletic clades for *S. cantharus* along its geographic range from Angola to the Mediterranean (McKeown *et al.*, 2020; Neves *et al.*, 2020).

Life-history

S. emarginatum is a protogynous hermaphrodite (Fairhurst *et al.*, 2007). It changes from female to male at either two or three years old and the size at which it does so depends on the selection pressures of the habitat (Tunley *et al.*, 2009). In the protected area of Langebaan Lagoon, the fork length size at sex change is 220 to 240 mm whereas in unprotected and fished areas such as Struisbaai, the size of sex change is reduced to ~180 mm (Tunley *et al.*, 2009). They can reach a maximum size of 450 mm but rarely exceed 250 mm, and can live up to seven years old (Fairhurst *et al.*, 2007). *S. emarginatum* populations follow a 1:2.6 male:female sex ratio and when sexually mature, the species is characterised by a large difference in gonadosomatic index (GSI) between the sexes (Attwood and Ensair, 2020). Female GSI is higher than that of males and that of other sympatric sparid species, with an average GSI of 7.5 to 10% for ripe ovaries, compared to 2% or lower for males (Attwood and Ensair, 2020). The species also experiences important changes in body condition (essentially mass) throughout the year, with males undergoing a stark decline in condition between the second and third quarter, which is in line with the nesting period (Figure 8) (Attwood and Ensair, 2020). During the breeding period, the species is sexually dimorphic and *S. emarginatum* males are characterised by a distinct nuptial dress of black and white bands along with a yellow and blue stripe across the snout (Figure 9). Females in spawning colours are characterised by a small white band along their side and develop patches of white along their dorsal flank (Figure 9).

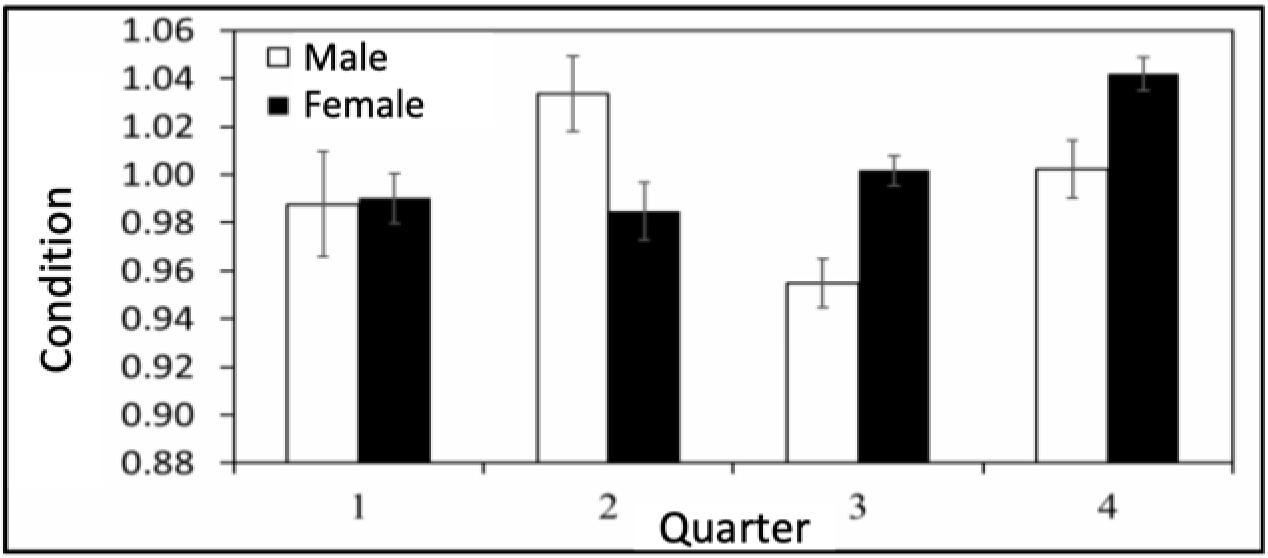

Figure 8. The average condition factor of *Spondyliosoma emarginatum*, in each quarter by sex (Attwood and Ensair, 2020). Quarter 1 represents the months from January to March. Error bars indicate one standard error. Condition is a surrogate for weight, for the exact formulas used see Attwood and Ensair, 2020

Figure 9. *Spondyliosoma emarginatum* colours. Top left: both males and females year-round. Bottom left: female in spawning colours, notice the white thick stripe along her side and the white blotches along the dorsal spine. Top right: Male in black and white banded colour. Bottom right: front view of a male's blue and white stripes on its forehead. Photographs credited to N. Faure Beaulieu

Parental Care in Spondyliosoma

During the spawning season, *S. emarginatum* display male parental care expressed as territorial and nesting behaviour (Penrith, 1972; Mann, 2013). The nesting behaviour as well as female activity during spawning remain mostly unknown and have only been documented in aquaria (Van Bruggen, 1965). What is known is that a male will construct a small depression in the substrate on which he attracts females to come and spawn, the male will subsequently guard the eggs until hatching. In addition, it is important to mention that while referring to *S. emarginatum* individuals as male or female is convenient it is also misleading in the context of life-history theory. Since the individual acts as both sexes throughout its lifetime, the energy allocation to reproductive effort or growth cannot be regarded as separate between the sexes. To understand the consequences of hermaphroditism and parental care co-occurring, a thorough description of the mating system is necessary.

Fisheries

S. emarginatum is often deemed too small and of little commercial value to trawl and line fishers (Tunley *et al.*, 2009; Mann, 2013). Currently, *S. emarginatum* is only used as bait or fished in the absence of more profitable species (Mann, 2013). There is a daily bag limit of 10 pieces per person per day but stock status is currently unknown (Mann, 2013). *S. emarginatum*'s congener, *S. cantharus*, is conversely of high commercial and recreational value as it is a good food fish as well as used for fish meal and oil (Capenter and De Angelis, 2016). It is fished along its range by line, pelagic and bottom trawls, beach seines and traps and plays a particularly important commercial role in the UK (Pinder *et al.*, 2017), Portugal (Gonçalves and Erzini, 2008) and Senegal (Capenter and De Angelis, 2016). *S. emarginatum* could grow to become a valued species in South Africa due to a demanding fisheries sector (FAO, 2018) and as commonly caught linefish species are depleted (Griffiths, 2000; Mann, 2013). The combination of being a nest builder and protogynous species renders them particularly vulnerable to overexploitation. Life-history and population data is required to ensure that the species is not at risk from a rapidly expanding recreational fishery.

1.5. Aims

This dissertation is exploratory in nature and my aim is to reveal new insights into the reproduction of *S. emarginatum*, a protogynous sparid with male-only parental care. The main themes I will aim to cover are the nesting habitat and the nesting behaviour. To answer these questions, I will use non-invasive methods, which include exploratory diving and underwater video monitoring.

Chapter 2 will focus on finding and describing the nesting habitat and spawning system. A mention on the techniques used to find a nesting site will be described as this represented a considerable amount of time and energy due to the lack of knowledge on nesting sites in South Africa and how to find them. I then hope to understand how long the spawning period lasts for, by using the first and last set of spawned eggs as a proxy. I will also gather information on the competitiveness of the system by measuring the density and size of nests on the site as well as the proportion of nests to receive eggs. Finally, I will also describe the physical characteristics of the nesting site.

Chapter 3 will focus on behaviour. Using remote underwater video, male behaviours while on the nests will be monitored and this should uncover how their behaviours change through different stages of nesting: nest building, courtship, and nest-guarding. Female behaviours will also be captured indirectly as they swim by or visit monitored nests.

Knowledge from these two chapters should provide new insights into the life-history of a protogynous sparid with male-only parental care, which appears to be a novel evolutionary strategy in the Sparidae. This information will also help direct conservation efforts locally and globally. This genus is a commercially important species and its vulnerability during nesting needs to be taken into account for sustainable exploitation.

2. Chapter 2 - Discovery of a *Spondyliosoma emarginatum* nesting site in False Bay, South Africa

2.1. Introduction

For demersal fish spawners, and especially species that maintain and guard nests, the availability and quality of adequate spawning grounds are vital for successful reproduction (Barber, 2013). In marine species these spawning grounds are often located in sheltered shallow coastal habitats or estuaries (Nagelkerken *et al.*, 2015; Macura *et al.*, 2019). Unfortunately, these coastal habitats have been exposed to overexploitation, habitat degradation, and pollution over the past few centuries (Lotze *et al.*, 2006; Brown *et al.*, 2019). An extreme example showcasing the damages caused to coastal habitats comes from the Baltic sea. A case study in the Stockholm archipelago revealed that coastal spawning-ground habitat for commercially important species such as northern pike (*Esox lucius*), eurasian perch (*Perca fluvialutis*) and roach (*Rutilus rutilus*) declined by 0.5-1% per year since 1960 (Sundblad and Bergström, 2014). A poor understanding of spawning habitat requirements can lead to uninformed marine spatial planning, the degradation of crucial spawning and nursery grounds, and the collapse of many commercially and ecologically important species (Brown *et al.*, 2019).

Fisheries management plans often fail to incorporate knowledge on essential habitats for reproduction (reviewed by Sundblad et al., 2014). The lack of knowledge on important spawning grounds is also made harder for temperate species where turbid and cold conditions are often not as suitable for either underwater observations or habitat mapping (Ebeling and Hixon, 1991; Sundblad *et al.*, 2014). This is also evident in the literature where there is a bias towards the study of tropical reef fish behaviour and reproduction (Thresher, 1984; Ebeling and Hixon, 1991). The proportion of fish that are demersal spawners is higher in temperate compared to tropical environments, but data on temperate species' parental care behaviour and larvae development are lacking (Leis *et al.*, 2013). In addition, many demersal spawning fishes are commercially important (Sánchez Lizaso *et al.*, 2020), and so understanding spawning habitat requirements is crucial for conservation and coastal economies.

One such temperate nesting species is *Spondyliosoma emarginatum* in South Africa. South Africa's coastline is smooth with few embayments and enclosed seas (Hutchings *et al.*, 2002). This smooth coastline is characterised by high short-term environmental variability, a strong western boundary current on the east coast (Aghulas current) and intense upwelling and shelf-edge jet currents on the west coast (Hutchings *et al.*, 2002). The combination of a smooth coast and dynamic coastal conditions has resulted in relatively few suitable nursery grounds, and most fish are serial broadcast spawners of pelagic eggs (Hutchings *et al.*, 2002). *S. emarginatum* is the only species in South Africa known to lay demersal eggs in nests.

Available nesting records for *Spondyliosoma* species are sparse (Table 5). Most records are for *S. cantharus* and there are few observations of *S. emarginatum*. Multibeam side-scan sonar surveys have helped in the discovery of impressive nesting sites off the south coast of the UK (Figure 10) whereas popular diving literature contain various photographs of impressive *Spondyliosoma* nest sites. A common feature of nesting habitats of *Spondyliosoma* species seems to be the availability of low-profile reef buried under a thin layer of sediment. The nests are made by removing a layer of sand or silt to expose the hard-bottom substratum. This feature seems consistent across both species (Figure 11). There are reports of *S. emarginatum* juveniles sampled in the Swartkops and Sundays estuary in South Africa (Beckley, 1983, 1984), but it is unlikely nests form there due to the instability of the sediment.

Table 5. Nesting records for *Spondyliosoma* spp. The first three are for *S. emarginatum* and the following two are for *S. cantharus*. n/a indicates that the information was not available or is not applicable. References: (1) Van Bruggen, 1965, (2) Penrith, 1972, (3) Burger, 1990, (4) Collins et al., 2012, (5) James et al., 2010

Location	**Month**	**Season**	**Nest width (cm)**	**Distance between nests (m)**	**Depth (m)**	**Substratum**
Port Elizabeth aquarium, South Africa	September - November	Spring	80 - 100	0 (limited tank space)	n/a	Sandy
False Bay, South Africa	January	Summer	50	3-10	18 - 30	Coarse shell grit and fine sand
Storm's River mouth, South Africa	November	Spring	50	n/a	10	Sandy
Central south coast, UK (five sites)	May - June	Spring - Summer	100 - 250	n/a	9 - 23	Mixed: sand, gravel, silts, shell, cobble, buried boulders
Central south coast, UK	n/a	Spring - Summer	100 - 200	n/a	5 - 25	Sandy gravel; thin sediment on bedrock

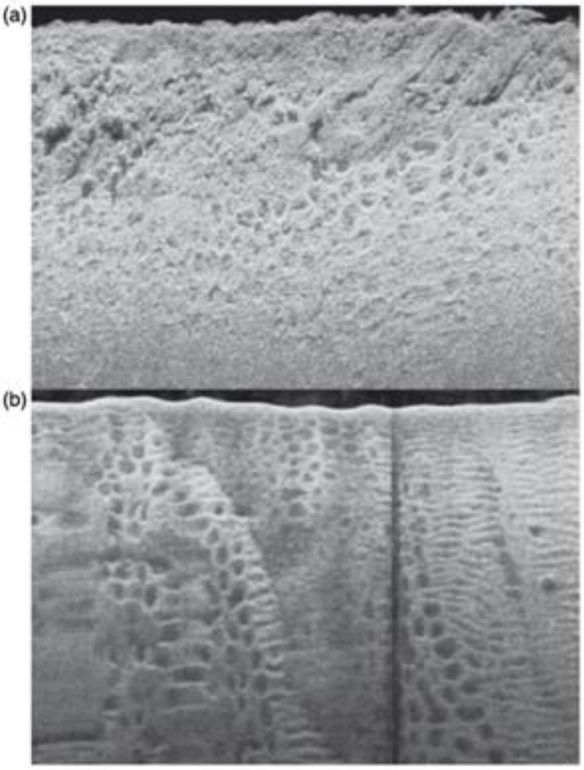

Figure 10. Side scan sonar surveys reveal *Spondyliosoma cantharus* nest craters off the central south coast of the UK (Collins and Mallinson, 2012)

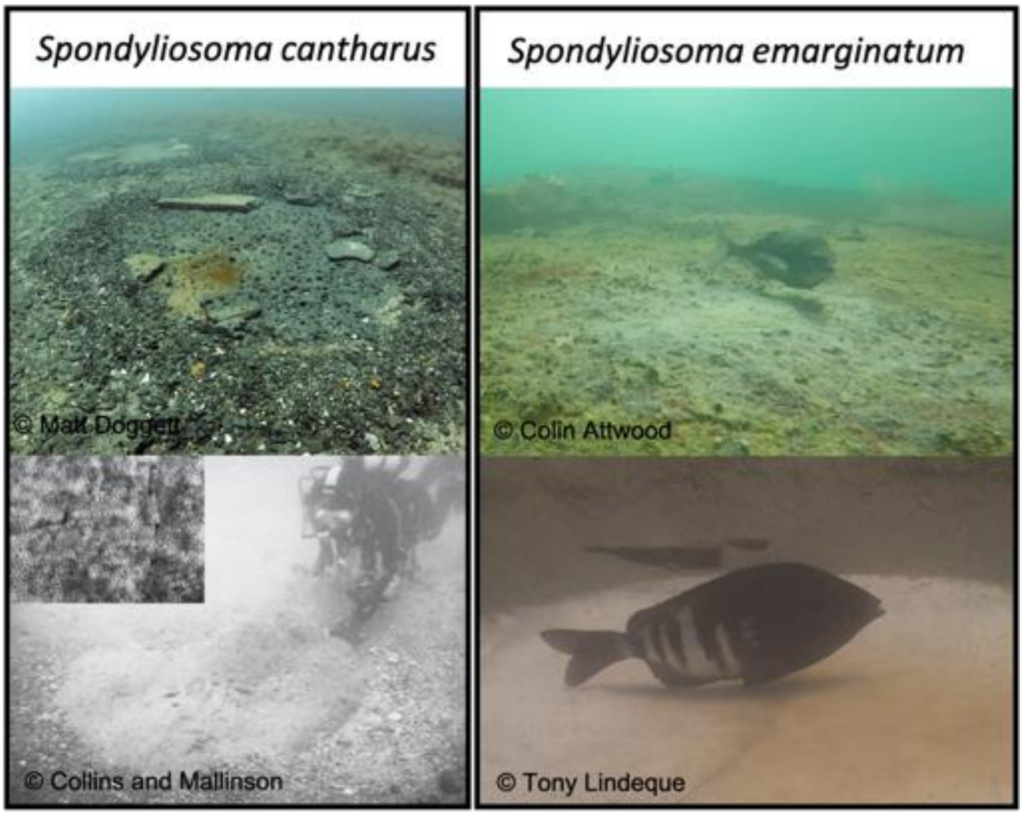

Figure 11. *Spondyliosoma* nesting sites. Left top and bottom: *S. cantharus* nests along the Dorset coast in the UK. Right top and bottom: *S. emarginatum* nests in False Bay, South Africa

Spondyliosoma species also share similarities in their distribution across the coastal zone. It is known that *S. cantharus* overwinters in deeper waters but comes up to shallower depths during spring to establish spawning grounds (Collins and Mallinson, 2012). This pattern also appears in *S. emarginatum* sightings from BRUV surveys in False Bay (Figure 12) (De Vos *et al.*, 2015). In the summer months, there are few sightings deeper than 30 m, whereas in the winter months the pattern is reversed with little to no sightings between 0 and 10 m (Figure 12). The reduced sightings in spring/summer could also be due to a high frequency of nesting individuals that are unlikely to travel to a baited camera.

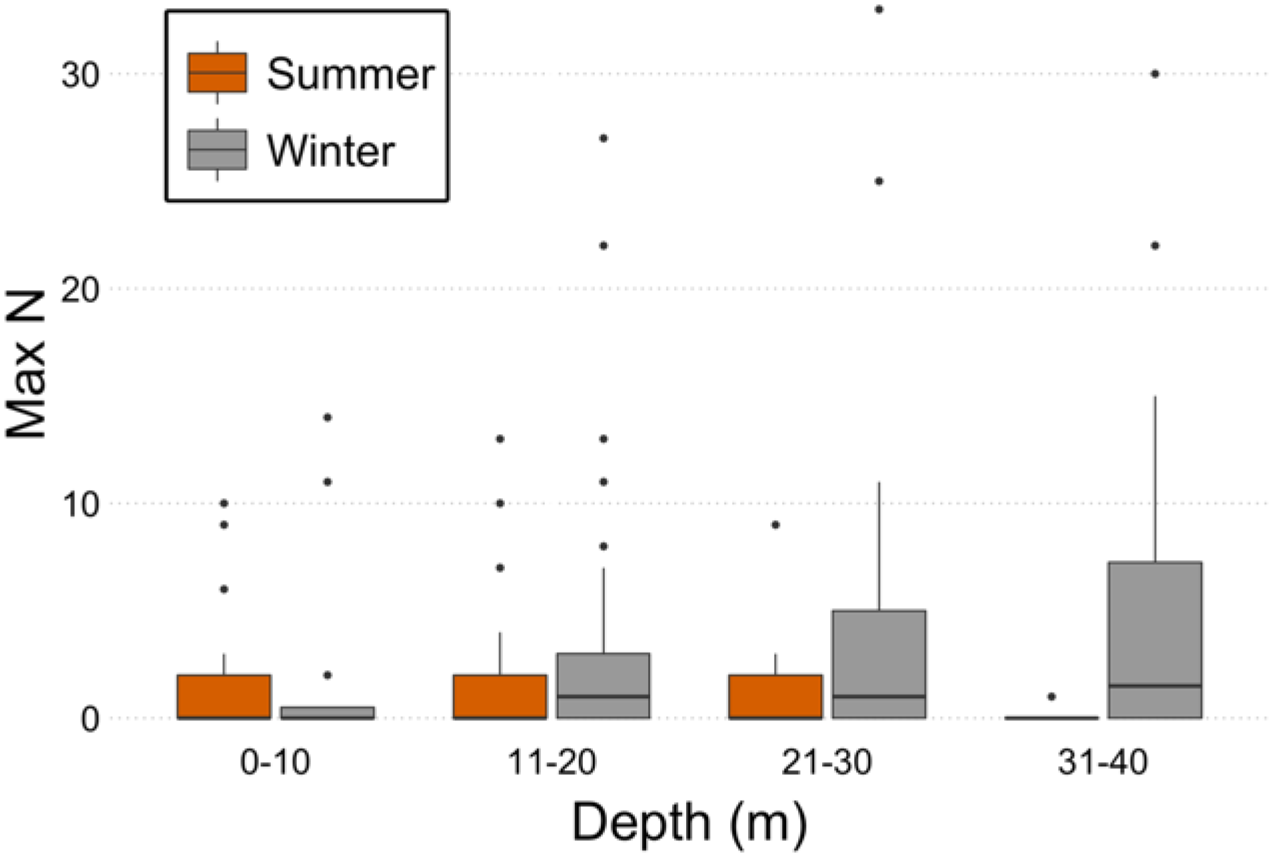

Figure 12. *Spondyliosoma emarginatum* sightings from baited remote underwater video surveys (BRUVS) in False Bay. Data extracted from (De Vos *et al.*, 2015)

2.2. Aims

This study aims to find and describe a nesting site of the temperate nesting species *S. emarginatum* in South Africa. *S. cantharus* is a commercially important species (Collins and Mallinson, 2012) and *S. emarginatum* could grow to become a valued species in South Africa due to an expanding small scale coastal fisheries sector (DAFF, 2016; FAO, 2018) and particularly so if more valued linefish species become further depleted (Griffiths, 2000; Mann, 2013). A proper description of the characteristics and dynamics of one or a few *S. emarginatum* nest sites could lead to the discovery of other sites, which will have implications for marine spatial planning.

2.3. Materials and methods

2.3.1. Study site

This study was conducted in False Bay, on the south west coast of South Africa (Figure 13). False Bay is less than 85 m deep and is rectangular in shape with an area of ~1000 km^2 (Dufois and Rouault, 2012; Pfaff *et al.*, 2019). False Bay is influenced by a dynamic exchange of cool temperate and warm temperate water masses (Dufois and Rouault, 2012; Pfaff *et al.*, 2019). The seabed is made up of 40% reef, of three rock types (Wells *et al.*, 1989). Sea surface temperatures (SST) are affected by cold south-east wind driven upwelling events and warm water influx originating from the east coast Agulhas current (Pfaff *et al.*, 2019). Most of the water column in the bay is almost isothermal during winter. During summer it is strongly stratified with an 8 to 9 °C difference between the surface and 50 m depth (Dufois and Rouault, 2012). Strong south-easterly winds in summer months lead to upwelling events that weaken stratification.

The study site is located in the north-western region of the bay, where bottom topography is characterised by Cape Peninsula granite overlaid by coarse and medium sand (Terhorst, 1987). This region is exposed to lower wave action compared to the rest of the bay (Terhorst, 1987; Pfaff *et al.*, 2019) and experiences a semi-diurnal upper microtidal (<2 metre tidal range) environment, which means that tidal driven currents are weak (Terhorst, 1987). SSTs in the north-western part of the bay average at 18.8 ºC in summer and 15 ºC in winter (Dufois and Rouault, 2012).

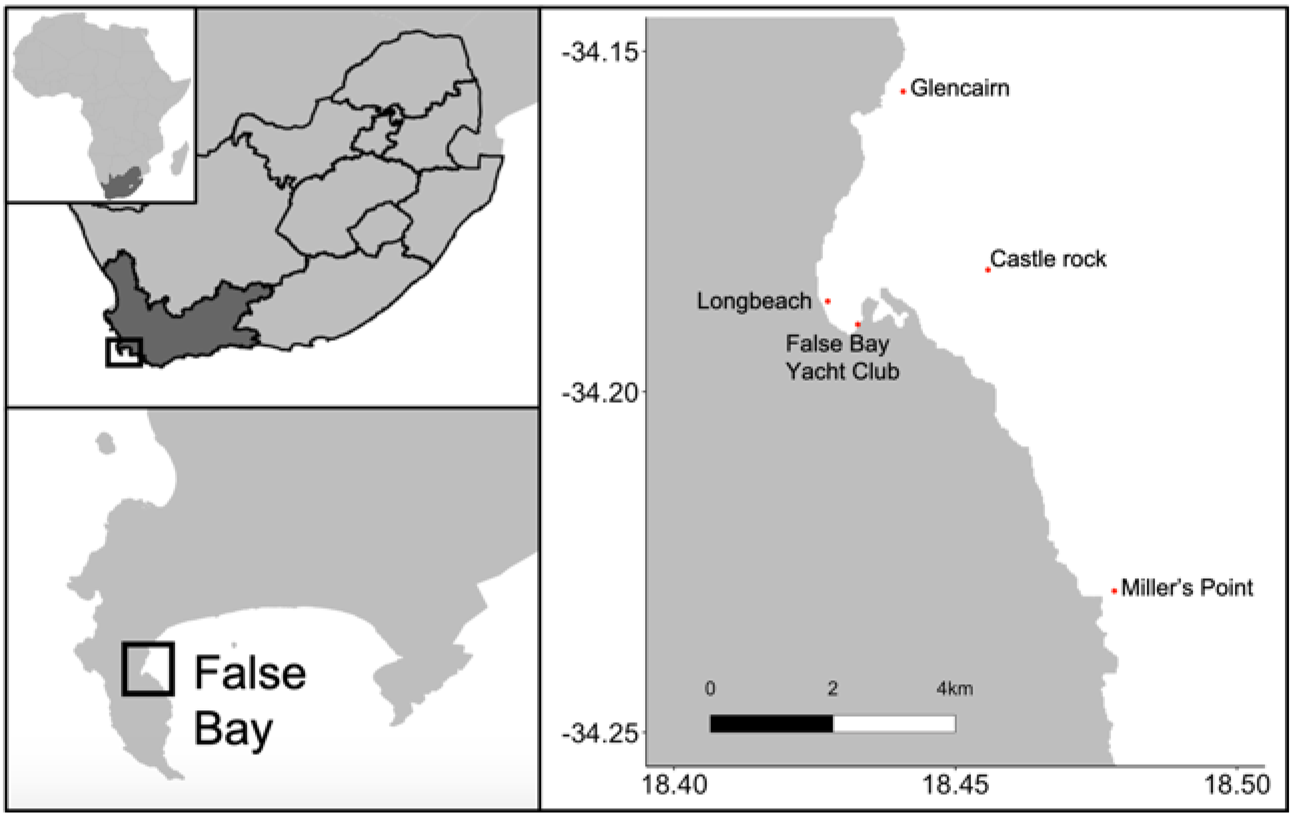

Figure 13. The study site is located in False Bay, South Africa. Sites that were surveyed for *Spondyliosoma emarginatum* nests are marked in red. The large nesting site was eventually located at Glencairn and one nest was located in the False Bay Yacht Club harbour

2.3.2. Exploratory surveys

Exploratory surveying efforts were focused at three main sites: (1) in the False Bay Yacht Club (FBYC) harbour in Simon's Town, (2) off Longbeach in Simon's Town, and (3) a few hundred meters off the coast of Glencairn. These sites were chosen due to prior sightings, and local opinion that *S. emarginatum* nests in the area. Two other sites, Miller's Point and Castle Rock, were also monitored but on a less frequent basis (Figure 13). The surveying methods included: baited remote underwater video systems (BRUVS), self-contained underwater breathing apparatus (SCUBA) dives and free-dives.

BRUVS were deployed to monitor for the abundance of *S. emarginatum* and the presence or absence of nesting males, characterised by a distinct nuptial dress of black and white bands. For a full description of the BRUVS set up see De Vos *et al.*, 2015. The only difference in this setup was the camera (GoPro Hero+™ HD) and bait (chopped *Sardinops sagax*). From the 26th of June to the 20th of August, a total of 14 BRUVS were deployed. At each deployment, the BRUV was lowered to the seafloor by means of rope and recorded continuously for 60 min. The footage was analysed for presence of *S. emarginatum* using MaxN (maximum number of individuals in a single frame) as a measure of abundance. The proportion of normal, slightly banded and heavily banded individuals was recorded and used as an indicator of the presence of a nearby nesting site.

Diving time for SCUBA dives and free-dives was limited to 45 min due to air consumption and/or cold water. Each buddy team was given a camera to film any sightings. A total of 14 SCUBA dives and 13 free-dives were conducted from the 12th of June to the 28th of August across all sites.

2.3.3. Environmental variables

A CTD (conductivity, temperature, depth) instrument was initially used to capture the temperature on the Glencairn nesting site. It was deployed regularly to the sea floor near the site (~13 m) prior to the procurement of *in situ* sensors.

In situ oxygen and temperature sensors, courtesy of Sea Technology Services (STS) (Pty) Ltd, were placed on the Glencairn nesting site at 13 m depth. The temperature sensor operated from the 7th of September until the 10th of October, and the oxygen sensor operated from the 13th to the 25th of September. Granger causality tests were performed to understand the causal relationship between oxygen and temperature levels. The null hypothesis for the tests was that temperature fluctuations do not cause oxygen fluctuations and vice versa.

Hourly wind direction, speed and air temperature data was also provided by the South African Weather Service (SAWS) from the 1st of August to the 31st of December 2019. Data came from the two coastal Automatic Weather Stations (AWS) closest to the nesting site: Cape Point (-34.355983, 18.4832966) and Strand (-34.1173884, 18.8123537). The strand station was deemed more appropriate to characterise wind conditions in False Bay since Cape Point is very exposed. Wind direction and speed were used to build overall, monthly and daily windroses using the R package *openair* (Carslaw and Ropkins, 2012).

2.3.4. Nesting site

Site topography

A multibeam scan of the site was performed using a Furuno DFF3D Multi-Beam Sonar Module, which has a 120° swath width (~ 200 m). Through successive tracks over several days, an area of 41 094 m^2 was surveyed encompassing 10 462 depth points. This allowed for a reconstruction of the nesting site topography.

Cluster size and nest density

The nests on the compound nesting site was organised in clusters. Throughout each dive the number of nests per cluster was measured. The total number of nests per cluster was divided by the area of the cluster to obtain a nest density (nests per m^2). The perimeter of each cluster was measured on the 11th of November using a measuring tape. Three or four measurements were taken along the edges of each cluster. These measurements were then used to calculate the area (A) covered by each cluster. For clusters with three sides (a, b, and c), Heron's formula was used as per equation (1) and (2).

$$A = \sqrt{s(s-a)(s-b)(s-c)} \tag{1}$$

$$s = \frac{a + b + c}{2} \tag{2}$$

For clusters with four sides (a, b, c, and d), Brahmagupta's formula was used as per equation (3) and (4).

$$A = \sqrt{s(s-a)(s-b)(s-c)(s-d)} \tag{3}$$

$$s = \frac{a + b + c + d}{2} \tag{4}$$

Cluster reconstructions

Each cluster was filmed from above by swimming back and forth in a "scanning" pattern at a relatively constant height. One frame per second was extracted from each video and the frames were stitched together using Panorama Stitcher© to build a composite bird's eye view of each cluster. A scale was not deemed appropriate for the composite because photos are slightly distorted or adjusted during the stitching process, meaning that the scale in the foreground and background can differ. To compensate for the lack of an overall scale, each picture contains the size of one nest. These pictures do not represent all nests on the site as many other nests were also scattered in between clusters.

2.3.5. Nest size

Nest pictures

Individual nest pictures were taken on the 3rd, 7th, 8th, 10th, 21st, 25th, and 26th of September. Nests were identified using tagged lead sinkers placed in the vicinity of nests at the start of the study period. Every picture from the 3rd to the 21st was taken from a standardized height using a camera (GoPro Hero 4) fixed to the end of a slender rod. A picture of a 20 by 20 cm quadrat was taken using the same method to later scale the pictures. Pictures on the 25th and 26th were instead taken using only the 20 by 20 cm quadrat to scale each frame, instead of using the rod, which proved impractical.

Nest area

All nest pictures were processed using ImageJ© (Schneider *et al.*, 2012). For every picture, the scale was set using the 20 by 20 cm quadrat. The area of each nest was then estimated three times by drawing the outline of the nest using the freehand drawing tool. The mean of the three areas was taken as the final nest area and a one metre scale bar was added to each picture.

Statistical analysis – change in rate of nest area over time

The rate of change of nest area was calculated by fitting a regression line to nest area (m^2) vs time (days) for any nests with three or more days of area measurements.

2.3.6. Eggs and larvae

During each dive on the nesting site, all the nests were examined for the presence or absence of eggs. The frequency of nests with eggs was monitored over time. Some egg samples were collected from selected nests. The vials with eggs were then brought back to the boat and the seawater was immediately injected with formalin to 5% strength. The samples were kept at room temperature until further analysis. The eggs were photographed with a Nikon DS-Fi 1 Digital Camera fitted to a Nikon SMZ1500, stereo dissecting microscope interfacing with NIS Elements Basic Research 3.2 imaging software. This was used to capture developmental stages, identify different substrata that eggs may attach to, and identify if eggs of different developmental stages were present on one nest at any one time.

2.4. Results

2.4.1. Exploratory surveys

Each surveying method provided information that would help locate *S. emarginatum* spawning grounds.

BRUVs

S. emarginatum was observed at all sites and in all BRUVS except for one. MaxN ranged from zero to 24. The extent of nuptial dress colouration was captured on a three-stage scale (Figure 14). The earliest sighting of a banded male was on the 26th of June at Longbeach. The proportion of banded males was highest at Glencairn on the 16th of July where one BRUV revealed five banded males in a MaxN of 14. Longbeach also held a relatively high proportion of banded males but no nearby nesting site was ever found despite numerous dives on the site. Finally, no banded individuals were ever noticed on the two Miller's Point BRUVS, both conducted on the 27th of July.

Figure 14. Three-stage scale used to identify the extent of male nuptial dress colouration from BRUV footage. Photographs credited to N. Faure Beaulieu

SCUBA and free-dives

It quickly became apparent that *S. emarginatum* is a “diver-negative” species, which means that the fish do not come close to SCUBA divers. Free-dives have a slightly greater chance of spotting them, probably due to reduced noise and bubbles. One individual was spotted at Longbeach during a free-dive, and a school of individuals was spotted in the FBYC during a SCUBA dive. A single nest was found in the FBYC on the 24th of August. On the 28th of August, a compound nesting site was found during a SCUBA dive at Glencairn.

2.4.2. Environmental monitoring

Water temperature rose from 11 ºC on the 27th of August to 16 ºC on the 9th of September (Figure 15). During this increase, on the 30th of August, the first nests with eggs were noticed on the Glencairn nesting site. Temperatures thereafter fluctuated between 13 and 17 ºC. A 2 ºC dip in temperature occurred on the 20th of September and a near 4 ºC drop between the 3rd and 5th of October (Figure 15).

Oxygen concentrations ranged between 5 and 8 mgL^{-1} and were correlated to temperature fluctuations, falling and rising on similar days (Figure 15). A granger causality test was performed and revealed that while temperature was a good predictor of future oxygen values ($p=0.01$, lag=3 days), oxygen was not a useful predictor of temperature values ($p=0.62$, lag=3 days).

The monthly windroses for the Strand weather station shows the increasing wind speeds and decreasing calm periods from the end of winter (August), through spring (September and October), with especially strong south-easterly winds in November and December (Figure 16). Both dips in *in situ* temperature observed on the 20th of September and on the 3rd of October (Figure 15) were preceded by two to three days of strong south-easterly winds.

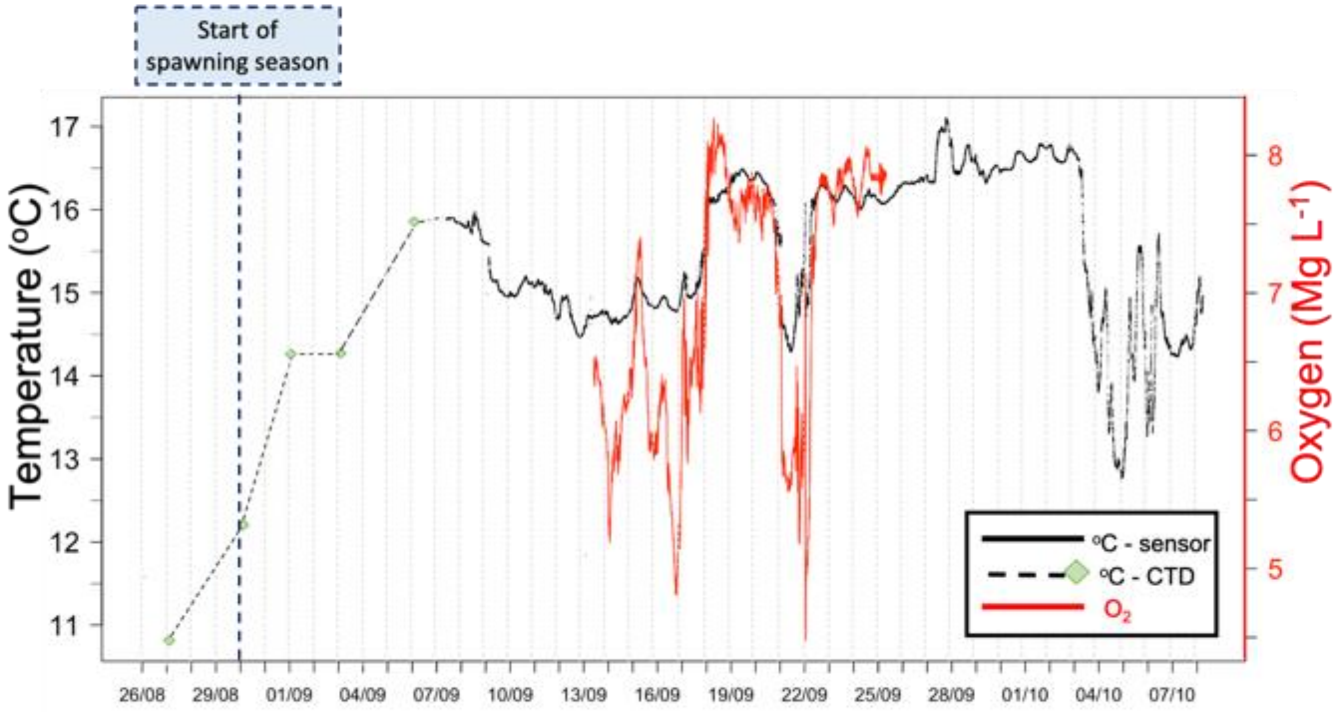

Figure 15. *In situ* oxygen and temperature observations on the nesting site at 13 m depth. Oxygen measurements span from the 13th to the 26th of September

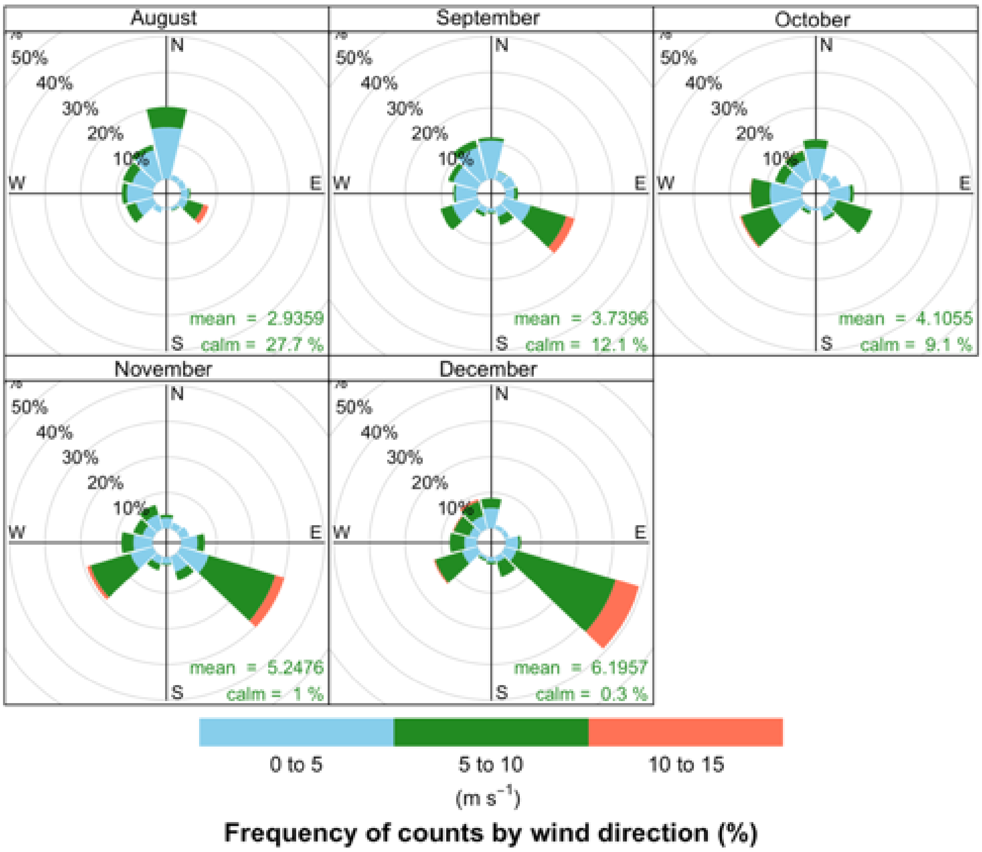

Figure 16. Monthly windrose diagrams showing the frequency of counts by wind direction (%) for the Strand weather station (-34.1173884, 18.8123537). Data: South African Weather Service (SAWS). Wind-roses were built using R *openair* package (Carslaw and Ropkins, 2012)

2.4.3. Nesting site

Habitat description

The single FBYC nest was found on a hard, rocky surface surrounded by sand. The nests within the compound nesting site were scattered above and in between large rocky granite outcrops (Figure 17). The bottom topography was as a mixture of sand and Cape Peninsula granite reef. Nests consisted of the granite surface from which the overlaying sand had been swept away and that was often covered by patches of thin coralline crust (*Phymatolithon foveatum*) (Figure 18). The nests were directly bordered by sand and calcareous debris, mainly comprised of mollusc shells (Figure 18). At increasing distance from the nest border (~30 cm), the seafloor was covered with a variety of ophiuroids, crinoids, holothuroids, sponges, sea fans and soft corals (Table 6). The most common assemblage directly bordering nests was beds of *Pseudocnella insolens, P. sykion* and *Ophioderma wahlbergii* (Figure 19). Many sea fans (*Eunicella* spp.) and sponges were also scattered over the site and on some occasions, sponges were found encrusting the nest surfaces.

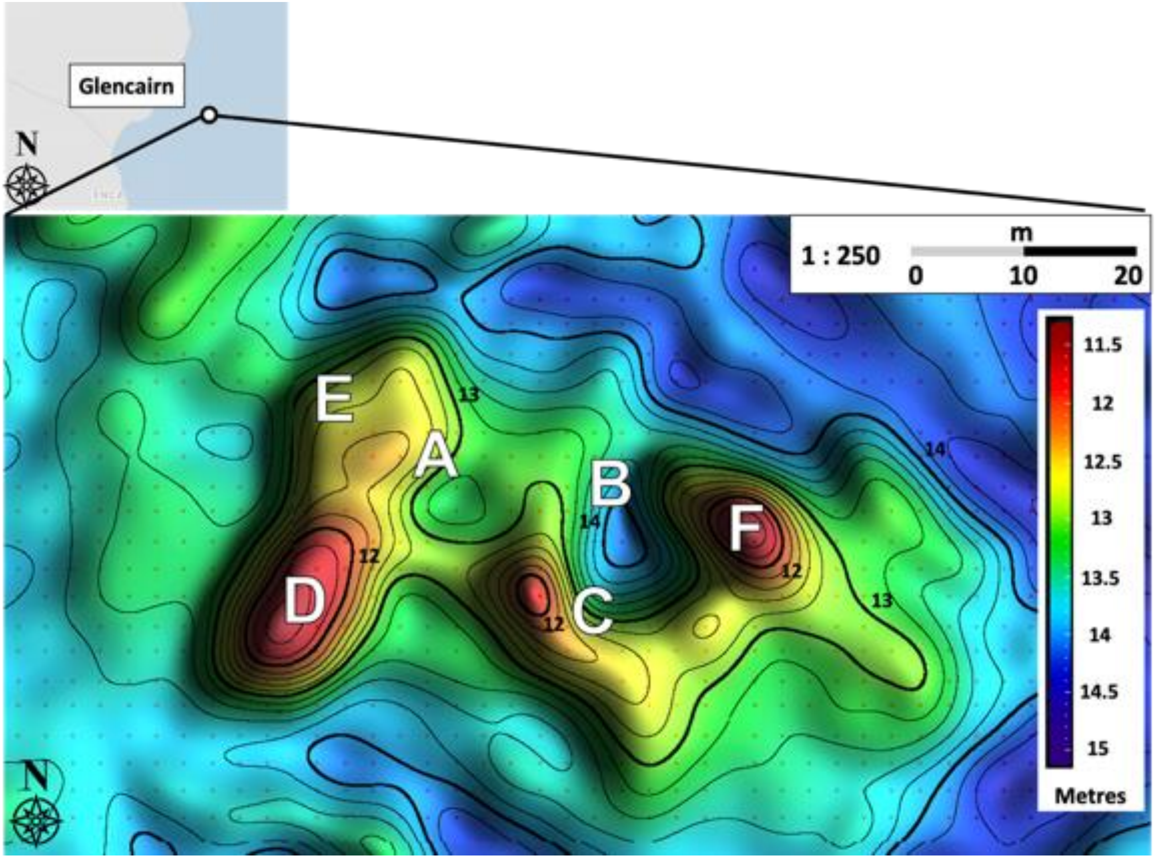

Figure 17. Topography of the nesting site at Glencairn. Letters A – F represent the different nest clusters. Small dots are individual depth soundings from which the bathymetry lines are interpolated. Bathymetry lines are spaced at 0.2 metre intervals. The contours were created using a Furuno DFF3D Multi-Beam Sonar Module

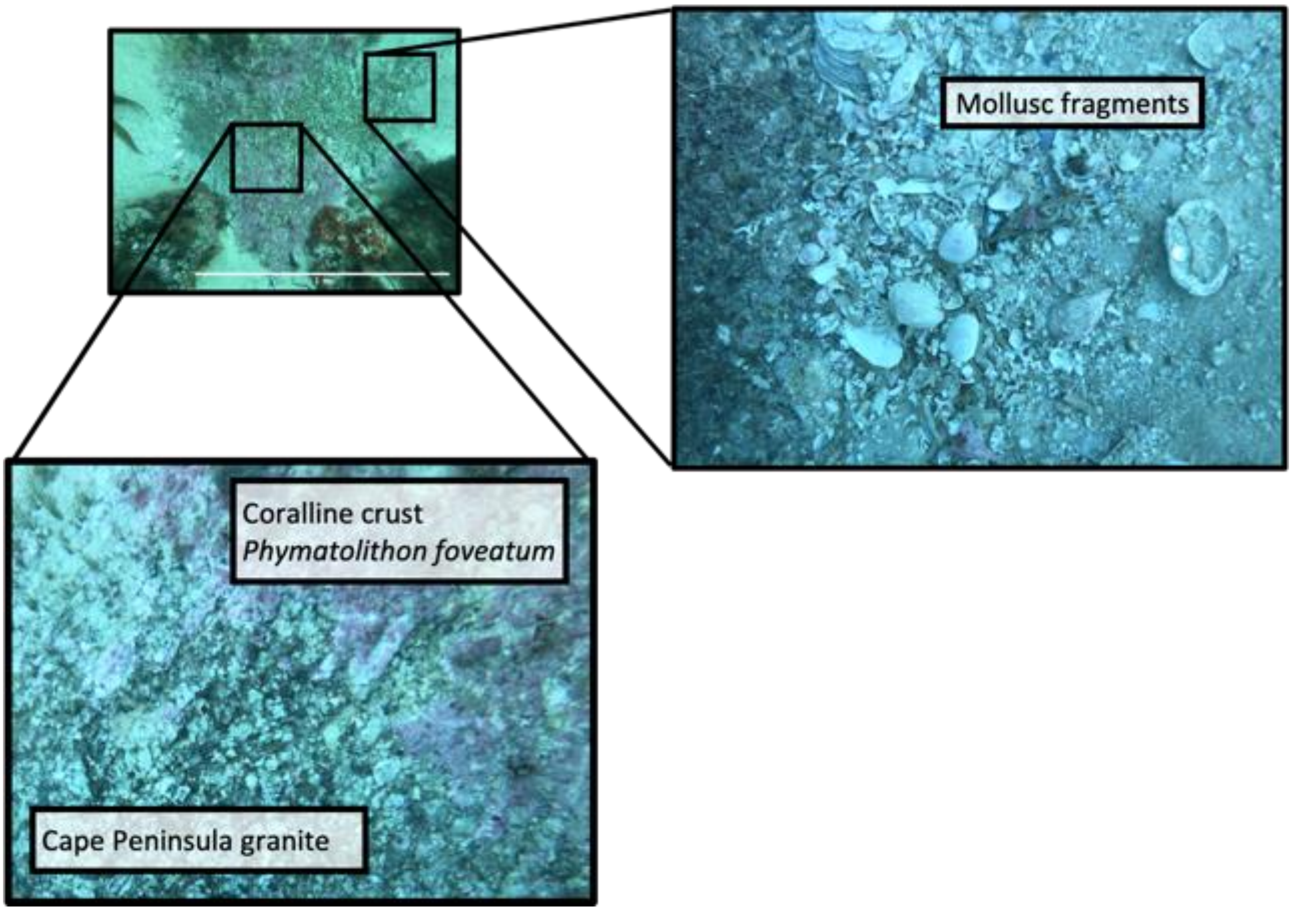

Figure 18. Picture of a nest (top left) and close-ups showing: (bottom left) coralline crust (*Phymatolithon foveatum*) over the Cape Peninsula granite nest surface, (top right) carbonate debris on the nest border comprised mostly of empty mollusc shells

Table 6. Most common invertebrate species observed on the Glencairn nesting site, identified to the highest possible classification

Phylum	Common name	Scientific name
Echinoderm	Serpent-skinned brittlestar	*Ophioderma wahlbergii*
Echinoderm	Spiny starfish	*Marthasterias africana*
Echinoderm	Elegant feather-star	*Tropiometra carinata*
Echinoderm	Red-chested sea cucumber	*Pseudocnella insolens*
Echinoderm	Cask sea cucumber	*Pseudocnella sykion*
Echinoderm	Pink sandstar	*Astropecten irregularis pontoporeus*
Echinoderm	Common feather-star	*Comanthus wahlbergii*
Cnidaria	Palmate sea fan	*Leptogorgia palma*
Porifera		*Polystamia spp.*

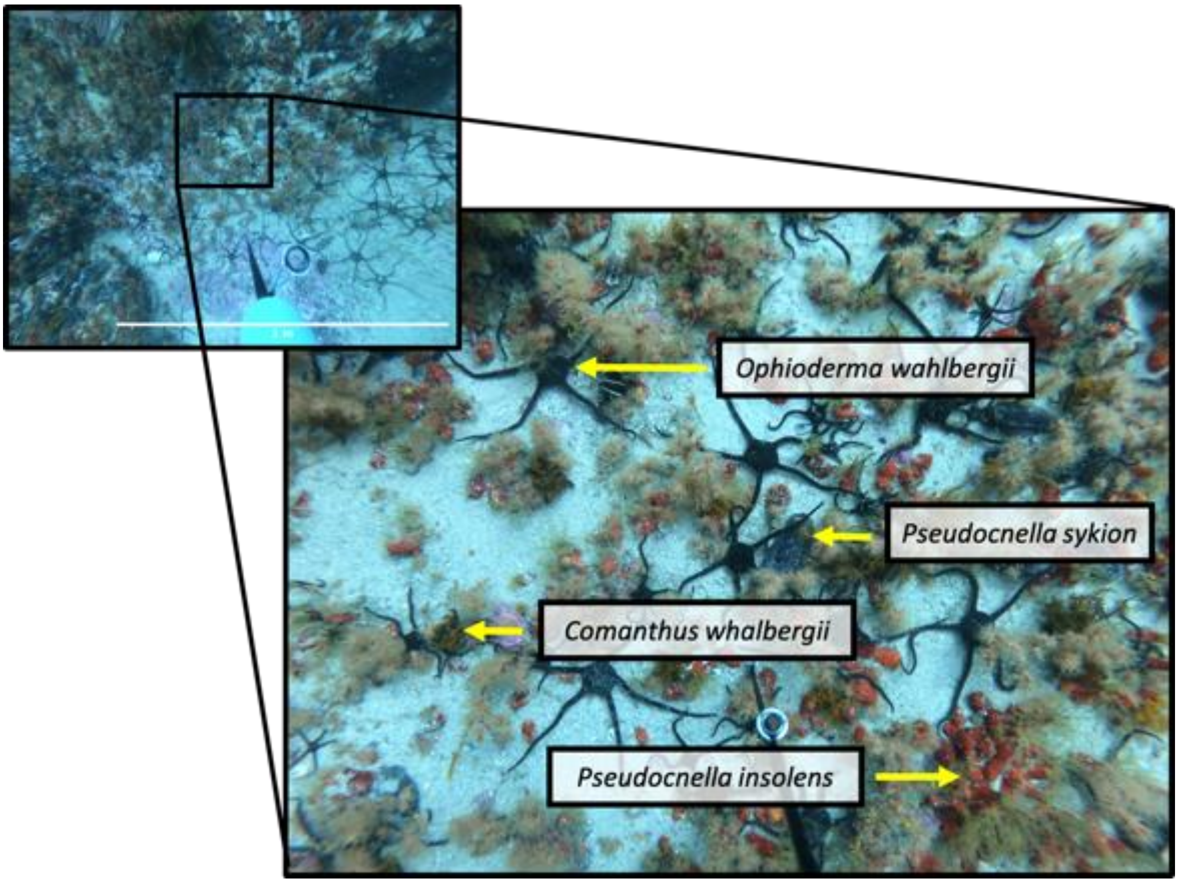

Figure 19. Common epifaunal community assemblages surrounding nests on the Glencairn site

Cluster size and nest density

The nesting site was split into six nest clusters, which were chosen based on the closeness of the nests in them. Four of the clusters (A-D) were on the sandy bottom, while the remaining two clusters (E-F) were on two different granite outcrops. The area covered by each cluster is displayed in Table 7. The clusters ranged in size from eight to 39 m^2 and the maximum density of nests per m^2 in each cluster ranged from 0.6 to 1.3 nests per m^2.

Table 7. Area of each nesting cluster in m^2. For clusters with three sides (a, b, c), Heron's formula was used ($A = \sqrt{s(s-a)(s-b)(s-c}$) and $s = \frac{a+b+c}{2}$). For clusters with four sides (a, b, c, d), Brahmagupta's Formula was used ($A = \sqrt{s(s-a)(s-b)(s-c)(s-d}$) and $s = \frac{a+b+c+d}{2}$)

Cluster	Area (m^2)	Maximum nº of nests	Nest/m^2
Cluster A	20	14	0.7
Cluster B	8	10	1.3
Cluster C	34	19	0.6
Cluster D	21	16	0.8
Cluster E	39	31	0.8
Cluster F	26	18	0.7

Cluster reconstructions

Nest cluster reconstructions show the densely packed nature of nests on this site (Figures 20 to 24). The presence of dense invertebrate communities surrounding the nests, especially in cluster B and F (Figure 21 & Figure 24), highlights the amount of effort males carry out to keep the nest surface bare. Cluster F was the only cluster at a different depth (Figure 24), it was on an elevated platform at 9 to 10 m depth compared to rest of the site, which was at 13 to 14 m depth. Cluster E was not included as it appeared later in the nesting season and the only video taken was on a day with poor visibility rendering the quality of the images too poor for photo stitching.

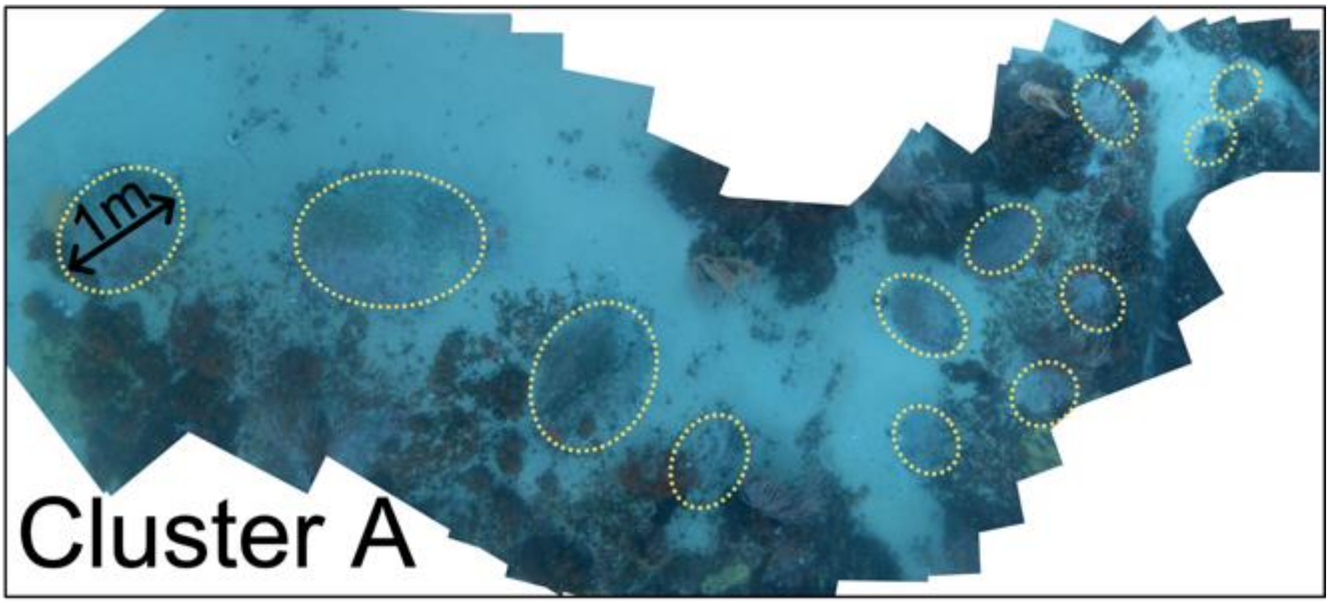

Figure 20. Nesting cluster A of the *Spondyliosoma emarginatum* nesting site

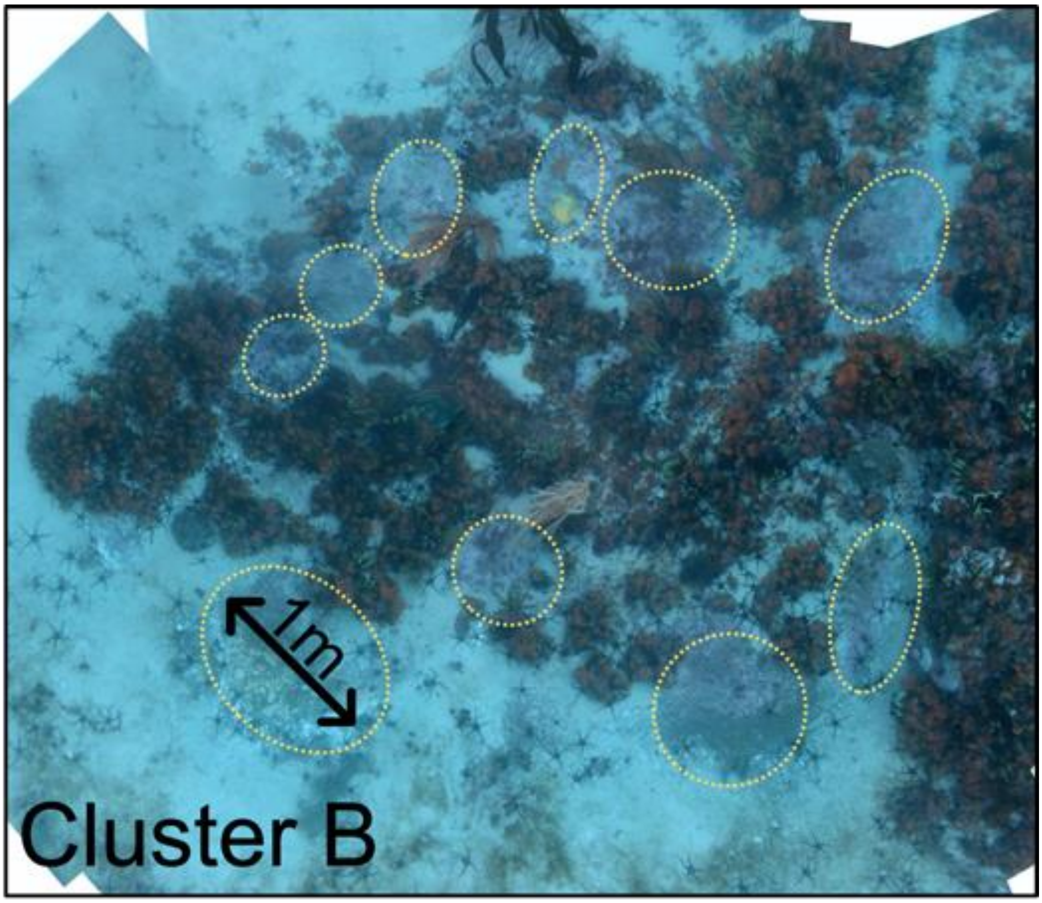

Figure 21. Nesting cluster B of the *Spondyliosoma emarginatum* nesting site

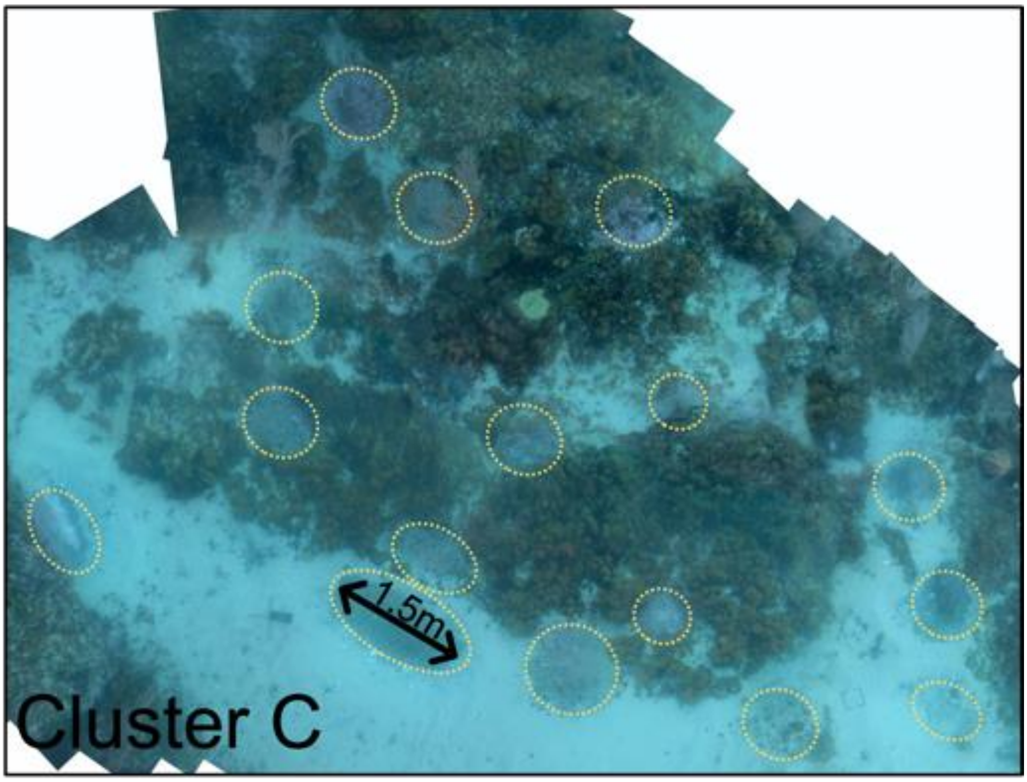

Figure 22. Nesting cluster C of the *Spondyliosoma emarginatum* nesting site

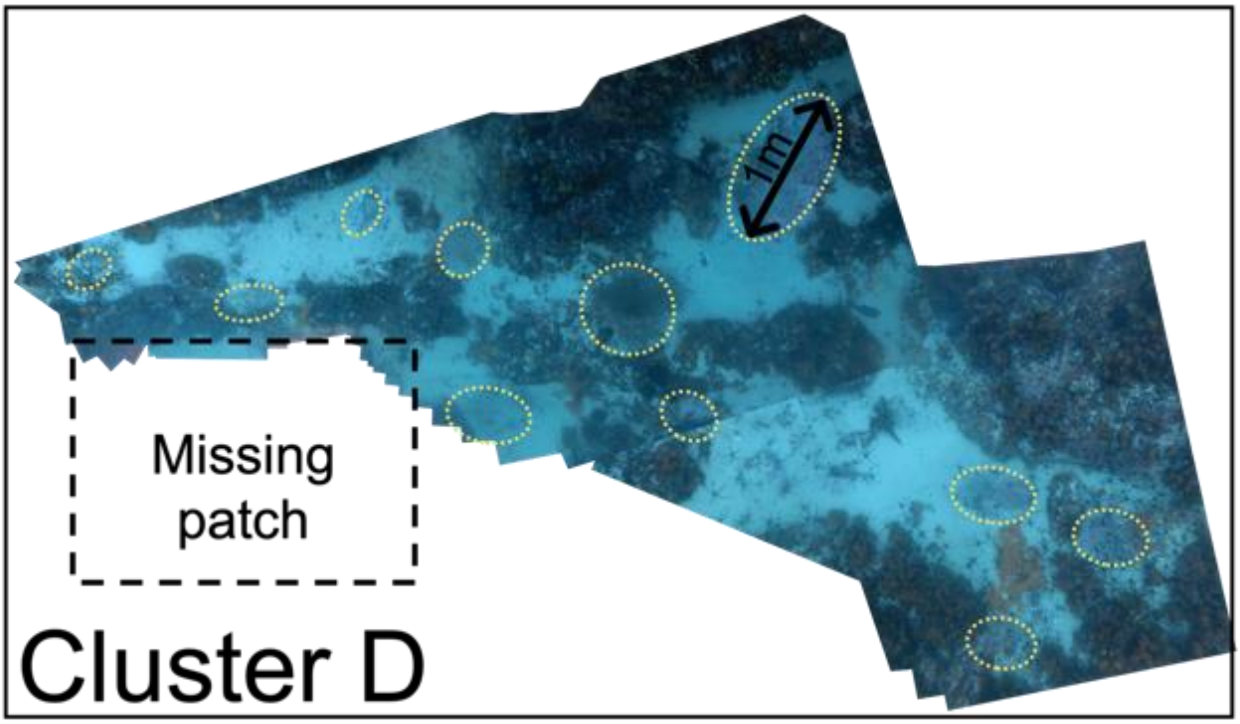

Figure 23. Nesting cluster D of the *Spondyliosoma emarginatum* nesting site. The missing patch represents an area of the cluster not recognised by the photo stitching software

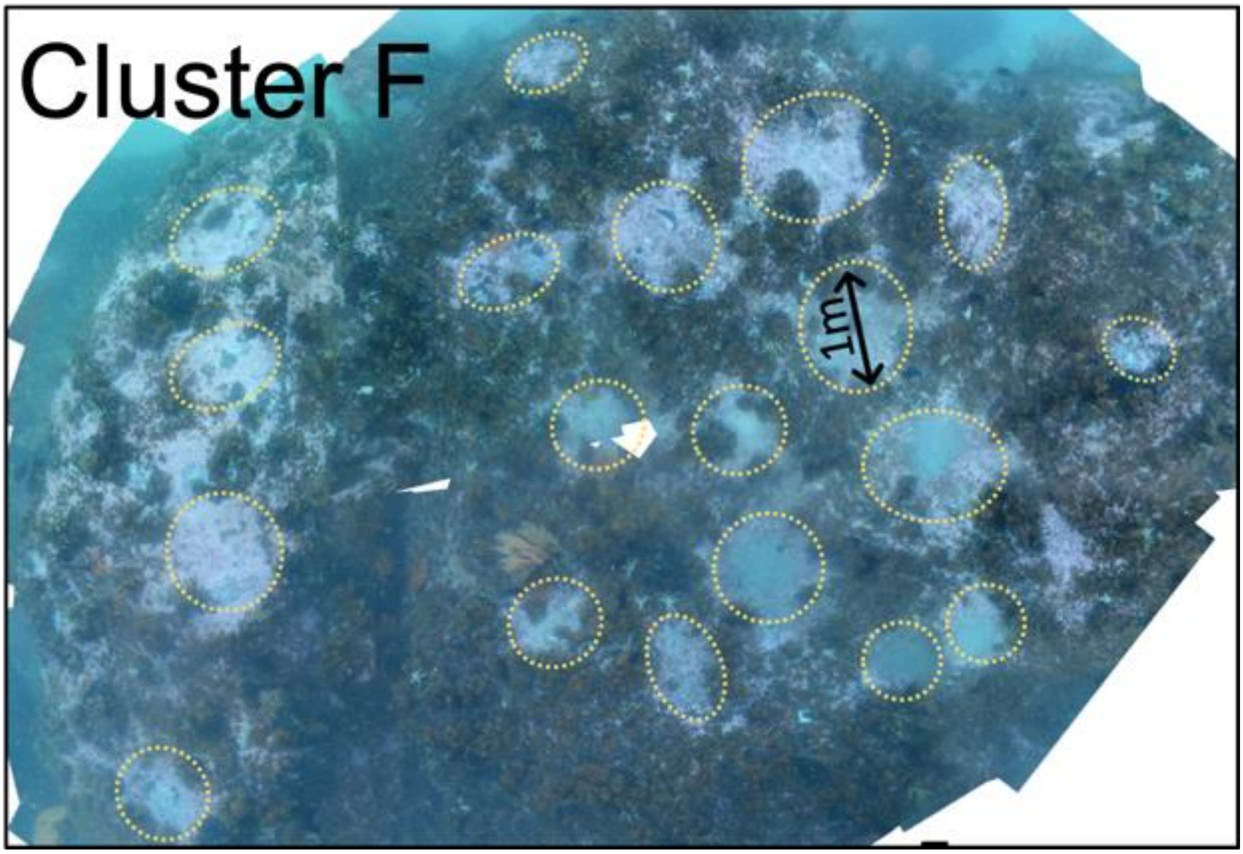

Figure 24. Nesting cluster F of the *Spondyliosoma emarginatum* nesting site

2.4.4. Nest size

Sample size

In total, 40 different nests were measured over seven days during the nesting period. Over 15 nests were captured on all but two days (Table 8), the reduced number of pictures on the 10th and 26th of September were due to reduced diving times. Twenty-two nests were captured on at least three days, whereas 18 nests were only captured on one or two days (Table 9).

Table 8. Total number of nests pictured each day

Date	Number of nests pictured
03/09/2019	26
07/09/2019	21
08/09/2019	18
10/09/2019	14
21/09/2019	21
25/09/2019	16
26/09/2019	9

Table 9. Total number of pictures taken per nest

Nest ID	Total days of pictures
3, 11B, 23B, 26, 33, 35, 36, 3B, 9	1
4, 16, 22, 25, 34, 37, 38, 39, 40	2
12, 17, 19, 2, 32, 32B	3
18, 20, 27, 31, 3A	4
1, 14, 15, 23,29, 30	5
10, 11, 13, 21, 28	6

Nest area

Nest area increased slightly from a median of below 0.25 m^2 on the 3rd of September to a median of near 0.5 m^2 on the 21st of September. Median nest size then dropped below 0.25m^2 on the 25th of September before rising again to above 0.25m^2 in one day (Figure 25). However, since each day represents a different combination of nests, this graph only provides an overview of the distribution of nest sizes over the entire site rather than how individual nests change in size over time.

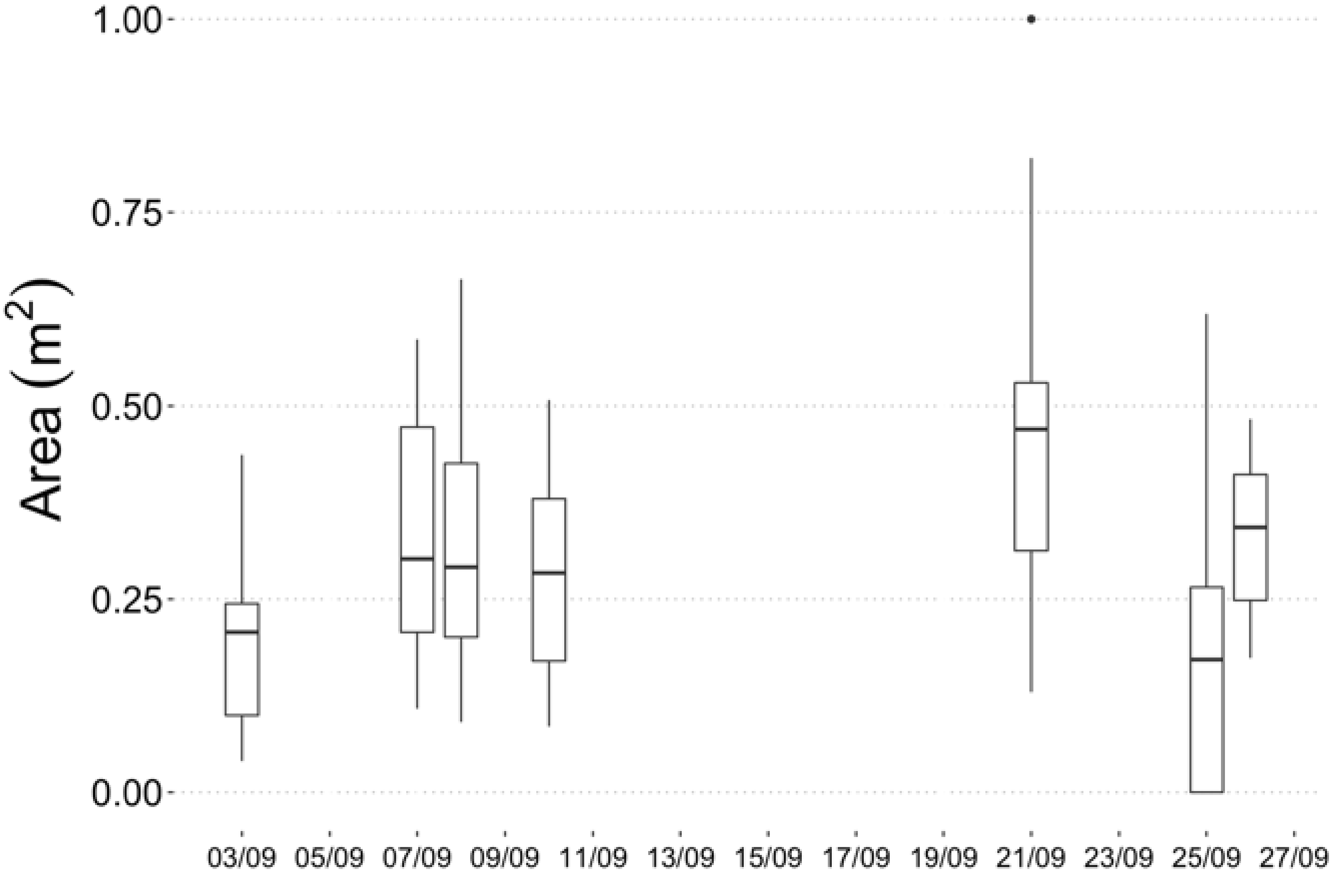

Figure 25. Variation in *Spondyliosoma emarginatum* nest area (m^2) throughout September

Change in rate of nest area over time

Out of the 20 nests analysed (

Table 10), five saw a significant change in size over time. An increase in size of 0.01, 0.03 and 0.04 m^2 was noticed for nests 13, 14 and 23 respectively, while a decrease in size of 0.02 and 0.04 m^2 was noticed for nests 21 and 3A respectively. These changes remain small and most nests saw no significant change in size over time. It is also important to consider unusual weather events during the period where nest area was monitored.

Throughout the nesting period, four consecutive days of south-easterly winds (5-15 ms^{-1}) occurred between the 21st and 25th of September. The structural integrity of most nests was affected to varying degrees (Figure 26).

Table 10. Linear regressions of nest area (m^2) against successive days for each nest with three or more measurements. Sample size (n), standard error (se). *$p < 0.05$

Nest ID	**n**	**Intercept**	**Area change per day (m^2)**	**se**	**R^2**	***p***	
1	4	148.67	-0.01	0.01	0.26	0.49	
2	3	-67.71	0	0.01	0.17	0.73	
3A	3	665.18	-0.04	0	1	0.01	*
10	5	-106.55	0.01	0.01	0.17	0.48	
11	5	57.98	0	0.01	0.1	0.61	
12	3	-219.93	0.01	0.04	0.09	0.8	
13	5	-162.25	0.01	0	0.78	0.05	*
14	5	-624.62	0.03	0.01	0.81	0.04	*
15	5	6.72	0	0.01	0	0.98	
17	3	-944.92	0.05	0.02	0.89	0.21	
18	4	-331.17	0.02	0.01	0.81	0.1	
20	4	-8.87	0	0	0.45	0.33	
21	6	448.54	-0.02	0.01	0.83	0.01	*
23	5	-701.9	0.04	0.01	0.91	0.01	*
27	4	74.65	0	0	0.31	0.45	
28	6	-22.23	0	0	0.02	0.79	
29	4	-140.67	0.01	0.02	0.1	0.68	
30	5	-73.79	0	0.02	0.01	0.86	
31	4	-175.52	0.01	0.02	0.07	0.73	
32	3	200.94	-0.01	0.08	0.02	0.91	

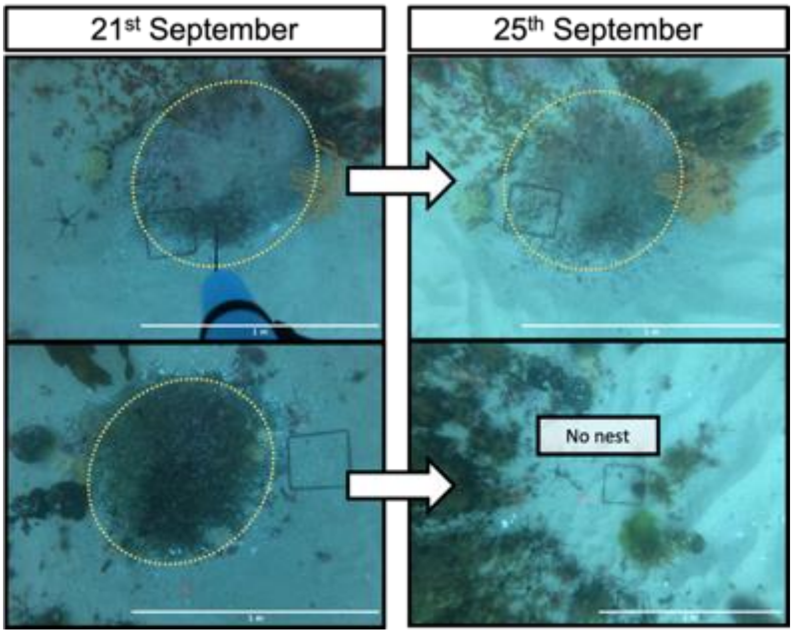

Figure 26. Two *Spondyliosoma emarginatum* nests before (left) and after (right) a south-easterly weather event that occurred between the 21st and 25th of September. The white line represents a one metre scale bar. The black quadrat is 20 by 20 cm

2.4.5. Eggs and larvae

Eggs where laid in dense layers over the nests, and were mostly directly attached to the carbonate nest surface (Figure 27) but in some cases the eggs were also attached to algae growing on or bordering the nest surface (Figure 28). The frequency of nests with eggs was monitored throughout the duration of the nesting period (Figure 29) as well as the maximum number of consecutive days a nest was seen with eggs. The first appearance of eggs was on the 30th of August at a temperature of 14.79 ºC. Temperatures recorded at the FBYC on the 19th of August were 12.4 ºC.

The number of nests with eggs steadily increased from the 30th of August until it reached a maximum of 58 nests with eggs out of 83 nests observed on the 24th of October. The number of nests with eggs on the site then decreased to zero on the 5th of November with no further increases, signalling the end of the nesting season. During the increase two dips in the number of nests with eggs occurred, one between the 21st and 26th of September and another between the 7th and 16th of October. The number of consecutive days a nest was observed with eggs ranged from two to nine days.

The earliest egg-stage identified with the aid of a microscope was the blastula stage (Figure 30-A), in which the blastomeres are arranged as a high mound of cells above the yolk cells. The next stage observed was the gastrula stage, in which the blastula is reorganised as a circle around the yolk (Figure 30-B). Two embryo stages were also observed. During these embryo stages, tissues and organs become apparent. In the earlier embryo stage, somatogenesis has started and the eyes are clearly visible (Figure 30-C). In the later embryo stage, organs such as the mouth and anus are clearly visible (Figure 30-D). None of the larvae samples collected were in pre-flexion phase, which is commonly characterised by full absorption of the yolk sac and flexion of the notochord. I found eggs of different developmental stages on the same nest such as seen in Figure 30-A, where there is an egg in the blastula stage and another in an early larval stage.

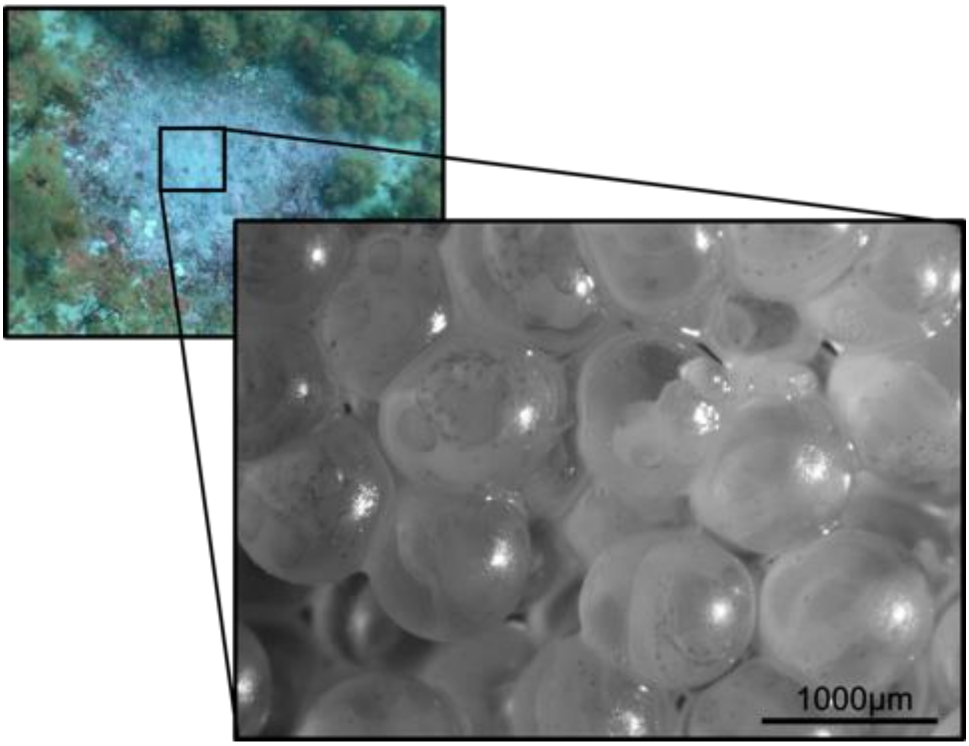

Figure 27. Photograph of a nest with eggs (top left) and photograph of *Spondyliosoma emarginatum* egg cluster collected from the nest (bottom right)

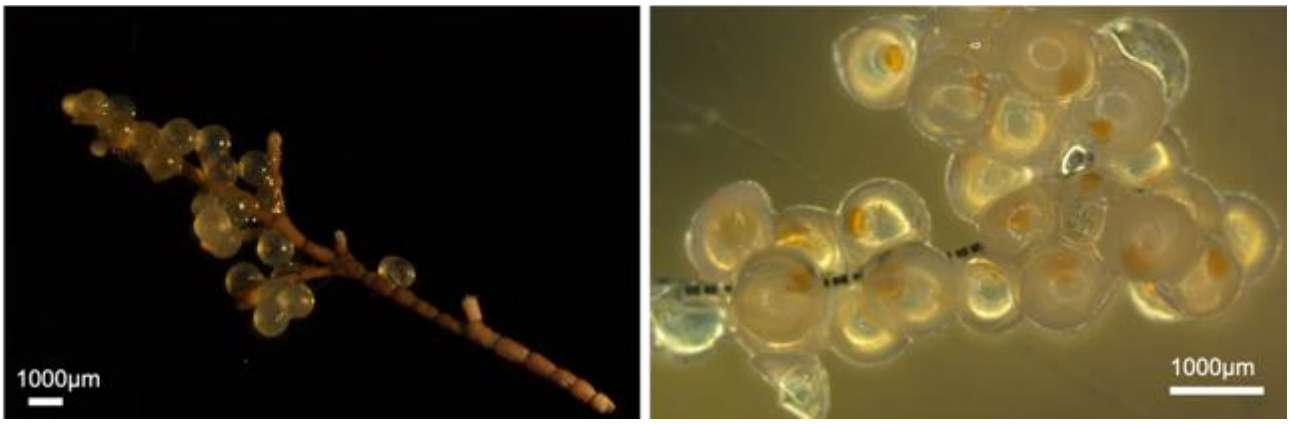

Figure 28. *Spondyliosoma emarginatum* eggs attached to different algae substrates

Figure 29. Number of nests with eggs on the site from the 30th of August until the 14th of November. The black line represents the lower cluster as well as the cluster on an elevated platform (cluster F), which was only noticed later on the 5th of October

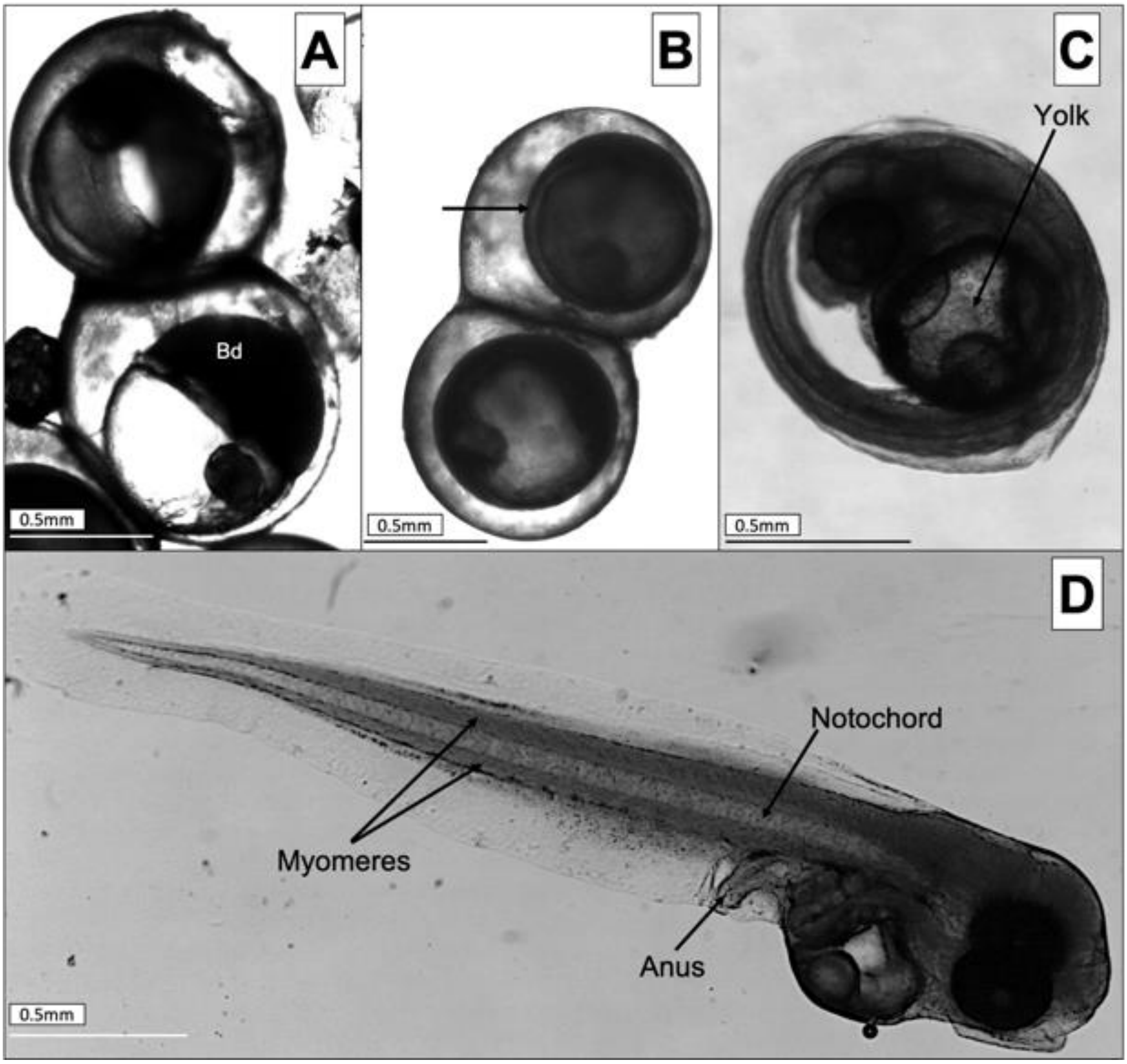

Figure 30. Embryonic and larval developmental stages in *Spondyliosoma emarginatum*. **A**, Blastula stage; Bd refers to the blastodisc. **B**, Gastrula stage; arrow points to embryonic shield. **C**, early larval stage; larvae is still curled around the yolk sac and organs are not yet clearly visible. **D**, later larval stage; somites within the myomeres are clearly visible, as are the eye, anus, and notochord

2.5. Discussion

Previous isolated observations of nesting and courtship of *S. emarginatum* were confirmed in this dedicated study. *S. emarginatum* is a nest-builder, and the nests are maintained for over a month. Whereas some isolated nests were discovered, the compound nest site I describe suggests that courtship and nesting is a highly social behaviour, similar to *S. cantharus*.

The clumped distribution of the nests made them difficult to locate and required careful monitoring for the presence of banded males in BRUVS, since banded males are likely an indication of a nearby nesting site. The two month time window suitable for nesting and associated harsh environmental conditions highlights the stressful environment in which this species reproduces.

Characterising the environmental variables associated with this nest site has provided vital information to help understand the suitable conditions under which this population spawns. An important insight is that this nesting site experiences stochastic environmental conditions due to recurring south-easterly gales, even if situated in a region of the bay which is usually sheltered to these gales (Terhorst, 1987).

Water temperature is an important factor affecting embryonic development and incubation time in fish eggs (Kamler, 2002; Yang and Chen, 2005). Warm water speeds up incubation time, which increases survival in nesting fish, since any extra time spent on the nest means a higher exposure to predation, unfavourable weather events and increased physical exertion for guarding males. Spawning started when temperatures increased above 14 ºC, and the majority of spawning happened at 15 ºC or higher, which coincides with the optimal spawning temperatures measured for *S. cantharus* (Gonçalves and Erzini, 2008). These spawning temperatures are lower than optimal spawning temperatures for most sparids (Sheaves, 2006), however most sparids spawn pelagic eggs, which may float to warmer surface waters.

It takes seven to ten days for *S. emarginatum* eggs to hatch (Beckley, 1989). This time is in agreement with this study's findings that nine days was the maximum number of consecutive days on which eggs could be observed on a single nest. This nesting population was also exposed to temperature fluctuations ranging from 13 to 17 ºC. This is characteristic of the north and north-western region of False Bay, where shallow water temperature varies frequently during spring and summer (Dufois and Rouault, 2012). Temperature fluctuations have strong effects on egg developmental times (Klimogianni *et al.*, 2004) and are likely to have important effects on *S. emarginatum* eggs. In addition, unlike a pelagic egg that stays in the water mass in which it was produced, demersal eggs are geostationary and vulnerable to current variations and associated temperature fluctuations. This adds even more uncertainty to egg developmental time.

The short time window suitable for spawning also explains why the spawning and nesting season differed slightly in length. Males had already established their nests on the 30th of August when the site was found, and the nesting period lasted just over two and half months. The spawning season is a little shorter and lasted just over two months with the first eggs appearing on the third of September and the last eggs recorded on the 13th of November. This suggests that males establish a nesting site prior to the correct environmental conditions for spawning. A spawning season of two months is relatively short in comparison to other Sparidae (Sheaves, 2006). This could be attributed to the male's energetic requirements of building and subsequently guarding a nest (Chapter 3), as well as the short time period during which the environmental conditions are suited for spawning in this region of False Bay.

While spring in the north-west region of the bay is the period during which average temperatures become suited to spawning, it also coincides with an increasing number of strong south-easterly gales (Pfaff *et al.*, 2019). The two dips in total number of nests with eggs on the site coincided with these south-easterly weather events, which cause periods of high turbidity, siltation and colder water. Complementing *in situ* data with local wind speed and direction from the Strand weather station was especially useful to gain a clearer insight into these weather events and their impact on the nesting site. The effect of successive days of south-easterly winds was evident by the measured *in situ* temperature drops that followed.

The vulnerability of the site and of nesting *S. emarginatum* males to these storms is twofold. Firstly, the south-easterly gales affect the structural integrity of the nests as was evident throughout the study as some nests were completely destroyed. Weather events have important effects on the success of nesting and the destructive effect of storms on nest was also noticed for other nesting species such as Pumpkinseed (*Lepomis gibbosus*) (Popiel *et al.*, 1996). This may be why *S. emarginatum* chose a fairly rocky site where boulders can offer protection from nest destruction and reduce the siltation of eggs. Secondly, strong south-easterly winds can cause local upwelling and sudden dips in temperature such as that seen on the 20th of September and 3rd of October.

Whilst no link could be found between oxygen concentration and behaviour, it is known that reduced oxygen levels increase the need for males to fan their eggs more regularly and expend more energy (Olsson *et al.*, 2016). Further research is needed to gain a clearer understanding of how these different environmental conditions interact to affect successful nesting and spawning.

The nesting population established its site on a subtidal rocky granite reef, characteristic of the western region of False Bay (Terhorst, 1987). The epifaunal assemblages consisting mostly of ophiuroids and crinoids is evidence that this is a relatively stable and low energy environment (Terhorst, 1987). The location of this nesting site at in 9 to 14 m may be the optimal combination of substrate suitability, turbulence, predation risk and water temperature. A higher proportion of rocky reefs and boulders exist closer inshore, and these sites would also be shallower and experience higher temperatures, which would speed up larval development.

There are trade-offs to consider for shallower or deeper sites. Shallower sites are closer to the shore and may experience a higher proportion of predation, especially from shore birds and visual predators such as *Loligo vulgaris*, *Pomatomus saltarix*, and *Sarda sarda*. This coast is frequently hit with wave height in excess of 3 m, and the effects of such turbulence will extend at least three times as deep as this measurement, making nests shallower than 10 m a poor choice. The shallower (5 to 9 m) nest in the yacht club was situated in the lee of the harbour, and not subjected to the turbulence of the Glencairn site. Nest destruction by storms for the three spined stickleback (*Gasterosteus* *aculeatus*) was also associated with depth and location of nests (Kynard, 1978), and I expect a similar relationship to apply to *S. emarginatum*.

Deeper waters, however, would be less turbulent and offer more protection to from nest destruction but deeper waters are colder, which would increase egg development time. The longer the eggs take to develop, the more energy the male must expend on nest guarding, without being able to replenish his reserves. Ultimately, this temperature-enforced delay will reduce the amount of eggs he can fertilize and hatch.

The tightly packed community of nests on the site is a common occurrence in nesting fish. Nesting aggregations can imply a scarcity of suitable habitat in the region, or a selective advantage conferred by spawning success or protection from predation (Gross and MacMillan, 1981). Bluegill sunfish (*Lepomis macrochirus*) and Green damselfish (*Abudefduf abdominalis*) also nest in tightly packed colonies, which has been shown to offer protection against brood predation (Gross and MacMillan, 1981; Tyler, 1995). Stand-alone nests as well as those in the periphery of *L. macrochirus* nesting colonies experienced brood loss at a rate of three times higher than nests in the colony (Gross and MacMillan, 1981).

The finding that many invertebrate species associated with the nest border or directly on the nest surface also suggests that these nests provide an important micro-habitat for macroinvertebrate species. Nests of the freshwater *Nocomis* spp. were shown to provide a microhabitat for 38 different families of macroinvertebrates (Swartwout *et al.*, 2016). Further research would be required to investigate the role of *S. emarginatum* nests on macroinvertebrate communities.

Identifying similar sites could help in the location of more nesting sites in the region. Some species can show extremely high nest-site fidelity and return to the same nesting sites year after year (King and Withler, 2005). In a temperate reef fish, Lingcod (*Ophiodon elongatus*), genetic markers showed that 86% of selected males returned to the site the following year and many to the same exact nest (King and Withler, 2005). It is therefore possible that this represents a recurring nesting site for this *S. emarginatum* population.

The average size of *S. emarginatum* nests in this study was smaller than those recorded for *S. cantharus,* whose nest sizes also vary significantly between sites due available substrate and site topology (Collins and Mallinson, 2012). This compound nesting site was a small rocky outcrop surrounded by sand so it may be that the amount of available nesting substrate was limited. It would be necessary to find other *S. emarginatum* nesting sites to understand the range of nest sizes for this species.

Most nests saw no significant change in size over time, which implies that males do not increase the size of their nest once built. The variability in nest destruction following south-easterly storms also implies that the location and features surrounding the nest have an effect on the nest's susceptibility to strong weather events.

Whereas the nesting site is in the Table Mountain National Park (TMNP) marine protected area, it is not in a no-take zone. Anglers and spearfishermen were observed over the site on several occasions during the study. In addition, False Bay has experienced a decline in many commercial linefish species as well as increase in illegal fishing (Pfaff *et al.*, 2019). This poses a risk to *S. emarginatum* populations during the nesting season, where nesting males are highly vulnerable. A fishing closure on spawning aggregation sites is recommended to conserve the species during this critical life-history stage. A study on the effects of catch-and-release practices above *S. cantharus* nesting grounds revealed that 17% of fish captured were at high risk of post-release mortality, in addition to vacated nests likely suffering high levels of predation (Pinder *et al.*, 2017).

3. Chapter 3 - A description of the mating behaviour of *Spondyliosoma emarginatum* on a large nesting site from remote submarine videography

3.1. Introduction

Nests and accompanying nesting behaviours are critical in determining the survival of offspring (Barber, 2013). Nesting fish species are widely distributed across the globe in freshwater and marine habitats, but studies of nesting behaviours are taxonomically restricted to a few families (Barber, 2013), namely Blenniidae (blennies) (Phillips, 1974), Pomacentridae (damselfishes and clownfishes) (Robertson, 1973), Cichlidae (cichlids) and Gasterosteidae (sticklebacks) (van Iersel, 1953). In addition, most of this research has focused on observations under experimental conditions in aquaria. These restrictions can be attributed to the difficulty of underwater *in situ* observations, and a historical lack of submersible video technology. Laboratory studies are a useful alternative, as they are often hypothesis directed and provide information on specific aspects of nesting behaviour. Nonetheless, *in situ* observations are also needed to provide a realistic overview of the system (Shaffer and Johnson, 2008).

Field studies on nesting behaviours were until recently restricted to visual observations by divers using snorkels or self-contained underwater breathing apparatus (SCUBA). These methods limit continuous observations to a maximum of 45 min, and divers introduce an added confounding effect of disturbance, which is known to affect natural fish behaviour (Emslie *et al.*, 2018). Parental care is energetically costly (Clutton-Brock, 1991), and long-term observations in the wild can help inform us on how behaviours change throughout the nesting sequence and in response to environmental conditions.

Only two genera show evidence of nesting in the Sparidae (*Spicara* and *Spondyliosoma*), and descriptions of their nesting behaviour are sparse. Aquarium observations are available for *Spondyliosoma emarginatum* (Van Bruggen, 1965) and *S. cantharus* (Wilson, 1958). Accounts of nesting behaviour *in situ* are only available from SCUBA observations for *S. cantharus* (Doggett, 2015) and *Spicara smaris* (Raffaelle, 1898; Harmelin and Harmelin-Vivien, 1976).

3.1.1. Nesting stages

Nesting behaviour in fishes can been categorised into three stages: nest-building, courtship and egg care (van Iersel, 1953; Sevenster, 1961; Timms and Keenleyside, 1975).

Nest building

While nest-building behaviours in the Sparidae remain poorly understood, the nest types documented are similar in that they all seem to involve a bare hard surface. *S. cantharus* nests were described as “an area of the slate floor of the tank cleared of its usual covering of small pebbles”

(Wilson, 1958) and as circular patches for *S. emarginatum* (Van Bruggen, 1965) and *S. smaris* (Harmelin and Harmelin-Vivien, 1976). In addition, research on *G. aculeatus* and *S. cantharus* has shown that nest building often starts in response to temperature cues but this remains undocumented in the wild for Sparidae species (van Iersel, 1953; Wilson, 1958). Some behaviours observed during nest building for *S. cantharus* include the chasing away of other males and an accentuation of nuptial colouration as black and white bands (Doggett, 2015). The onset of colouration was also noticed in aquaria for *S. emarginatum* where colours intensified in a matter of seconds in the presence of passing males or females (Wilson, 1958; Van Bruggen, 1965). The majority of nest building behaviours remains otherwise unknown, as do the pressures males face during nest building such as competition from other males or predation from other species.

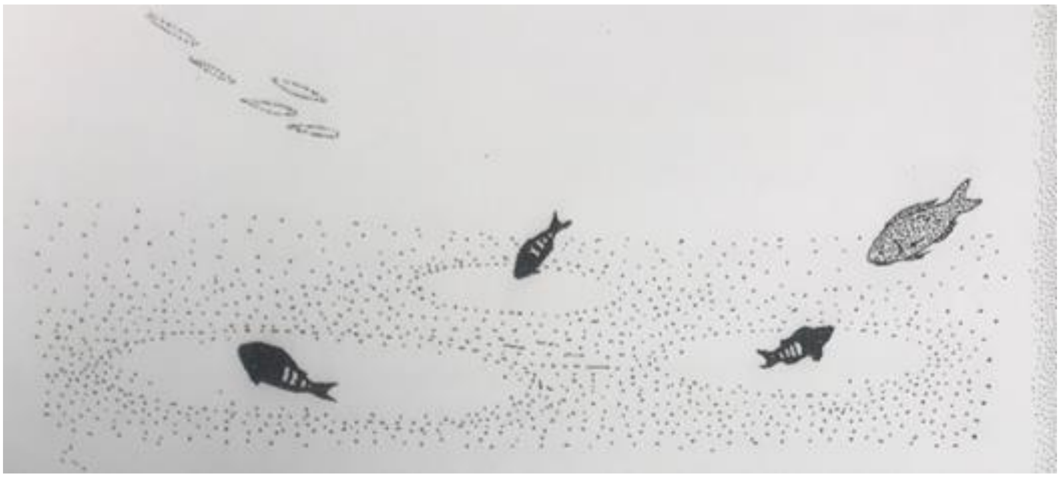

Figure 31. *Spondyliosoma emarginatum* nesting scene from observations at the Port Elizabeth aquarium. Males are seen in nuptial dress at the centre of their circular nests. Nests were also reported to border on each other (Van Bruggen, 1965)

Courtship

The main difference between nest building and courtship has been described for *G. aculeatus* as a readiness to accept females (van Iersel, 1953). This reaction varies across species but often involves distinct swimming “dances” and an accentuation of nuptial colours as the male attempts to lead females to their nest. Following gamete release, males of *G. aculeatus* show aggression towards the female and chase her away. This has been hypothesised to occur as a result of a sudden lowered sex drive post sperm release and also due to the absence of the female’s swollen abdomen as a cue for courtship (van Iersel, 1953). Courtship has been briefly observed for *S. cantharus* in the wild, where males are seen circling their nest to attract females (recognisable by their white horizontal stripe) to their nest (Doggett, 2015). Spawning has not been observed in the wild for any of the nesting Sparidae. It is evident that information on courtship, spawning, and mating systems is also greatly lacking and requires more attention.

Egg care

During the parental phase, the male takes care of the eggs through actions such as ventilating the eggs by fanning, chasing away fish predators and removing invertebrate predators from the nest.

Males should favour a high level of paternity in the young to justify the time and energy investments required for guarding a nest. Factors that decrease genetic relatedness on nests include brood parasitism by sneaker males, known as cuckoldery, or by nest-takeovers and egg thievery (DeWoody and Avise, 2001). None of these behaviours have been documented in nesting Sparidae.

The presence and type of predators surrounding nesting sites can be a useful indication of the predation pressure and energetic demands of nest defence by males. Predation pressure was briefly noted for *S. cantharus* and appeared to be site-specific as there were different predators at each site (Doggett, 2015). Aquarium accounts of *S. cantharus* during egg care included an instance whereby a male seized the antenna of a rock-lobster to drag it off the nest (Wilson, 1958). Such accounts are absent for *S. emarginatum* but are required to describe the energetic demands of the species and the communities present on nesting sites.

3.1.2. Energetic demands during nesting

Fanning

Fanning, sometimes referred to as skimming (Sale, 1971; Robertson, 1973), is a commonly described behaviours in nest-tending fish. Fanning consists of the pectoral, pelvic, caudal, or anal fin beating regularly over a surface (Blumer, 1982). The function of this action has several roles (Sevenster, 1961). One is to remove detritus from a surface to keep it clean. Another is to ventilate and remove metabolic waste as well as any silt or debris from the eggs (Sale, 1971). Fanning is expected to increase with egg development to match the oxygen demands of developing embryos. A study on male common gobies (*Pomatoschistus microps*) revealed that fanning frequency increases over the parental care period and that the frequency and rate of fanning also increased in reduced oxygen conditions (Jones and Reynolds, 1999). The energetic demands of fanning was sufficiently high that male gobies in low oxygen treatments suffered weight loss, suggesting fanning to be an important factor in the loss of condition experienced by nesting species (Jones and Reynolds, 1999).

Nest maintenance

A common behaviour in nesting fishes is the regular cleaning of debris and or items deemed unsuitable on the nesting surface. Individuals will remove unwanted items with their mouth and carry them away from the nest (Robertson, 1973; Timms and Keenleyside, 1975). These items can be pieces of vegetation or rock or even benthic invertebrates that wander onto the nest surface. This behaviour is likely to be energetically demanding to males. The types and quantities of invertebrates removed might reflect the predation pressure on the eggs.

Guarding and territoriality

Territoriality and guarding of the nest is defined as “Displaying towards and/or actively chasing conspecifics and heterospecifics that approach the eggs or fry, or the site where they are located” (Blumer, 1982). Interactions between conspecifics are common in fishes (van Iersel, 1953; Sale, 1971; Phillips, 1974). The message behind these displays are however not always clear. Some studies have mentioned that displays are especially useful in colourful fish or fish with accentuated sexual dichromatism during the mating season. This is because it has been proven that fish are capable of associative learning and there is evidence that colour displays are used in social interactions to establish hierarchy and dominance (Reese, 1975; Stacey and Chiszar, 1978). For example, in brightly coloured Chaetodontids, interactions between conspecifics may serve to reinforce social structure in the population (Reese, 1975). In addition, a study on wild nesting Sunfish (*Lepomis* spp.) found that when exposed to model fish with body patterns, this elicited a heightened aggressive response compared to simple colourless models (Stacey and Chiszar, 1978). Interestingly, this study also showed that when exposed to female colour patterns, male reduced aggressive behaviours and started carrying out pre-spawning activities. It is possible that such social interactions occur in many territorial and coloured fish species and understanding these displays are an important step to understanding their social structure.

3.2. Aims

This study aims to provide a detailed qualitative description of the reproductive behaviour of *Spondyliosoma emarginatum* using remote, non-invasive underwater videography. Where possible, behaviour involving durations and rates will be quantified, to provide a basis for gauging the relative energetic costs, as such costs could not be quantified in units of energy. The central hypothesis that will be tested is that the frequency of male behaviours changes once eggs are deposited on the nest. Positive affirmation of this hypothesis may confirm the utility of certain behavioural actions. These include time spent on the nest, the frequency of fanning and the chasing and clearing of egg predators. The responses of males to other males, females and other species will be closely examined and described.

3.3. Materials and methods

3.3.1. *Study site and period*

The study began on the 24th of August and ended on the 7th of October 2019. Two sites were studied, both located in western-most part False Bay, South Africa. The first site was at the False Bay

Yacht Club (FBYC) at a depth of 7 m, and the second site was at Glencairn in False Bay at an average depth of 13 m. Only one nest was recorded at the FBYC. The second site was a large compound nest site at Glencairn (Chapter 2).

3.3.2. Video deployments

Individual nests were filmed using cameras (Hero 7 Black (x2), Hero 4 silver, Hero 3+, Hero (x2), Hero 1; GoPro Inc., San Mateo, CA, USA) with waterproof housings fixed onto custom made stands. Each stand consisted of two perpendicular metal bars, wired to a 1 kg lead dive weight. A metal camera fitting was screwed to a plastic plate that was itself screwed to the weight (Figure 32).

At the start of the study, nests were tagged using small lead sinkers to which a numbered plastic label was attached by means of a short length of fishing line. The sinker was placed in the vicinity of the nest, but not in the nest.

A camera stand was placed about 30 cm from each nest and the camera turned on (Figure 32). The tag for that nest was then shown to the camera so that it could later be identified properly during analysis. The presence or absence of eggs on the nest was noted using a pencil and slate. On a subsequent dive, the camera on the stand was collected and replaced with another camera. The stand was then either moved to another nest or left to film the nest it was on. This study had access to a total of seven cameras. As cameras were retrieved, they were replaced with freshly charged cameras, which meant that either three or four cameras could film simultaneously. I chose different combinations of nests for filming on each dive, in an attempt to simultaneously capture nests from different clusters and to sample a mix of those with and without eggs (see Chapter 2 for details on nest cluster characteristics and locations on the site).

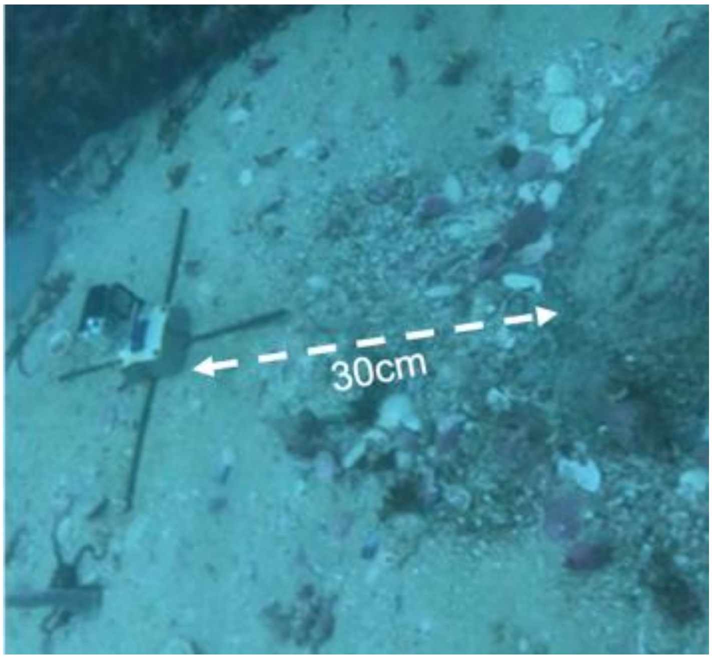

Figure 32. Camera stand placement 30 cm away from a *Spondyliosoma emarginatum* nest

3.3.3. Video analysis

This study is purely observational, and no manipulations of conditions were carried out. Male behaviours were characterised using an ethogram, which is as a list of behaviours performed by that animal (Huntingford, 1986). Fish display an extremely wide variety of behaviours and so this study focused on select nest-tending behaviours chosen for their frequency or importance during the nesting period (

Table 11).

Throughout the study period, a total of 97 videos were collected over 23 days and 27 dives. All the footage was captured between 08:00 am and 16:00 pm at a mean time of day of 11:00 am. Video length varied from 18 to 157 min, with a mean time of 92 min, due to differences in battery charge. I carried out an initial sorting of the videos, and some footage was discarded due to poor quality, bad camera placement or nest abandonment. After that, 74 videos of 19 males were kept for analysis, totalling 113 h of footage. Each male was named using a three-digit number i.e. 001. Each video was analysed in full using the behavioural analysis software called BORIS (Friard and Gamba, 2016). To account for any distress caused by camera placement and nearby divers, video analysis started 5 min from when the male first returned to his nest. In addition, behaviours within 3 min of diver sightings were also excluded and that time removed from analysis time. If a male left the frame and failed to return before the end of the video, the end of the analysis was marked as the last shot of the male in frame. To investigate nest fidelity among males, males were identified from their individual markings and bands.

Table 11. *Spondyliosoma emarginatum* behaviours that were recorded in the ethogram. Measured parameters for each behaviour include frequency (F) (count/h), and duration (D) (min/h)

Behaviour	**Description**	**Parameters measured**
Aggressive bout	Continuous back and forth chases between a nesting male and a neighbour or male swimming by	F, D
Chasing – conspecifics	Chasing away other male or females that are either on the nest or swimming by	F
Chasing - other species	Chasing away or attempts to chase another species that is either on the nest or swimming by	F
Clearing	Actively removing items or animals from the nest surface. This is done by picking the object or invertebrate up with his mouth and swimming away from the nest with it or removing it from the nest surface.	F
Courtship display	Actively courting a female	F, D
Diver in shot	Divers in shot and swimming by or carrying out fieldwork activities. were recorded so that diver disturbance can be accounted for during analysis.	F
Fanning	Rapid beating of the caudal fin over or near the nest surface	F
Female on nest	A female is on the nest	F, D
Leaving the nest	Leaving the nest was caused by actions that included: clearing, chasing, predator avoidance, disturbance by *Chrysoblephus laticeps*, wandering or hovering. In cases where leaving was a wander or hover, the male was only marked as having left when he was three or more body heights above the nest.	F, D
Nest visitor - conspecifics	This includes any *S. emarginatum* that stops on the nest to inspect it or attempt to claim the nest as his own.	F
Nest visitor - other species	This includes any species other than *S. emarginatum* that stop on the nest surface. This is different from a swim-by, in that the organism has to be touching the nest surface or stopping noticeably on it rather than a simple swim by.	F
On nest	The male is on the nest.	D
Other	Any behavioural event deemed important and not represented in the ethogram	F
Out of frame	The male is out of frame.	F, D
Spawning	Both sexes release gametes.	F
Swim-by	This occurs when any species swims over or nearby the nest. These observations help describe the community around the nesting site.	F

3.3.4. Statistical analyses

Behaviour frequency and duration

A maximum of two variables was measured per behaviour, frequency (count/h) and duration (min/h). These were calculated per video as per formula (1) and (2).

$$\text{Behavioural frequency (count/h)} = \frac{total\ counts}{analysis\ time\ (s)} \times 3600 \tag{1}$$

$$\text{Behavioural duration (min/h)} = \frac{total\ time\ (s)}{analysis\ time\ (s)} \times 60 \tag{2}$$

If a behaviour was absent from a video, it was assigned a behavioural frequency of 0 count/h. This ensured all behaviours had a frequency per video. Duration was not measured for all behaviours (Table 11). In addition, if a behaviour was absent (frequency=0 count/h) then it was not assigned a duration. For example, if a video had a courtship display frequency of 0 count/h, then no courtship display duration was given since assigning a duration of 0 min/h is misleading and would affect later calculations of average courtship display duration.

In summary, each behaviour in each video has a frequency value and when applicable a duration value. Since the total number of videos per male varied, this resulted in a different number of total frequency and duration values per behaviour per male.

Time on nest

The time each male spent on the nest was a behaviour that was calculated per video by subtracting all the times that a male spent off the nest from analysis time. If a male left the nest and failed to come back into shot before the end of the video, then analysis time stopped just before that last leaving event. While that last leaving event was included as a leaving count, the duration of that leaving event was not included as it is impossible to know when the male would have returned to the nest.

Effect of fieldwork on behavioural analyses

A prerequisite to the statistical analyses was to ensure that experimental effects such as analysis time and the time of day at which the video was taken had no effect on the frequency or duration of behaviours. A first linear regression was conducted to look at the effect of analysis time on the time spent by each male on the nest. Three additional linear regressions were conducted to test the effect of the time at which the videos were taken each day on date, egg presence and analysis time. These tests were done to check for any bias in how the videos were collected.

Descriptive statistics

For each behaviour, an average behavioural frequency and duration (where applicable) was taken per male by averaging across all videos for that male. Descriptive statistics (mean, standard deviation, standard error and coefficient of variation) were then calculated for each behavioural variable by averaging across all males (n=19). For some behaviours, the sample size for behavioural duration statistics was less (n<19) since not all behaviours were captured for all males.

Similar descriptive statistics were also carried out for the different species swimming by nests. A mean swim-by rate (count/h) for each species was calculated by averaging across videos per male. Absence of presence was accounted for by assigning the absence of a swim-by for a species in a video with a count of 0.

Effect of egg absence or presence on behaviours

All but two males (male 003 and male 009) were either filmed only on empty nests (no egg group) or only on nests with eggs (egg group). To allow for a nested ANOVA design, no male could have behavioural observations in both groups. When a nested design was necessary, behavioural observations from videos in the egg group for males 003 (n=2) and 009 (n=4) were removed from the analyses, resulting in a remaining 67 videos from the original 74 videos.

Levene's test

A Levene's test for equality of variances was conducted for each behavioural variable to compare variances between observations in the no egg group and egg group. A significant result ($p<0.05$) indicates heteroscedasticity.

In these tests, observations from each video were included and not averaged per male. For behavioural frequency, each behaviour had 31 observations in the no egg group and 36 observations in the egg group. For behavioural duration, the number of observations differed per group per behaviour since not all males carried out all behaviours. The sample sizes per behaviour per group are reported in the test results.

Nested analysis of variance (ANOVA)

For each behaviour parameter, if Levene's test was not significant a nested analysis of variance (ANOVA) was performed. Egg absence or presence was set as the main effect, and individual males were set as the error term (or nested effect). For each behavioural frequency (count/h), there were 31 observations from six males in the no egg group, and 36 observations from 13 males in the egg group. As a result, the total observations in both groups are balanced. Sample sizes for tests on behavioural duration are reported per test in the results since the number of males and observations per male vary per behaviour.

Welch's t-test

For behavioural parameters where Levene's test revealed heteroscedasticity ($p<0.05$), a Welch's t-test was carried out. Omitted values for male 003 and 009 were returned since the tests no longer needed to be nested. Welch's t-test is less powerful as it disregards variation among the males, by lumping all data, and so for each behaviour, behavioural variables were averaged per male ($n=19$).

A Welch's t-test was conducted per behavioural variable comparing observations between the no egg group and egg group. For behavioural frequency, the no egg group had six observations and the egg group had 15 observations. Sample sizes for tests on behavioural duration are reported per test since the number of observations per group vary per behaviour.

Behaviour specific t-tests

A series of behaviour-specific t-tests were performed for more insight into the effect of egg absence or presence on select behaviours. Each test looked at the effect of select behaviours or events between males in the no egg group ($n=6$) and egg group ($n=15$). For all tests, absence of presence was accounted for by assigning absence of a group or event with a count of 0 per video.

The effect of egg presence or absence was investigated on the types of items cleared from the nest. The clearing frequency (count/h) of eight items was calculated per video and then averaged per male. The effect of eggs was also examined for *S. emarginatum* swim-bys by sex (male, female, unknown) over nests. Similarly to the items cleared, the frequency of each group swimming by a nest was counted per video and averaged per male. Finally, similar to the swim-by t-tests, the effect of egg absence or presence on type of *S. emarginatum* sex chased was tested.

3.4. Results

3.4.1. Sample size

A total of 74 videos were retrieved (

Table 12) and additional Date, subject number, egg presence and analysis time are also listed (Supplementary table 1). Only one male (001) was filmed in the FBYC, whereas all the others were filmed at the Glencairn nesting site. The total number of videos per males varied from one to 13, and the total analysis time per male varied from 40 min to 22.7 h (

Table 12).

Table 12. Summary of footage acquired per *Spondyliosoma emarginatum* male. On some days more than one video was taken per male, which explains why total videos is sometimes greater than the sum of the number of days filmed with and without eggs i.e. male 003

Male	**Total videos**	**Total analysis time (min)**	**Days filmed (no eggs)**	**Days filmed (eggs)**
001	2	176	1	0
002	1	135	1	0
003	17	1360	11	2
006	10	823	7	0
007	2	135	2	0
008	6	447	0	5
009	6	427	2	4
010	7	544	0	6
011	3	331	0	3
013	2	113	0	2
014	2	39	0	2
015	1	136	0	1
016	3	177	0	2
017	2	152	0	2
018	5	523	0	4
019	2	213	0	2
020	1	124	0	1
021	1	137	0	1
022	1	155	0	1

3.4.2. Fieldwork effect on behavioural analyses

There was no significant effect of video length on the duration of time each male spent on the nest (p=0.37, R^2=-0.002, df=72, n=74). Equally, there was no significant effect on the time at which videos were taken of either date (p=0.253, R^2=0.004, df=72, n=74), the presence of eggs (p=0.79, R^2=-0.01, df=72, n=74), and analysis time (p=0.75, R^2=-0.01, df=72, n=74).

Once the camera was placed and turned on, it took males a mean time of 4 min 23 s to return to the nest. Diving related disturbances resulted in 171 min of footage being omitted from analysis times across 22 videos, equivalent to a mean loss of 8 min per video.

3.4.3. Summary statistics for all nesting behaviours

Video examples of each behaviour are available at: https://shysteentjies.com/nesting-behaviours and https://www.youtube.com/playlist?list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo. From the videos, 11 male behaviours were observed as well as four other regularly occurring events (

Table 13). Males remained on their nest on average for 46 min/h (

Table 13). The least frequent event observed was spawning (0.19 counts/h) and the most frequent event was fanning (80 counts/h). By duration, the shortest behaviour was also spawning (0.19 min/h) and the longest behaviour was males being out of shot (12 min/h) and chasing away conspecifics (10 min/h) (

Table 13).

Table 13. Frequency and duration of male *Spondyliosoma emarginatum* nesting behaviours and other events. Standard deviation (sd), sample size (n), standard error (se), coefficient of variation (cv). For each behaviour, a link is provided to example online video footage

Behaviour	**Parameter**	**Mean**	**sd**	**n**	**se**	**cv**	**Video example Link**
Male behaviour							
Aggressive bout	count/h	1.61	3.08	21	0.67	1.91	https://www.youtube.com/watch?v=Ha31T9q36jo
	min/h	0.21	0.24	13	0.07	1.15	
Chase - other species	count/h	3.72	2.78	21	0.61	0.75	https://www.youtube.com/watch?v=jtzZGJq9DSU&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=13
Chase - conspecifics	count/h	9.73	8.73	21	1.9	0.9	
Cleaning with mouth	count/h	26.91	43.97	21	9.6	1.63	https://www.youtube.com/watch?v=-eo0jksPqkY&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=4
	min/h	0.45	0.73	21	0.16	1.63	
Clearing	count/h	7.05	4.92	21	1.07	0.7	https://www.youtube.com/watch?v=l1yjm_bJYEw&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=3
	min/h	0.71	0.49	21	0.11	0.7	
Courtship display	count/h	4.91	6.69	21	1.46	1.36	https://www.youtube.com/watch?v=LuHUfeQbHuw&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=12
	min/h	2.53	4.21	10	1.33	1.67	
Fanning	count/h	79.44	51.18	21	11.17	0.64	https://www.youtube.com/watch?v=QuB2Vx0nbqI
	min/h	1.32	0.85	21	0.19	0.64	
Spawning	count/h	0.19	0.50	21	0.11	2.71	https://www.youtube.com/watch?v=eI_H5CXONSA&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=11
Nest departures	count/h	13.98	5.18	21	1.13	0.37	https://www.youtube.com/watch?v=-9kMhHXWCmo
	min/h	4.79	3.93	21	0.86	0.82	
On nest	min/h	45.64	11.78	21	2.57	0.26	https://www.youtube.com/watch?v=E2cPpgiGY-k&feature=youtu.be
Out of shot	count/h	76.58	37.7	21	8.23	0.49	-
	min/h	12.19	12.06	21	2.63	0.99	
Parasite sweep	count/h	3.12	3.07	21	0.67	0.98	https://www.youtube.com/watch?v=Q26q8v36KOI
Other events							
Female on nest	count/h	1.49	2.53	21	0.55	1.7	Female on nests can be seen in the videos on courtship, spawning and nest visitors.
	min/h	2.74	4.39	8	1.55	1.6	
Nest visitor - conspecifics	count/h	0.86	1.25	21	0.27	1.46	https://www.youtube.com/watch?v=4qQYiLhZF-4&t=1s
Nest visitor - other species	count/h	2.4	5.66	21	1.24	2.36	
Chrysoblephus laticeps on nest	count/h	1.22	4.16	21	0.91	3.41	https://www.youtube.com/watch?v=I_Fc-Sxfvno&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=10
	min/h	0.70	1.21	6	0.49	1.74	
Swim by - conspecifics	count/h	13.1	16	21	3.49	1.22	https://www.youtube.com/watch?v=tIx3WlCtksE&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=5
Swim by - other species	count/h	4.39	3.78	21	0.82	0.86	https://www.youtube.com/watch?v=BTXFhrJwc8w&list=PLpl_RpSR8nmo8tO9bXGgqI96t1IwaXLeo&index=14

3.4.4. Behavioural effect of egg presence

Levene's test

A total of six behaviours were affected by heteroscedasticity ($p<0.05$), three of which were male behaviours and three were other events (Table 14). These included: the frequency of chasing other species, the duration of courtship, the duration of clearing, and the frequency of nest visitors from conspecifics, other species, and *C. laticeps*.

Table 14. Results of Levene's tests of the differences in the variance of *Spondyliosoma emarginatum* male nesting behaviour variables (frequency and duration) and other variables between the absence or presence of eggs. Statistically significant results indicate heteroscedasticity. Degrees of freedom (df). *$p<0.05$

Behaviour	**Parameter**	***F***	**df**	***p***	
Male behaviours					
Aggressive bout	count/h	0.45	18,48	0.97	
	min/h	0.58	10, 19	0.81	
Chase - conspecifics	count/h	0.86	18,48	0.62	*
	count/h	1.97	18,48	0.03	
Cleaning with mouth	count/h	1.48	18,48	0.14	
	min/h	1.44	18, 44	0.16	
Clearing	count/h	1.69	18,48	0.07	
	min/h	2.1	18, 39	0.03	*
Courtship display	count/h	0.61	18,48	0.87	*
	min/h	3.69	8, 21	0.01	
Fanning	count/h	0.88	18,48	0.61	
	min/h	1.12	18, 43	0.37	
Gamete release	count/h	0.62	18,48	0.87	
Nest departures	count/h	1.03	18,48	0.44	
	min/h	1.04	18, 48	0.44	
Out of shot	count/h	1.21	18,48	0.29	
	min/h	0.91	18, 48	0.57	
Parasite sweep	count/h	0.6	18,48	0.88	
Time on nest	min/h	1.04	18,48	0.44	
Other events					
Female on nest	count/h	0.67	18,48	0.82	
	min/h	0.38	6, 12	0.88	
Nest visitor - conspecific	count/h	2.05	18,48	0.02	*
Nest visitor - other species	count/h	14.78	18,48	0	*
Chrysoblephus laticeps on nest	count/h	1.99	18,48	0.03	*
	min/h	1.41	4, 11	0.29	
Swim by - conspecific	count/h	0.58	18,48	0.9	
Swim by - other	count/h	0.76	18,48	0.74	

Effects of egg presence on behaviour frequency and duration

Male behaviours that were unaffected by egg presence include: chasing other species, clearing, fanning, gamete release, and parasite sweeps (Table 15, Table 16). Other events that were also unaffected by egg presence include: nest visits by other species and *C. laticeps* (Table 15, Table 16).

Male behaviours that were affected by egg presence in frequency and duration or simply in frequency when no duration value was taken include: time spent on the nest, chasing conspecifics, cleaning, leaving – dash, nest departures and out of shots (Table 15). Other events that were also completely affected by egg presence include: nest visits by conspecifics, and swim bys by other species and conspecifics (Table 15, Table 16). The direction of each effect is reported in further detail below.

For some behaviours, only their frequency was affected by egg presence and include aggressive bouts, courtship displays, females on the nest, and leaving – wander (Table 15). Only for hovering was it the case that the duration but not the frequency was affected by egg presence (Table 15).

Table 15. Results of Welch's two sample t-tests of the effects of eggs (absence or presence) on *Spondyliosoma emarginatum* nesting behaviour. Degrees of freedom (df). **p*<0.05

Behaviour	**Parameter**	***t***	**df**	***p***	
Chase - other species	count/h	0.58	6.62	0.58	
Nest visitor - other species	count/h	1.78	5.03	0.14	
Nest visitor - conspecifics	count/h	4.08	5.22	0.01	*
Chrysoblephus laticeps on nest	count/h	1.19	5.01	0.29	
Clearing	min/h	1.04	7.44	0.33	
Courtship display	min/h	-2.41	3.01	0.09	

Table 16. Results of two-factor nested analysis of variance (ANOVA) of the effects of eggs (absence or presence) and individual *Spondyliosoma emarginatum* male (n=19) on nesting behaviour. Degrees of freedom (df), Sum of squares (SS), Mean sum of squares (MS). **p*<0.05.

Behaviour	**Parameter**	**Term**	**df**	**SS**	**MS**	***F***	***p***	
Male behaviours								
Aggressive bout	count/h	Eggs	1	72.78	72.78	6.94	0.02	*
		Male	17	178.17	10.48			
		Error	48	595.95	12.42			
	min/h	Eggs	1	0.68	0.68	4.7	0.06	
		Male	9	1.31	0.15			
		Error	19	3.62	0.19			
Chase - conspecifics	count/h	Eggs	1	1640.34	1640.34	14.2	0	*
		Male	17	1963.83	115.52			
		Error	48	6097.16	127.02			

Cleaning with mouth	count/h	Eggs	1	41782.54	41782.54	29.41	0	*
		Male	17	24148.06	1420.47			
		Error	48	77973.02	1624.44			
	min/h	Eggs	1	34.67	34.67	33.17	0	*
		Male	17	17.77	1.05			
		Error	44	55.52	1.26			
Clearing	count/h	Eggs	1	163.65	163.65	1.83	0.19	
		Male	17	1519.43	89.38			
		Error	48	4320.1	90			
Courtship display	count/h	Eggs	1	1247.11	1247.11	8.97	0.01	*
		Male	17	2363.35	139.02			
		Error	48	15811.94	329.42			
Gamete release	count/h	Eggs	1	0.79	0.79	2.53	0.13	
		Male	17	5.35	0.31			
		Error	48	29.14	0.61			
Fanning	count/h	Eggs	1	7816.37	7816.37	1.41	0.25	
		Male	17	94340.38	5549.43			
		Error	48	287598.19	5991.63			
	min/h	Eggs	1	2.38	2.38	0.56	0.46	
		Male	17	72.28	4.25			
		Error	43	199.87	4.65			
Leaving - Dash	count/h	Eggs	1	5696.89	5696.89	21.77	0	*
		Male	17	4448.98	261.7			
		Error	48	28270.41	588.97			
	min/h	Eggs	1	10731.23	10731.23	26.15	0	*
		Male	17	6975.49	410.32			
		Error	48	12990.93	270.64			
Leaving - Hover	count/h	Eggs	1	52.27	52.27	1.11	0.31	
		Male	17	803.79	47.28			
		Error	48	1107.65	23.08			
	min/h	Eggs	1	164.9	164.9	6.27	0.03	*
		Male	14	368.28	26.31			
		Error	33	1740.49	52.74			
Leaving - Wander	count/h	Eggs	1	194.04	194.04	14.85	0	*
		Male	17	222.2	13.07			
		Error	48	1019.37	21.24			
	min/h	Eggs	1	13.35	13.35	0.85	0.39	
		Male	7	110.03	15.72			
		Error	16	616.88	38.56			
Nest departures - all	count/h	Eggs	1	9338.73	9338.73	24.74	0	*
		Male	17	6418.34	377.55			
		Error	48	35194.21	733.21			
	min/h	Eggs	1	15675.49	15675.49	48.82	0	*
		Male	17	5458.06	321.06			
		Error	48	17587.43	366.4			
Out of shot	count/h	Eggs	1	90260.96	90260.96	63.36	0	*
		Male	17	24218.56	1424.62			
		Error	48	120311.54	2506.49			
	min/h	Eggs	1	14801.44	14801.44	42.72	0	*
		Male	17	5889.77	346.46			
		Error	48	22251.92	463.58			
Parasite sweep	count/h	Eggs	1	17.66	17.66	1.03	0.32	

		Male	17	291.33	17.14			
		Error	48	455.21	9.48			
Time on nest	Count/h	Eggs	1	5643	5643	48.83	0	*
		Male	17	1965	116			
		Error	48	6331	131.9			
		Other events						
Female on nest	count/h	Eggs	1	74.65	74.65	7.03	0.02	*
		Male	17	180.58	10.62			
		Error	48	1308	27.25			
	min/h	Eggs	1	844.15	844.15	5.26	0.07	
		Male	5	802.52	160.5			
		Error	12	111.38	9.28			
Chrysoblephus laticeps on nest	min/h	Eggs	1	43.31	43.31	0.46	0.55	
		Male	3	284.11	94.7			
		Error	11	519.76	47.25			
Swim by - other	count/h	Eggs	1	120.28	120.28	4.81	0.04	*
		Male	17	425.44	25.03			
		Error	48	467.03	9.73			
Swim by - conspecifics	count/h	Eggs	1	1571.15	1571.15	18.12	0	*
		Male	17	1474.15	86.71			
		Error	48	4789.82	99.79			

Fanning was the most frequent behaviour in the absence and presence of eggs, followed by nest departures and clearing (Figure 33). For graphing purposes, the chasing of conspecifics and other species, as well as aggressive bouts were grouped in the territorial behaviour category (Figure 33). Cleaning heavily decreased in the presence of eggs. The outlier for cleaning came from one obsessive male (002), which in the absence of eggs cleaned his nest with a frequency of 196 counts/h (Figure 33). Cleaning also took up the most time on nests with no eggs. The two most fastidious males spent 9.7% and 6.1% of their time cleaning (Figure 34).

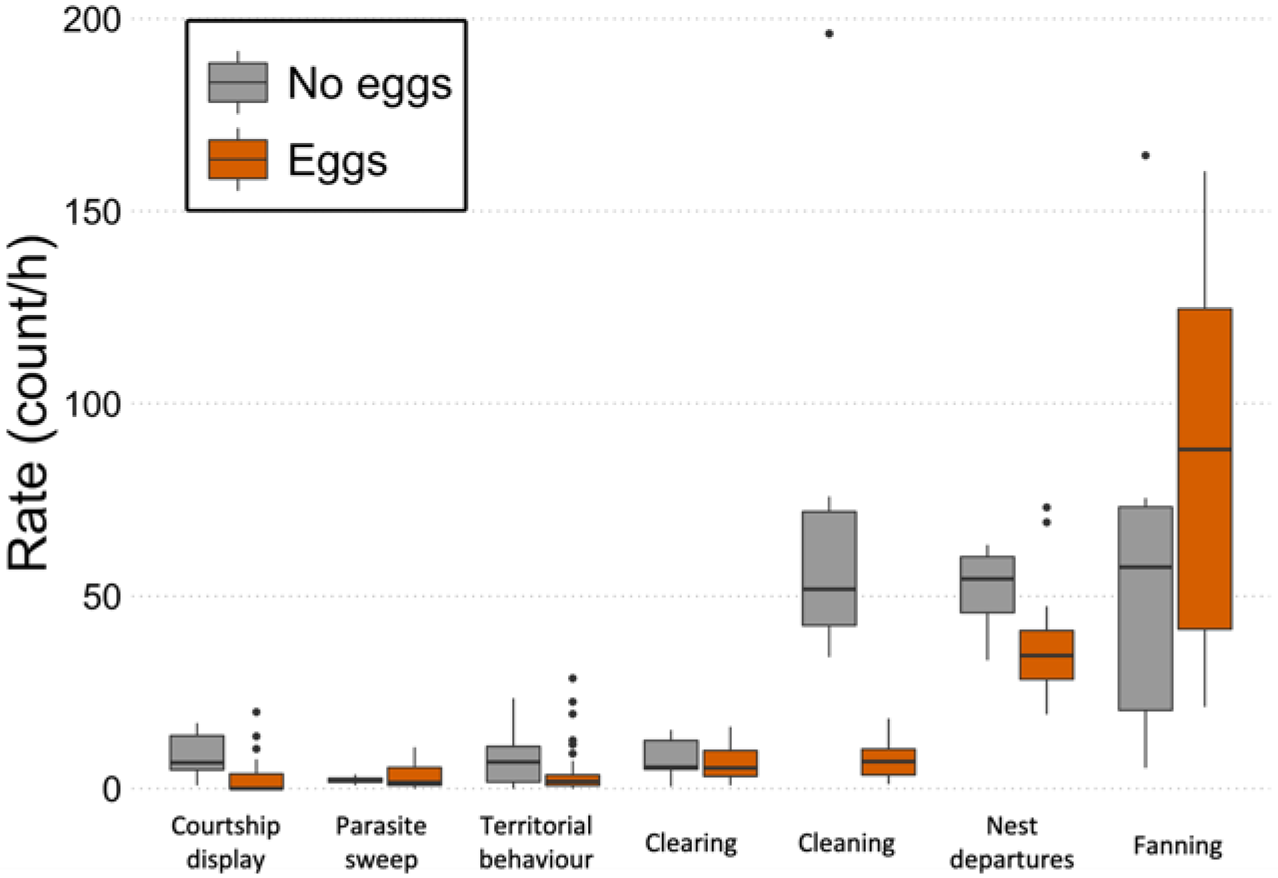

Figure 33. Frequency of *Spondyliosoma emarginatum* nesting male behaviours in the absence or presence of eggs on their nest

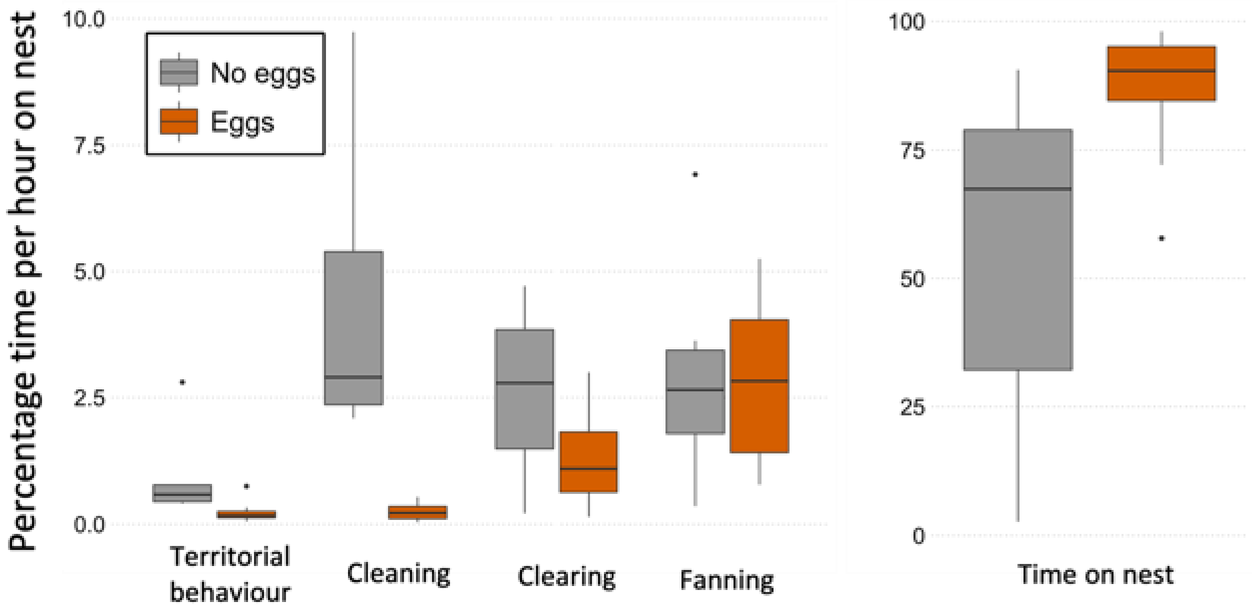

Figure 34. Percentage of time *Spondyliosoma emarginatum* males spent on the nest spent carrying out the most common behaviours

3.4.5. Description of individual behaviours

Time on nest and nest departures

Males increased their time spent over the nest by 70% in the presence of eggs, from 30 to 52 min/h (Figure 34). Increased nest presence with eggs was also accompanied by a 28% decrease in the frequency of nest departures and a 72% decrease in the duration of these departures. Males were also 78% less "out of frame" in the presence of eggs. The longest departure times were attributed to predator avoidance (Figure 35), but this was not what caused males to leave their nest most frequently (Figure 36). The most departures by count were attributed to chases and unknown dashes (Figure 36). And while chasing was one of the most frequent causes of departures, it was also the action that led to the smallest departure times (Figure 35).

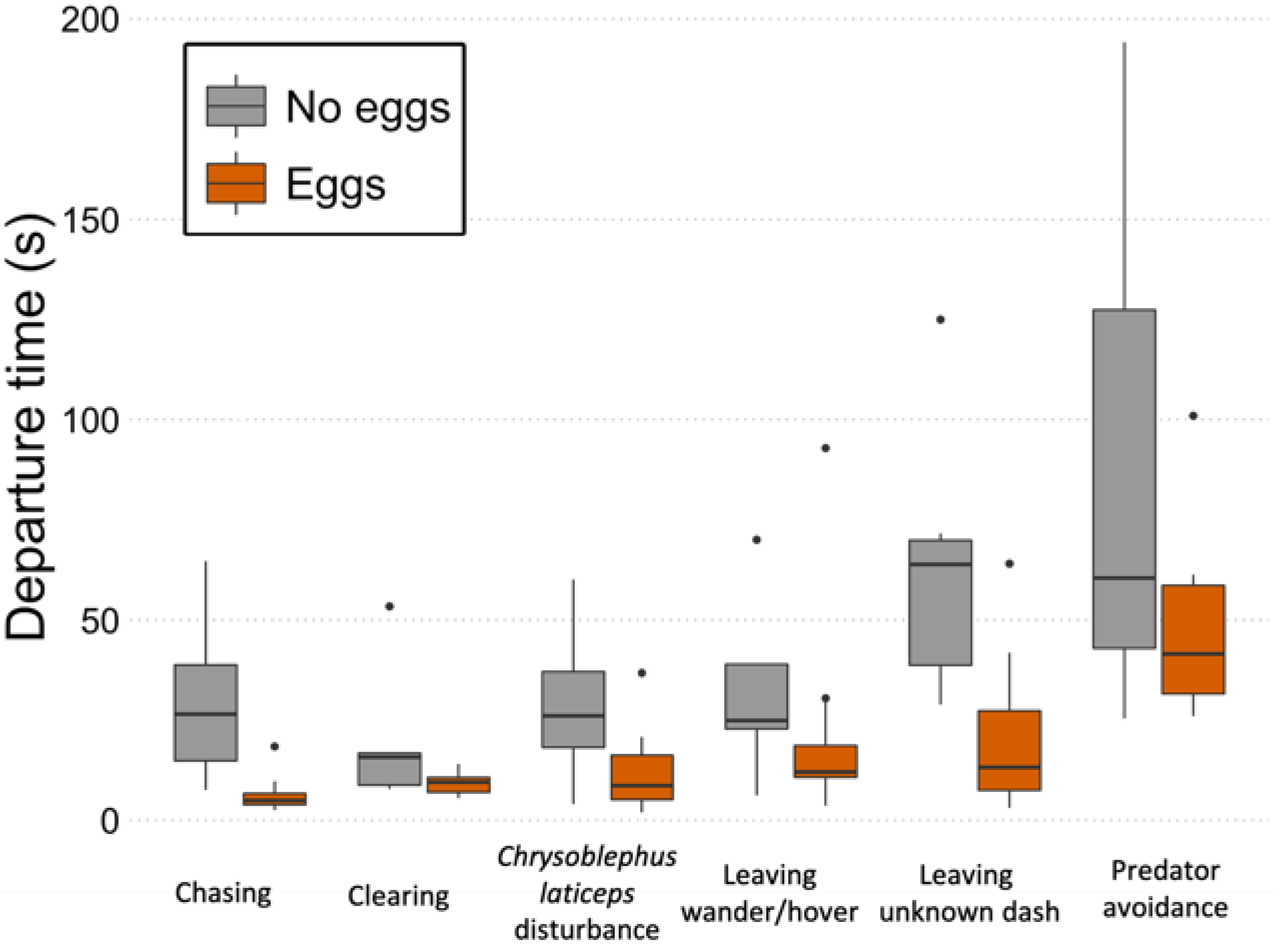

Figure 35. Mean duration of departures from the nest per activity by male *Spondyliosoma emarginatum* in the absence and presence of eggs

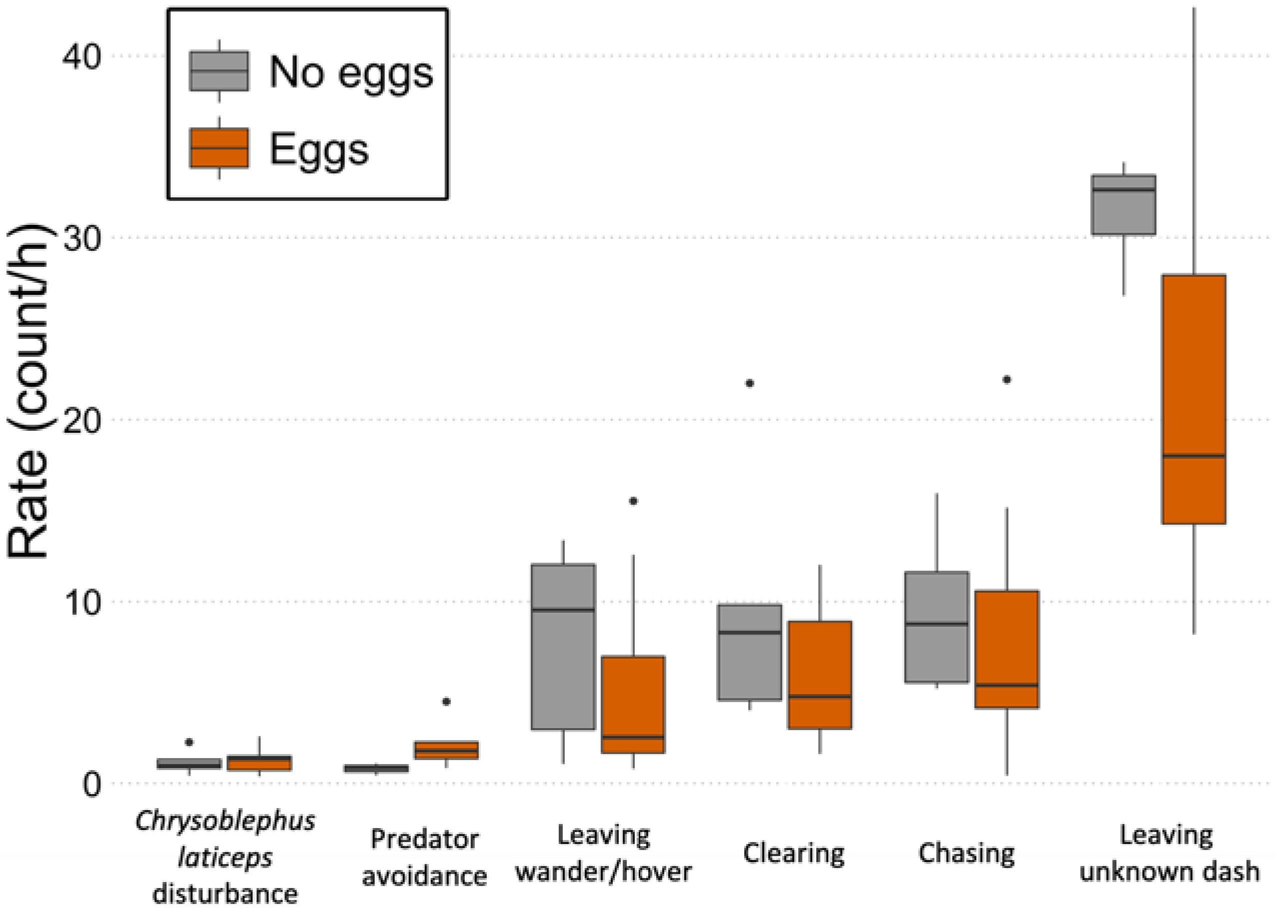

Figure 36. Mean frequency of departures from the nest per activity by male *Spondyliosoma emarginatum* in the absence and presence of eggs

Chrysoblephus laticeps disturbance

C. laticeps was abundant on the site and were observed staying over the nesting surface of five males (Figure 37). While disturbances by *C. laticeps* led to the lowest frequency of departures (Figure 36), these departures lasted longer than clearing or chasing departures (Figure 35). This was particularly apparent for male 006, for which *C. laticeps* individuals visited the nest at a frequency of 19 counts/h, staying on the nest for a few seconds to up to 3 min.

Figure 37. Roman (*Chrysoblephus laticeps*) hovering over the nest of *Spondyliosoma emarginatum* male 006 (left) and feeding near the nest boundary of male 018 (right)

Predator avoidance

Predator avoidance was easily distinguishable in videos as it resulted a large school of fish leaving the site simultaneously. In many cases, the predator was next seen swimming in the background (Figure 38). Predator avoidance behaviours were noticed in 15 videos. The range of departure times due to predator avoidance ranged from 25 to 194 seconds in the absence of eggs and decreased to a range of 26 to 100 seconds in the presence of eggs (Figure 35). The main predators observed included the Cape fur seal (*Arctocephalus pusillus*), the white-breasted cormorant (*Phalacrocorax lucidus*), and the African penguin (*Spheniscus demersus*) (Figure 38).

Figure 38. Predator sightings at the nesting site. Top left: White-breasted cormorant (*Phalacrocorax lucidus*), Top right: African penguin (*Spheniscus demersus*), Bottom: Cape fur seal (*Arctocephalus pusillus*)

Clearing and cleaning

Cleaning and clearing are distinguished from each other in the size of the item cleared and the action of the male. Cleaning involves picking at sand or small pieces of vegetation on the nest and eating or spitting them out straight away. In contrast, clearing involves the male actively picking up and swimming away with the item or organisms to clear it off the nest. Cleaning was significantly affected by egg presence (Table 16) and males cleaned their nest surface 90% less in the presence of eggs (Table 16). On the 30th of August, one male (002) cleaned his nest by picking at algae growing on the surface 196 counts/h, which is an outlier in Figure 33.

The clearing of unwanted items or organisms from the nest was one of the most charismatic behaviours observed (Figure 39). As males cleared their nests throughout the site, this often resulted in them dropping the item into the nest of another male. Clearing occurred on average 7 counts/h (

Table 13). The most common item cleared was full shells, and while it is highly likely that most of these shells were hermit crabs, this was not possible to confirm from the footage (Figure 40). Sea cucumbers (*Pseudocnella insolens* & *P. sykion*) were the least cleared item in the presence and absence of eggs (Figure 40). Hermit crabs were the only item cleared significantly more in the presence of eggs (*p*=0.04, df=10.93, n=21).

Figure 39. *Spondyliosoma emarginatum* male clearing a Serpent skinned brittle star (*Ophioderma wahlbergii*) (left) and a hermit crab (*Diogenese* spp.) (right)

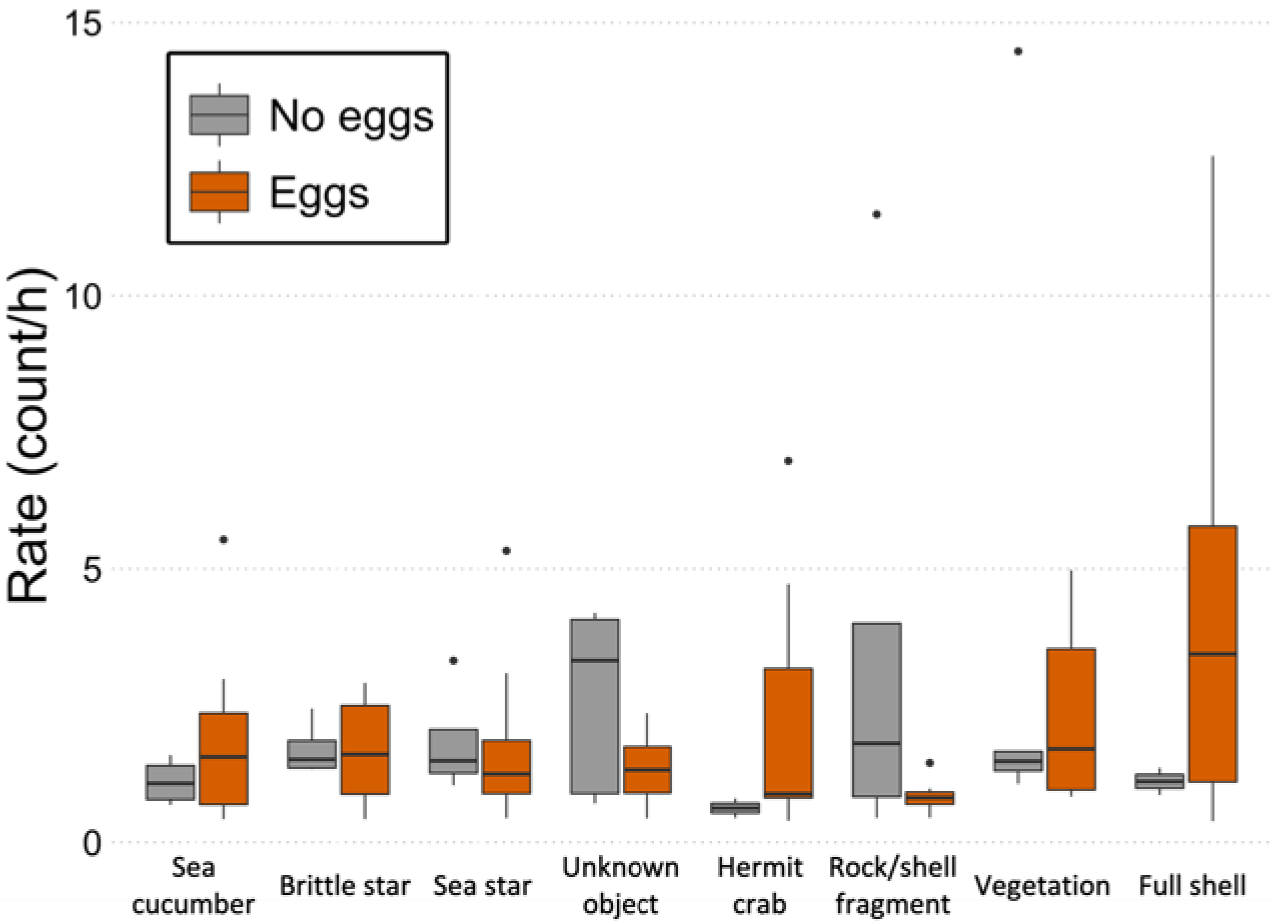

Figure 40. Frequency of items cleared per *Spondyliosoma emarginatum* male in the absence and presence of eggs

Swim-bys

Swim-bys by other species and conspecifics were significantly affected by the presence of eggs (Table 16). The most frequently observed species swimming by male nests in terms of total days observed were *Clinus* spp., *Pachymetopon blochii*, and *C. laticeps* (

Table 17). Less frequently observed were *Octopus vulgaris* and Red Stumpnose (*C. gibbiceps*), who were only observed on two days each (

Table 17). On the 26th of September, a school of five White Steenbras (*Lithognathus Lithognathus*) were observed, these are endemic to South Africa and are classified as endangered on the IUCN red list (Mann *et al.*, 2014).

Table 17. Most commonly sighted species swimming by *Spondyliosoma emarginatum* male nests. Scientific name is reported to the lowest possible classification level. Standard deviation (sd), sample size (n), standard error (se), coefficient of variation (cv)

Common name	**Scientific name**	**Days observed**	**Mean swim-by (count/h)**	**sd**	**n**	**se**	**cv**
Red Roman	*Chrysoblephus laticeps*	19	8.74	7.01	21.00	1.53	0.80
Hottentot	*Pachymetopon blochii*	20	3.74	3.82	21.00	0.83	1.02
White Stumpnose	*Rhabdosargus globiceps*	15	2.37	4.00	21.00	0.87	1.68
Klipfish	*Clinus* spp.	20	1.84	1.56	21.00	0.34	0.85
Barehead Goby	*Caffrogobius nudiceps*	15	1.58	2.52	21.00	0.55	1.59
Red fingers	*Cheilodactylus fasciatus*	17	1.51	1.68	21.00	0.37	1.11
Shyshark	*Haploblepharus spp.*	10	0.71	1.58	21.00	0.35	2.24
Cuttlefish	*Sepia* spp.	9	0.49	0.65	21.00	0.14	1.33
Blacktail	*Diplodus capensis*	11	0.47	0.65	21.00	0.14	1.39
Common octopus	*Octopus vulgaris*	2	0.07	0.21	21.00	0.05	3.20
Red Stumpnose	*Chrysoblephus gibbiceps*	2	0.06	0.20	21.00	0.04	3.31

Two tailed t-tests of the difference in *S. emarginatum* swim-bys by sex over nests in the absence or presence of eggs (Figure 41) revealed that only males significantly decreased in swim-by frequency over nests with eggs (*p*=0.05, t=2.44, df=6.16, n=74).

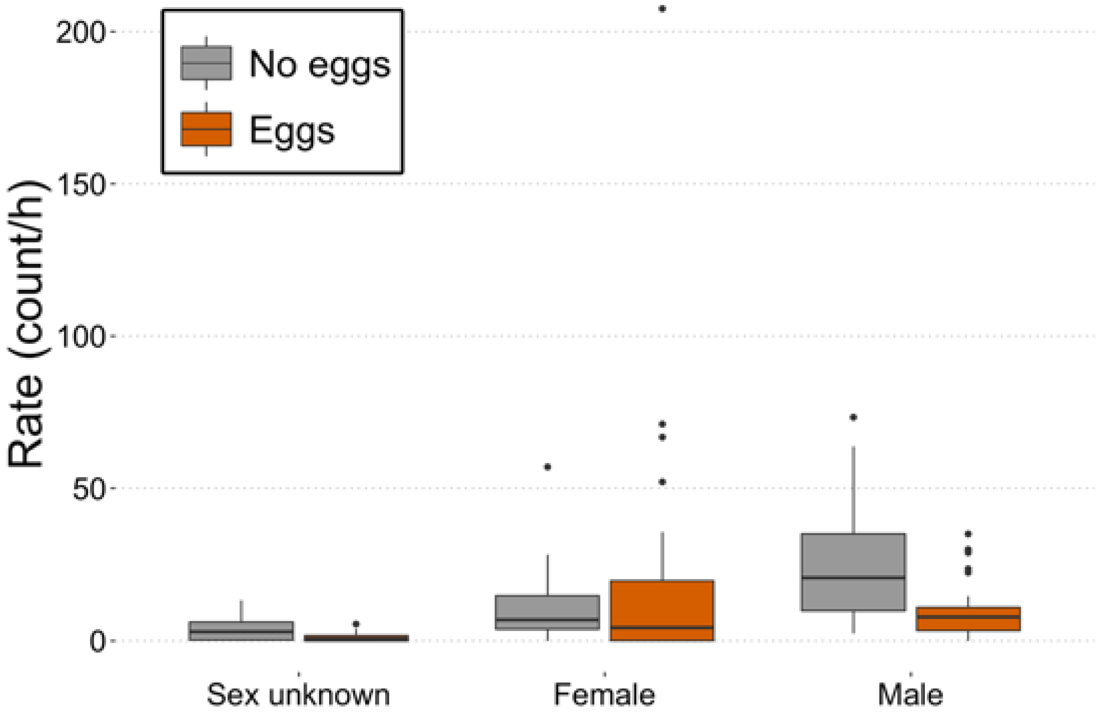

Figure 41. Frequency of conspecifics swimming by nesting *Spondyliosoma emarginatum* males

Territoriality

Territorial behaviours were characterised as either chasing away conspecifics and other species from the nest, or as aggressive bouts between males. Aggressive bouts are characterised by continuous back and forth chases between two males, who were often neighbours, and lasting an average of eight to 107 seconds (

Table 13). The effect of these territorial behaviours was also visible in some males that appeared to look damaged with scars along their body and broken lower lips.

Multiple male aggression

On two occasions a multiple male exchange was observed during which some males developed a colouration that differed from the usual black and white bands. The top half of their body was much darker than the bottom half, a colouration that was not observed in any other instance (Figure 42). In addition, pairs of males seemed to engage in a "duel" in which they would swim in circles parallel to each other and regularly curve their body from snout to tail (Bottom panes, Figure 42).

Figure 42. Multiple *Spondyliosoma emarginatum* male aggression. Left pane: multiple males are seen aggregating over a single nest. Right pane: two male colour morphs engaged in a paired "duel"

Chasing

T-tests revealed that nesting males chased females 300% more often in the presence of eggs (Figure 43), increasing from 2 counts/h in the absence of eggs to 7 counts/h in the presence of eggs (*p*=0.04, t=-2.34, df=9.78). There was no significant decrease in the number of females swimming by over nests with or without eggs. Nesting males chased males swimming by 64% less in the presence of eggs, decreasing from 10 to 4 counts/h (*p*=0.02, t=3.05, df=6.78). In contrast to female swim-bys however, there were less male swim-bys over nests with eggs (Figure 41).

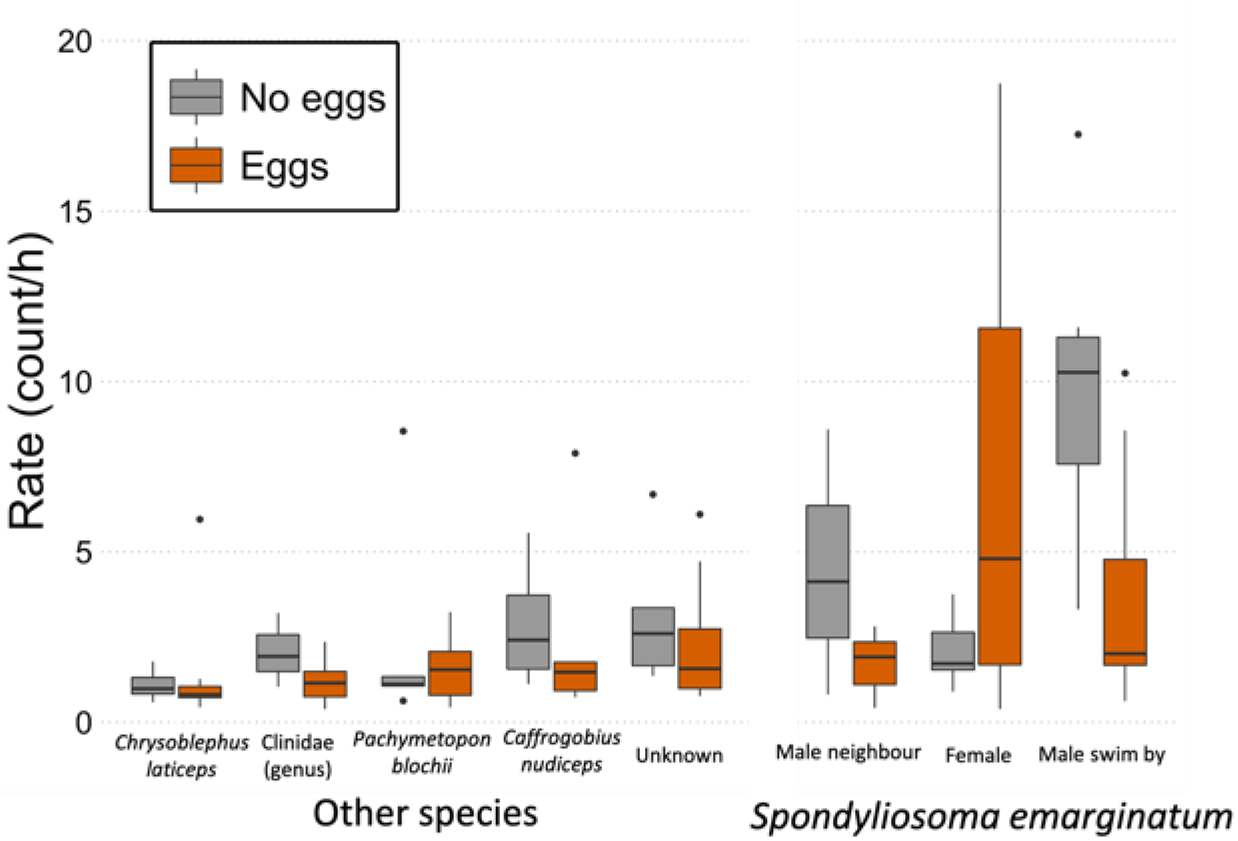

Figure 43. Frequency of chasing behaviours per target by *Spondyliosoma emarginatum* males on nests in the absence or presence of eggs

Courtship and Spawning

Courtship displays occurred an average of 5 (± 1.30) counts/h, with each display lasting on average 2 min 30 s (± 1 min 20 s) (

Table 13). There was no effect of egg presence on courtship display duration or frequency (Table 16). Courtship displays involved the male swimming in circles at a tilted angle over the nest surface to display accentuated nuptial dress colours to females swimming above (Figure 44). Once the female was on the nest and inspecting the nest surface, the male repeatedly swam up and down around her and frequently nuzzled her cloaca. If the female left the nest the male frequently chased after her. There was one exceptional case where a male (009) successfully attracted three females to his nest at the same time. While males often chased away any other female if a female was present on his nest, this male did not chase them off (Figure 45).

Spawning was captured on three separate occasions, each involving different males (Table 18). Two events occurred around 13:00 (male 010 and male 009), whereas the other event happened around 10:30 (male 017). For male 010 and 017, spawning occurred with the same female who released her eggs in bouts, and she stayed on the nest the entire time. For male 009, it was not possible to confirm if all spawn came from the same female, as the female swam in and out of shot between spawnings and there were no physical features strong enough to confirm if she was the same one.

Table 18. *Spondyliosoma emarginatum* spawning events observed throughout the study period

Male	Date	Eggs on nest	Number of spawnings	Time of event	Avg. temperature (°C)
010	07/09/2019	Yes	5	13:05 – 13:16	15.89
009	14/09/2019	Yes	8	13:04 – 13:29	14.67
017	02/10/2019	Yes	3	10:32 – 10:35	16.57

Figure 44. *Spondyliosoma emarginatum* male in courtship display behaviour. They circle the nest at an angle to show off their nuptial dress colours to a female swimming overhead

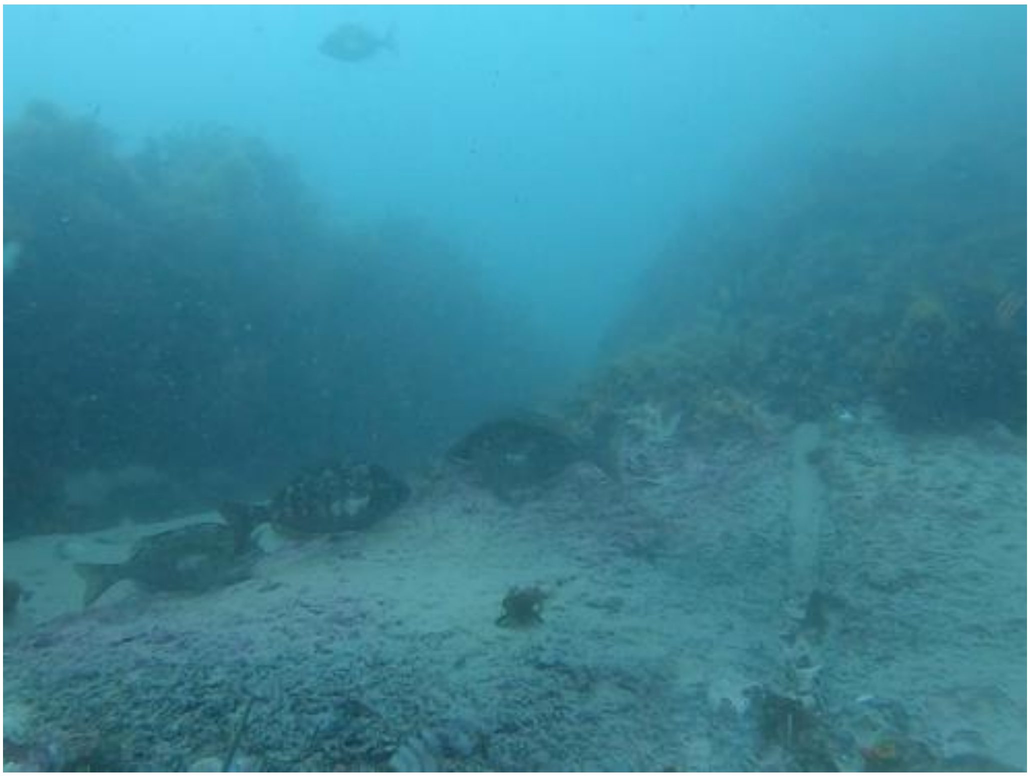

Figure 45. Three *S. emarginatum* females examine a male’s nest, which has pre-existing eggs

Sneaker males

A sneaker male was captured on the 7th of September between 12:00 and 13:00. A male attempted to sneak into a paired spawning event between a male courting a female from his nest (Figure 46). As the nesting male is courting a female to his nest, another male, herein referred to as sneaker male, can be observed waiting in the background hiding behind rocks and vegetation. As the male and female join for gamete release, the sneaker male darts in between them. The female dashes off the nest and the nesting male attacks and bites the sneaker male who also eventually leaves. There is no obvious release of gametes from the footage suggesting the sneaker male was unsuccessful on this occasion.

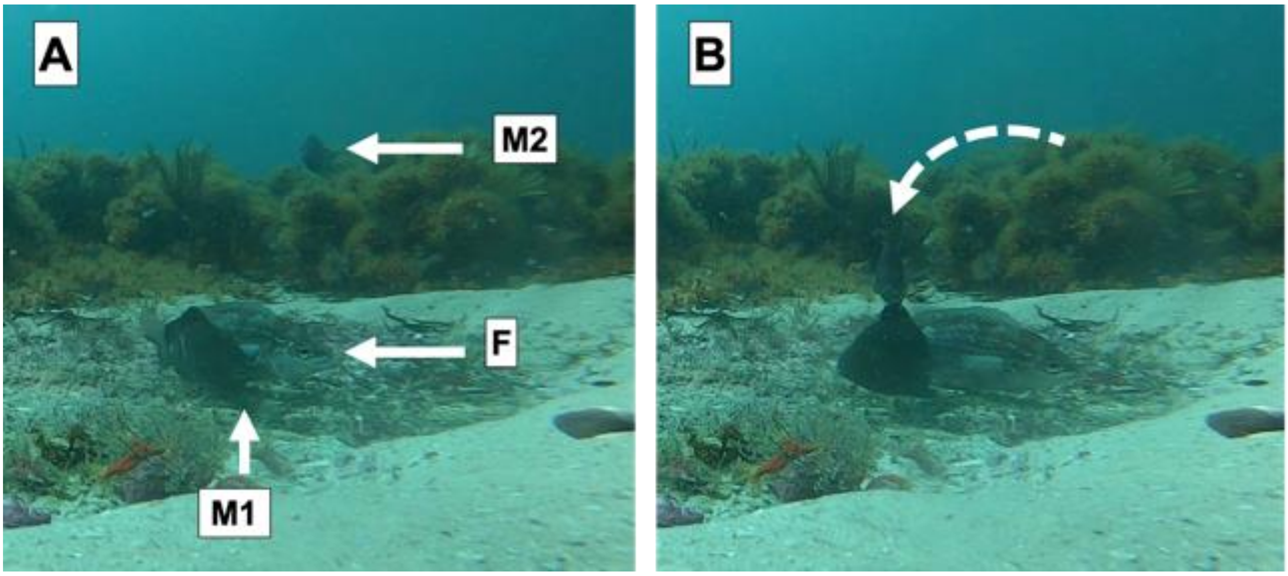

Figure 46. Sequence of events in a sneaker male intrusion. Panel A shows the sneaker male (M2) hiding in the background as the nesting male (M1) and female (F) are getting ready for spawning. Panel B shows the sneaker male jolting out of his hiding place to attempt a sneak fertilization. Following this, the nesting male bit and chased off the sneaker male and the female swam away

3.5. Discussion

This is one of the few studies on *in situ* nesting behaviours and the first for an *S. emarginatum* nesting site in South Africa, which means there are few data with which to compare the results. Therefore, many new insights into the reproductive behaviour of *S. emarginatum* have been revealed for all three stages of the nesting period: nest building, courtship, and guarding.

Nesting males spend little time off their nest, up to 52 min/h in the presence of eggs, and they focus all of their activities to nesting, courtship and egg defence. This amount of nest residency is in line with *Chromis crusma* (Navarrete-Fernández *et al.*, 2014) and *Micropterus salmoides* (Maxwell *et al.*, 2018). The limited time they spend off the nest also suggests they devote little to no time on foraging and feeding. There is a possibility that the small pieces of vegetation males cleaned off their nest were sometimes ingested but no other evidence of feeding was observed. Energetically demanding behaviours, such as clearing and fanning, were not affected by egg presence. This suggests that males are continuously busy over the nest surface and explains the extreme loss in condition that males have been shown to experience post nesting (Attwood and Ensair, 2020). Males also appeared to look damaged in some videos, particularly on the lips and fins. Such damage is likely due to aggressive encounters with other males. By contrast, damage from predators is usually seen on the flanks (Attwood, Pers. Comm.).

Activities that affected the nest surface or eggs directly were cleaning, clearing and fanning. All three behaviours help keep a clear nest surface during nest building and courtship. In particular, cleaning occurred mainly for nest preparation, since it was observed at its highest rates early on in the nesting season (30/08/2019) and decreased by 90% in the presence of eggs. This is the only behaviour that may provide occasional nutrition to the males and so indicates that little to no foraging and feeding occurs in the presence of eggs.

In the presence of eggs, clearing keeps egg predators away whereas fanning keeps the eggs well ventilated and removes metabolic waste and silt or sand build up (Wootton and Smith, 2014). Fanning rate increases with brood size and correlates with weight loss in Bluegill sunfish (*Lepomis macrochirus*)(Coleman and Fischer, 1991). Experiments on Three-spined stickleback (*G. aculeatus*) also revealed that parental activities (with a focus on fanning) caused an expenditure rate of 12.3 J g^{-1} h^{-1}, which was significantly higher than the expenditure of 3.9 J g^{-1} h^{-1} for non-parental males (Smith and Wootton, 1999). The findings that fanning occurred at similar rates throughout the entire nesting period for *S. emarginatum* irrespective of egg presence highlights the potential for large energetic expenditures throughout the nesting period and is likely to be an important limiting factor for brood size and recurrent male spawnings during a season. This also points to a dual use for fanning as a means of building and clearing a nest as well as for egg ventilation.

Clearing was regular throughout the nesting period irrespective of egg presence, but the types of items cleared did change. Hermit crabs were cleared significantly more in the presence of eggs, which suggests they may be an important egg predator at this site. No other invertebrate was removed significantly more in the presence of eggs, however it is also possible that the regular fanning is enough to keep lightweight predators off such as Red-chested sea cucumbers (*P. insolens*), Cask sea cucumbers (*P. sykion*) and Serpent-skinned brittlestars (*O. wahlbergii*).

Other activities that also relate to large energetic expenditures are nest defence and territoriality. The nest-bound males are exposed to a regular threat from predators, and aggressive intrusions by other conspecific males on the site. Increased predator presence causes increased energetic depletions in nesting *Micropterus dolomieu* males (Steinhart *et al.*, 2005). On multiple instances, when nests were abandoned, hottentots and other *S. emarginatum* individuals took advantage of an empty nest to feed on eggs.

A regular non-predatory disruption was the visits by Roman (*C. laticeps*) to certain males' nests. This occurred regularly for male 006, as a *C. laticeps* individual seemed to have his territory under a rocky overhang adjacent to the male's nest. Acoustic monitoring has shown that *C. laticeps* occupies small home ranges and enjoys rocky reefs with small crevices and caves (Kerwath *et al.*, 2007), which were widespread throughout the nesting site. During these visits, the nesting male would actively circle around the nest and occasionally get closer in what seemed like an attempt to chase away the *C. laticeps* individual. This was likely to be quite energetically demanding to the male.

The frequency but not the duration of intraspecific aggressive bouts decreased in the presence of eggs. When two males faced each other in the multiple male aggression scenes, they changed colours and seemed to be displaying dominance signals. This is in line with findings in other species that colour displays establish hierarchy and dominance (Reese, 1975; Stacey and Chiszar, 1978). These displays could result in nest takeovers, a phenomenon observed in other nest-tending species (Wootton and Smith, 2014). Nest takeovers allow males to take advantage of the nest building effort from other males. In some cichlid species, a male may takeover a nest, spawn with a female and then leave to allow the former male to return to his nest. The practice is known as piracy and allows a male to cheat the system and reduce his energetic investment in parental care (Wootton and Smith, 2014). These nest takeover events may also imply a limited availability of suitable nesting sites.

There was no significant difference in the number of *S. emarginatum* females swimming by over nests with or without eggs. However, the frequency of chases towards females increased by 300% in the presence of eggs. This could be due to males reaching a maximum clutch size. On empty nests males may not chase away females since their goal is to find a mate. Once they cannot take up more clutches from gravid females, they may have to chase them away as they try to approach the nest. Females may prefer to spawn in nests with eggs in a bet-hedging strategy to maximise their broods' survival and reduce the chances of their eggs being predated upon (DeWoody and Avise, 2001; King and Withler, 2005). This is known as the dilution effect. Another explanation for the increase in female chases could be as a courtship display. Observations from *S. emarginatum* courtship displays have shown that males will chase females off the nest until they eventually rest on the nest to lay eggs (Wilson, 1958).

Finally, the decrease in males swimming by nests with eggs could be due to an overall decrease in males that are not attending their own eggs.

In terms of courtship and spawning, these analyses have revealed that *S. emarginatum* carry out paired simultaneous spawning, but with evidence of polygyny. The finding that eggs of different developmental stages were found on one nest (Chapter 2) also suggest that either males will spawn multiple times per nesting season with either the same or a different female. In addition, this study has revealed that spawning does not only occur at dawn or dusk as previously suggested (Wilson, 1958). Males attracted multiple females to their nest and also guarded eggs of different developmental stages on the same nest (Chapter 2). This is in line with genetic studies that found nest-tending males to commonly have polygynous mating systems (DeWoody and Avise, 2001). These are important factors for nest-tending species, as mating systems affect reproductive success and the certainty of paternity between a male and his brood (DeWoody and Avise, 2001). While there was not enough evidence to show that females spawn in multiple nests (polyandry), there is evidence that females spawn with the same male in temporally discrete bouts. Polyandry has also been documented in other nest-tending species such as the Redbreast sunfish (*Lepomis auritus*) and the Tessellated darter (*Etheostoma olmstedi*) (DeWoody *et al.*, 1998, 2000). The frequency of female visits that did not end in spawning does suggest that females visit several nests to assess the quality distribution of males and their nests before committing her gametes. In Sphinx blenny (*Aidablennius sphynx*), where females visited up to nine nests before choosing a mate (Kraak and Weissing, 1996).

A sneaker male is defined as a male phenotype that sneaks into the territory of a conventional male to mate with a female (Balshine and Sloman, 2011). Genetic evidence has revealed that sneaker males are relatively common among nesting fishes (Taborsky, 1994). Across species, nest-tending males are typically related by 70 – 95% to the embryos in their nest (DeWoody and Avise, 2001). Much remains unknown about the factors controlling the presence of sneaker males in a population. Some suggest that the prevalence of sneaking may be attributed to nesting site availability (DeWoody and Avise, 2001), but an experimental study using sand gobies (*Pomatoschistus minutus*) revealed that nest-availability had no effect on the presence of sneaker males, and neither did the owning of a nest (Singer *et al.*, 2006).

In summary of what was learned from the video analysis, I can say that the protogynous *S. emarginatum* display most, if not all, of the nesting behavioural acts recorded in gonochoristic species of nest-builders from other families across marine and freshwater settings. These behaviours include nest cleaning and clearing, oxygenation of eggs, intra-and interspecific aggression, colour-mediated displays, polygyny, and sneaker males. Males invest substantial amounts of energy, and lose body condition, by nest-building and egg-guarding, over a period not exceeding two months. During this time, males are exposed to predation. Their investment and risk are not shared by males of pelagic-spawning seabreams, which dominate the family.

4. Chapter 4 – General discussion

A critical aspect of this study was locating nests. *S. emarginatum* is a diver-negative species, so SCUBA and BRUV deployments were necessary to find spawning grounds. Similar methods were deployed in the UK to locate *S. cantharus* nests (Collins and Mallinson, 2012). Finding a nesting site remains challenging due to the clumped nature of the nests and the plasticity in nesting habitat used by this species. Whereas this site was found on granite outcrops, other *S. emarginatum* nests have been spotted on wrecks and sandy bottoms without exposed rock. Despite this variation, a unifying feature found across *Spondyliosoma* spp. nests is that they are all built on a hard surface. *S. emarginatum* can therefore be described as either a lithophil or polyphil according to Balon's classification scheme (Chapter 1)(Balon, 1975).

S. emarginatum males establish a nesting site, spawn and guard the eggs during a period of two months (Chapter 2). This period coincides with rising temperatures during spring (September and October). The spawning season ends before south-easterly gales become frequent in summer (from November). Stochastic environmental conditions might have influenced the evolution of the nesting reproductive strategy of the ancestral *Spondyliosoma* spp. This can be explained in light of Baylis's rate-limit hypothesis (Chapter 1) that states that environmental stochasticity are selection pressures for demersal eggs and parental care (Baylis, 1981). Stochastic environmental conditions may also have influenced the present distribution of *S. emarginatum* in South Africa. *Spondyliosoma* is widely distributed over a range that covers a variety of oceanographic domains. The wind-driven upwelling system off South Africa is very different from the tidally-dominated English Channel and the calm coast of Angola.

The nesting site was found in a relatively sheltered region of False Bay, where it is unaffected by north-westerly storms and their associated significant swell heights (<4 m) that occur commonly along the South African west and south coasts. The only *S. emarginatum* population on the west coast of South Africa is found in the only sheltered bay along the west coast (Saldanha Bay) (Tunley *et al.*, 2009), which suggests that turbulence is an important deterrent to the establishment of nests. *S. emarginatum* is widely distributed along the South African south coast, from Cape Point to Algoa Bay (McKeown *et al.*, 2020). I predict that nest sites are found in the many half-moon bays along the coast that host high densities of *S. emarginatum* (Attwood and Ensair, 2020; McKeown *et al.*, 2020) and protect from the predominantly westerly swell: Gansbaai, Struisbaai, Mossel Bay, Buffalo Bay, Plettenberg Bay, Jeffries Bay and Algoa Bay.

Because the water in the east is warmer than in the west, it is also likely that nests will be found progressively deeper from west-to-east since deeper nests are more sheltered from large swell and turbulence. Other species also increase their depth range from west-to-east, as the mass of overlying Agulhas Current water suppresses the 16° C thermocline (Awad *et al.*, 2002; Attwood and Ensair, 2020).

Even when sheltered, nests are exposed to highly variable weather conditions. During spring, strong south-easterly winds with daily mean speeds of between 8 to 10 ms^{-1} are common (Pfaff *et al.*, 2019). These winds are likely to be destructive for nests, based on the damage seen during the gale reported in Chapter 2. Apart from the destructive element, strong winds likely also contribute to egg siltation and add to the energetic requirements of nesting males due to increased fanning of their eggs to keep them clear of debris. The effect of south-easterly gales might diminish towards the east if nests are constructed in deeper water as I predict.

Wind-driven currents in False Bay are changing, and summer months experienced an increase in southerly winds and upwelling events in the 2000s (Blamey *et al.*, 2012; Pfaff *et al.*, 2019). Increased upwelling has led to reductions in some False Bay biota (Mead *et al.*, 2013) such as the indigenous brown mussel *(Perna perna*), a decline attributed to reduced recruitment due to cold-water conditions (Tagliarolo *et al.*, 2016). This trend also poses a risk to *S. emarginatum,* which is constrained in its spawning season by a short weather window and which would likely suffer from more frequent upwelling. Lower temperatures increase egg development time (Régnier *et al.*, 2018) and pose a greater risk to males due to exhaustion and increased exposure to predation.

The nesting site was characterised by a tightly packed community of nests, similar to nesting sites for the two other nesting Sparidae species: *S. cantharus* (Collins and Mallinson, 2012) and *Spicara smaris* (Harmelin and Harmelin-Vivien, 1976). Closely packed nests is a common occurrence for nesting fish species (Drazen *et al.*, 2003) and can be described as fish spawning aggregations (FSAs) (Chérubin *et al.*, 2020). A potential risk with FSAs is that these sites, once known, can attract a large number of predators including fishermen and so require careful management and protection (Erisman *et al.*, 2017).

Several factors can help explain FSAs (Winnicki *et al.*, 2020). A first is group defence from predators. Multiple large predators were sighted swimming over *S. emarginatum* nests, and many small invertebrate predators were also observed on and around nests (Chapter 3). Nesting in a group increases the chances of brood survival, as it decreases the chances of any single nest being targeted. In cooperatively breeding cichlids (*Neolamprologus pulcher*), individuals invested less in anti-predator defences (e.g. alarm calling and vigilance) at high densities (Jungwirth *et al.*, 2015). It is unknown if *S. emarginatum* use acoustic warning signals, but the sudden dispersal en-mass of *S. emarginatum* and other species, could provide the visual cue that a predator is nearby. In nesting Bluegill Sunfish (*Lepomis macrochirus*), nests on the periphery of the aggregation suffered higher rates of predation from other conspecific males and snails (*Viviparous georgianus*)(Gross and MacMillan, 1981).

FSAs may also result from sexual selection, as group nesting allows for an increased potential for mate-choice by females. Females often swam-by and visited nesting males without spawning (Chapter 3) and this could be part of a mate selection procedure. In colonial nesting grounds for shell-brooding cichlids (*Lamprologus callipterus*), females prefer to breed with males surrounded by many neighbours (Schütz *et al.*, 2016).

Finally, FSAs could also result from a scarcity of suitable nesting habitat. This is unlikely for *S. emarginatum* due to the known nearby similar habitat closer inshore (Terhorst, 1987; Pfaff *et al.*, 2019). However, the group aggressive displays uncovered in this study (Chapter 3) has revealed that males may steal higher quality nests from each other, a process known as nest takeovers (DeWoody and Avise, 2001). Nest takeovers could imply a lack of suitable nesting habitat or that some males evolve cheating strategies to avoid the energy-consuming, nest-building work.

A wide variety of behaviours previously undescribed for *S. emarginatum* were captured on this site. While many behaviours changed in frequency due to egg absence or presence, they never completely stopped. Energetically demanding behaviours such as fanning and clearing were continuous throughout the nesting period. This highlights the important energetic requirements from nesting males (van Iersel, 1953; Jones and Reynolds, 1999), and the effects of which are evident through the loss in male condition after the spawning season (Attwood and Ensair, 2020). This nesting strategy is well suited to a protogynous life-history since larger individuals will be more suited to building and guarding a nest, as they will have greater stamina and be less vulnerable to attack. Nesting behaviour and parental care most likely provide the size-advantage for males needed to meet Warner's requirement for protogyny (Warner, 1975) (Chapter 1).

These energetic demands help explain sneaker males (Chapter 3), who, when successful, can offload the energetic costs of nest-tending and guarding of their offspring to other males. When this event occurs in nests it is known as cuckoldery (DeWoody and Avise, 2001). Until now, sneaker males in the Sparidae is mentioned only for the Australasian snapper (*Chrysophrys auratus*)(Smith, 1986), and the Santer seabream (*Cheimerius nufar*)(Garratt, 1991). Both accounts are in aquaria and describe similar events: as a female swam along the surface of the tank, she was trailed by several males and when she released her eggs, several males released their sperm. I believe these events are more appropriately described as sperm competition in a spawning aggregation, where males are competing for a female. Sneaker males require a dominant male and other satellite males which does not seem to be the case in these accounts. The *S. emarginatum* sneaker event captured is likely the first account of sneaker males and cuckoldery in the wild for a Sparidae species.

S. emarginatum has evolved a unique life-history strategy compared to other Sparidae. This species is short-lived, 7 to 8 years (Fairhurst *et al.*, 2007; Tunley *et al.*, 2009), while many other sparids live up to 10 years, and some well above 30 years (Marengo *et al.*, 2014; Andrews *et al.*, 2018; Attwood *et al.*, 2019). *S. emarginatum* is also early-maturing and females only produce eggs for 2 to 3 years before changing sex (Fairhurst *et al.*, 2007; Attwood and Ensair, 2020). This short reproductive period explains why females have extremely high fecundity (Attwood and Ensair, 2020). It might be that the pressure on males to succeed at spawning is reduced by the possibility that they have already succeeded at spawning as females. This highlights the benefits of hermaphroditism, which allow species to adapt locally and in response to an individual's life-history (Buxton and Garratt, 1990).

S. emarginatum is dichromatic, a rare trait among Sparidae species, which is likely associated with the nesting habitat (Attwood and Ensair, 2020). Dichromatism is a sign of sexual selection (Darwin, 1875; Mank *et al.*, 2005) and points to the type of reproductive competition among males (Mank *et al.*, 2005). This competition may come from a scarcity of suitable habitats, a scarcity of females, or both. The male to female sex ratio for *S.emarginatum* and *S. cantharus* is 4.2:1 and 4.1:1 respectively (Fairhurst *et al.*, 2007; Gonçalves and Erzini, 2008). The other Sparidae nesting species, *Spicara smaris*, has an identical female to male sex ratio of 4.1:1 (Dulčić *et al.*, 2003). This suggests that a scarcity of males may have selected for sexual dichromatism. It is likely that this also affects the nesting strategy of males e.g. selection in favour of males that build bigger nests or maintain their nests for longer.

The *Spondyliosoma* life-history strategy can be described as opportunistic, as the generation time is short (Winemiller, 1992; Winemiller and Rose, 1992). *Spondyliosoma* has evolved life-history traits that allow for "efficient recolonization of habitats over relatively small spatial scales" (Winemiller and Rose, 1992). By contrast most Sparidae can be described as periodic strategists, with long generation times. Selection pressures resulting in an opportunistic strategy come from stochastic environments that change frequently over small spatio-temporal scales. *S. emarginatum* is one of the most abundant Sparidae among South Africa's 42 sparid species, and its success might be attributed to its ability to flourish in stochastic conditions. Highly stochastic environments are more common for freshwater compared to marine environments, which is also why nesting and an opportunistic strategy is mostly a freshwater phenomenon. This study has revealed that the nesting strategy evolved by *Spondyliosoma* shares many similarities with freshwater nesting species and that these environmental conditions select for similar strategies and behaviours.

5. References

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6. Supplementary material

Supplementary table 1. Summary of all 74 behavioural videos.

Video number	**Date**	**Male**	**Eggs (N or Y)**	**Analysis time (min)**
1	24/08/2019	001	N	120
2	24/08/2019	001	N	56
3	30/08/2019	002	N	135
4	30/08/2019	003	N	52
5	31/08/2019	003	N	71
6	01/09/2019	003	N	25
7	01/09/2019	003	N	77
8	01/09/2019	006	N	117
9	01/09/2019	007	N	74
10	01/09/2019	008	Y	60
11	02/09/2019	003	N	73
12	02/09/2019	006	N	130
13	02/09/2019	006	N	42
14	02/09/2019	007	N	61
15	02/09/2019	008	Y	39
16	02/09/2019	009	N	141
17	03/09/2019	003	N	49
18	03/09/2019	006	N	10
19	03/09/2019	008	Y	93
20	07/09/2019	010	Y	54
21	07/09/2019	003	N	101
22	07/09/2019	003	N	150
23	07/09/2019	006	N	98
24	07/09/2019	006	N	69
25	07/09/2019	009	N	72
26	08/09/2019	010	Y	71
27	08/09/2019	003	N	130
28	08/09/2019	006	N	55
29	10/09/2019	010	Y	48
30	10/09/2019	003	N	55
31	10/09/2019	006	N	102
32	13/09/2019	010	Y	149
33	13/09/2019	010	Y	84
34	13/09/2019	003	N	53
35	13/09/2019	003	N	78
36	13/09/2019	006	N	67
37	13/09/2019	006	N	133

38	14/09/2019	010	Y	73
39	14/09/2019	003	N	146
40	14/09/2019	009	Y	61
41	17/09/2019	011	Y	97
42	17/09/2019	003	N	75
43	17/09/2019	009	Y	34
44	18/09/2019	011	Y	142
45	18/09/2019	013	Y	38
46	18/09/2019	009	Y	33
47	21/09/2019	011	Y	92
48	21/09/2019	013	Y	74
49	21/09/2019	014	Y	25
50	21/09/2019	015	Y	136
51	21/09/2019	009	Y	87
52	25/09/2019	016	Y	24
53	25/09/2019	022	Y	155
54	25/09/2019	003	Y	72
55	26/09/2019	014	Y	13
56	26/09/2019	016	Y	79
57	26/09/2019	016	Y	74
58	26/09/2019	003	Y	81
59	26/09/2019	003	Y	71
60	02/10/2019	017	Y	78
61	02/10/2019	018	Y	147
62	02/10/2019	008	Y	138
63	03/10/2019	017	Y	74
64	03/10/2019	018	Y	72
65	03/10/2019	018	Y	133
66	03/10/2019	020	Y	124
67	03/10/2019	008	Y	66
68	03/10/2019	008	Y	51
69	05/10/2019	010	Y	64
70	05/10/2019	018	Y	87
71	05/10/2019	019	Y	60
72	07/10/2019	018	Y	84
73	07/10/2019	019	Y	152
74	07/10/2019	021	Y	137