Remote video analysis of an unusual fish life-history combination: nest-building, paternal care, and protogyny in a seabream

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Abstract Seabreams from two genera, Spondyliosoma and Spicara, have a unique life-history that combines nesting, paternal care, and protogyny. Whereas protogyny is a common sexual system among seabreams, all, except Spondyliosoma and Spicara spp., are broadcast spawners. We describe the nesting behaviour of Spondyliosoma emarginatum as a basis for analysing this unusual life-history combination. We remotely filmed males on a nesting site with over 80 nests in South Africa. It has been postulated, based on morphometric data and general observations, that males invest heavily in nest-building, courtship, and egg-guarding, although these behaviours had never been documented. Energy intensive behaviours, including the clearing of invertebrate invaders (7 counts h\(^{-1}\)) and fanning of nests (86 counts h\(^{-1}\)), remained constant before and after the appearance of eggs. Males spent 79.2% of their time on the nest. The remainder was spent chasing other fish species and neighbouring males (12 counts h\(^{-1}\)) and avoiding predation. Paired spawning events proceeded in batches. Nest take-overs and sneaker male attempts were recorded. The young leave the nest immediately after hatching. Males did not feed during the 67-day nesting period. Energetic costs of nest maintenance, starvation, and predation risk explain the condensed (relative to other seabreams) 51-day spawning season. S. emarginatum meets the requirements of the SAM as nest defence requires large male body size. Their short lifespan classifies Spondyliosoma spp. as opportunists, which may explain their success across a wide range of biogeographic zones from the cold temperate North Atlantic to the subtropical western Indian Ocean. These characteristics set Spondyliosoma spp. apart from the bulk of the seabreams, which are long-lived, broadcast-spawning, periodic strategists.

Keywords Reproduction · Hermaphroditism · Parental care · Sparidae · Spondyliosoma emarginatum

Introduction

Hermaphroditism, nest-building, and paternal care are phylogenetically versatile traits that add to the remarkable diversity of life-history strategies among fishes. The co-occurrence of these particular traits, however, is rare, partly because of their vastly unequal frequencies between fishes of freshwater and marine environments. Functional hermaphroditism (an individual acts as both a male and a female at some stage in its life) is very rare among freshwater...
frequencies have been advanced to explain this (Kuwamura et al. 2020). The first hypothesis relates to the size-advantage model (SAM), a frequently quoted model of the evolution of protogyny (female to male sex change) and protandry (male to female sex change). Its central tenet is that sex change occurs when one sex reproduces more efficiently when small and young, and the other sex when large and old (Kuwamura et al. 2020; Warner 1975). Warner and Lejune (1985) hypothesised that nesting males can spawn with only a limited number of females, which negates an advantage that would accrue to large, old males that spawns pelagically.

The second hypothesis advanced by Kuwamura et al. (2020) suggested that freshwater fishes and benthic egg-layers typically have large eggs, compared to marine broadcast spawners, which may require specialised ovarian development that prevents gonadal transition (Kuwamura et al. 2020).

Two Spondyliosoma species, Spondyliosoma emarginatum (Valenciennes 1830), and Spondyliosoma canthus (Linnaeus 1758), and the closely related Spicara smaris (Linnaeus 1758), are unusual among fishes in that they combine protogyny with nest-building and paternal care (Fairhurst et al. 2007; Harmelin and Harmelin-Vivien 1976; Van Bruggen 1965). This combination of traits is not known in any of the other 36 seabream (family Sparidae) genera and is exceedingly rare among fishes in general. Spondyliosoma emarginatum is considered endemic to southern Africa and is widely distributed around the shallow continental shelf. It is a small-bodied (maximum length = 312 mm FL), short-lived (maximum age = 8 years) species with early maturation (age at 50% maturity = 3 years), and sex change (age at 50% sex change = 5 years) (Fairhurst et al. 2007). The females have one of the highest annual fecundities among seabreams, whereas the male gonado-somatic index (GSI) is among the lowest (Attwood and Ensair 2020). Its temperate coastal habitat can be defined as stochastic and geographically diverse. During the breeding season, S. emarginatum is sexually dichromatic (unusual among the Sparidae) and the males express territorial and nesting behaviour (Mann 2013; Penrith 1972).

The nesting behaviour of S. emarginatum in an aquarium was briefly documented by Van Bruggen (1965) and prompted our search for the nests in the wild. No scientific account of the nesting behaviour
in the wild has been published for either *Spondyllosoma* species, although a citizen science project documented the nesting of *S. cantharus* in the English Channel (Doggett 2015). The nests of *Spirocarpa* sp. have been described in the Mediterranean (Harmelin and Harmelin-Vivien 1976).

In this paper, we report on an intensive nest survey and video-monitoring of the nesting and spawning behaviour of *S. emarginatum*. To understand the investments and risks involved in a combination of protogyny, nest-building, and paternal care, a thorough description of the reproduction strategy is necessary. Although paternal care of eggs is suspected and inferred, we have no proof of this practice in the wild for *S. emarginatum*.

We located a *S. emarginatum* nesting site and monitored nest-building and paternal care. We describe and quantify the activity of males prior to egg deposition and during egg development, and document the presence and activities of females, other fish species, and invertebrates insofar as they affect the nesting process and investment in reproduction. We were interested in the challenges that nest builders face in a space-limited coastal setting, rich in invertebrate and vertebrate predators. Evidence is presented to speculate on the scale of investment in paternal care, in relation to their short life-expectancy, high prior ovarian investment and the applicability of the SAM.

**Materials and methods**

**Study site and species**

This study was conducted between the 26th of June and the 5th of November 2019 in the north-western region of False Bay, on the southwest coast of South Africa (34° 15′ S, 18° 44′ W) (Fig. 1). Sea surface temperatures in the north-western part of the bay average at 18.8 °C in summer and 15.0 °C in winter (Dufois and Rouault 2012). This region is exposed to lower wave action compared to the rest of the bay (Pfaff et al. 2019; Terhorst 1987) and experiences a semi-diurnal upper microtidal (<2 m tidal range) environment, which means that tidal driven currents are weak (Terhorst 1987).

**Nesting site description**

On the 28th of August, during a SCUBA dive, a large compound nesting site with multiple nests was located between 9 and 15 m, at an average depth of 13 m. The site was arranged in clusters (Fig. 2; Fig. S1). The shape of each cluster was resembled to either a triangle or irregular quadrilateral to aid with area measurements. As such, the sides of each cluster were measured using a measuring tape, and labelled a to c (for triangle clusters) and a to d (for quadrilateral clusters). These measurements were used as per Eqs. (1) and (2) (Hess 2012) to first calculate the semi-perimeter of each cluster (s) from which the cluster area can be calculated (A).

\[
s = \frac{a + b + c + d}{2}
\]

\[
A = \sqrt{s(s - a)(s - b)(s - c)(s - d)}
\]

The number of nests per cluster was counted and divided by the area of the cluster to obtain a nest density (nests m\(^{-2}\)) per cluster.

Each cluster was filmed (GoPro Hero4, San Mateo, CA, USA) from above by swimming back and forth along a grid pattern at a constant height off the bottom. 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 photographs were 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 was labelled with the size of one nest (Fig. 2; Fig. S1).

Individual nest photographs were taken regularly to measure the size of nests. The presence of eggs on each nest was monitored. Every photograph was taken with a camera (GoPro Hero4, San Mateo, CA, USA) at a fixed height off the seabed. A photograph of a 20 by 20 cm quadrat was taken using the same method to later scale the photographs. All nest photographs were processed using ImageJ© (Schneider et al. 2012). For every photograph, the area of each nest was 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.
A CTD (conductivity, temperature, depth) instrument was used to record the bottom temperature on the nesting site during dive operations from the 27th of August to the 6th of September. The CTD was later replaced with an in situ temperature sensor (SBE 37-SMP-ODO, Sea-Bird Scientific), placed on the nesting site. The temperature sensor recorded continuously and operated from the 7th of September until the 10th of October. Hourly wind direction and speed was also provided by the South African Weather Service (SAWS) from the 1st of August to the 31st of December 2019. Weather data were provided by the Strand coastal Automatic Weather Station (−34.1174°, 18.8124°). Wind direction and speed were used to calculate the north–south wind vector using the equation:

\[ ns = w_s \ast \cos(w_d), \]  

(3)

where \( ns \) is the north–south wind vector, \( w_s \) is the wind speed, and \( w_d \) is the wind direction.

The north–south wind vectors helped classify the strength and types of weather events affecting the nesting site during the nesting period.

In an attempt to separate the duration of activities associated with courtship and nest preparation from paternal care, we used the proportion of nests with eggs observed on each dive to estimate a date at which half of the nests had eggs. We assume that this date represents the average transition from courtship (including nest preparation) to paternal care. We fitted a logistic model to the proportion of nests that had eggs over the development of the nesting season:
where $P(D)$ is the proportion of nests with eggs on Julian day $D$, $D_{50}$ is the Julian day at which half of the nests have eggs, and $\delta_D$ is a measure of the rate of increase in the proportion of nests with eggs. The model was fitted to the data by finding the values of $D_{50}$ and $\delta_D$ which minimised the sum of the squared differences between the model prediction and the observed proportion of nests with eggs.

Video deployments

Individual nests were filmed from the 30th of August until the 7th of October 2019 using cameras (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 weight. The camera mounts were designed to be < 10 cm high in an attempt to limit the intrusiveness to the nesting males. From the start of the study, nests were tagged using numbered plastic labels attached to small lead weights that were placed in the vicinity of the nest. These would allow nests to be identified during the analysis.

To film individual nests, the camera was placed ~30 cm from each nest. The presence or absence of eggs on the nest was noted. On subsequent dives, each camera was either moved to another nest or left to film the same nest. On average, three to four cameras were left to film simultaneously. We 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. All the footage was captured between 08:00 and 16:00, at a mean time of day of 11:00. Each video length varied from 18 to 157 min, with a mean time of 92 min. See Table S1 for a summary table of all footage captured.

Video analysis

After an initial sorting of the videos, some footage was discarded due to poor quality and bad camera placement (2 out of 24 nests) or nest abandonment (4 out of 24 nests). The suitable 72 videos that remained covered the behaviour of 18 males (100 h of footage). Males were named using three digit numbers from 001 to 018.

Each video was analysed in full using the behavioural analysis software BORIS (Friard and Gamba 2016). BORIS is an open-source software used for
event-logging of video or audio recordings. A pre-determined set of behaviours was chosen, based on our perceived relevance to the nesting and spawning processes (Table 1). The table of behaviours (ethogram) was loaded into the software and each behaviour was assigned a letter key. Then any time a behaviour was observed on the video, the appropriate key was pressed and the software recorded the given behaviour with a timestamp. BORIS was used only for event logging and all further statistical analyses were carried out in R (R Core Team 2021). 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 prior to and post any diver sightings in the frame were excluded and that time was 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. The frequency (counts h\(^{-1}\)) of each behaviour was measured per video. If a behaviour was absent, it was assigned a value of 0 counts h\(^{-1}\). For some behaviours (i.e., off nest, female on nest, aggressive bouts), the total duration (min h\(^{-1}\)) and mean event time (s) of each behaviour were recorded. Similarly to frequency, if a timed behaviour was absent from a video, it was given a duration of 0 min h\(^{-1}\). However, if a behaviour was absent from a video, it did not contribute a mean event time value. In summary, each behaviour in each video has a maximum of three variables: a total frequency (counts h\(^{-1}\)) and, when applicable, a total duration (min h\(^{-1}\)) and mean event time (s) (Table 1).

Table 1  Recorded *Spondyllosoma emarginatum* behaviours. Measured parameters for each behaviour include frequency (F) (count h\(^{-1}\)), duration (D) (min h\(^{-1}\)), and event time (E) (s)

| Behaviour                  | Description                                                                 | Parameters measured |
|----------------------------|-----------------------------------------------------------------------------|---------------------|
| Aggressive bout            | Continuous back and forth chases between a nesting male and a neighbour or male swimming by | F, D, E             |
| Chase — *conspecific*      | Chasing away other male or females that are either on the nest or swimming by | F                   |
| Chase — 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, E             |
| 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, E             |
| Nest departures            | 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, E             |
| Nest visitor — *conspecific* | 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                   |
| Out of shot                 | The male is out of frame                                                    | F, D, E             |
| 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                   |
Behavioural effect of egg absence or presence on the nest

Descriptive statistics (mean, standard deviation, and coefficient of variation) were calculated for each behaviour variable by averaging across all males \((N = 18)\). Most males were filmed on more than one day, so variables were first averaged across videos per male to get one value per male, to give each male an equal weighting. Sixteen males were filmed in only one egg group, and two were captured with and without eggs. The same descriptive statistics were then calculated by averaging across only males guarding empty nests \((n = 5)\) (no egg group) and then only males guarding nests with eggs \((n = 15)\) (egg group). Only two males were recorded in both groups, and in these cases, the variables were first averaged across videos per egg group for each male.

A nested analysis of variance (ANOVA) design was implemented to compare the difference in behavioural parameters between the egg groups. Egg presence or absence was set as the main effect, and the male identity was set as the nested effect. To comply with the conditions of a nested design, we removed the two males with observations in both groups from the egg group, since the egg group contained more males than the no egg group. For the nested ANOVA, each video was included, without averaging variables across videos per male first as was done for the descriptive statistics. Nested ANOVA assumes equal variance between groups, which was assessed using a Levene’s test for each behavioural variable.

For behavioural variables where Levene’s test revealed heteroscedasticity \((p < 0.05)\), a Welch’s \(T\)-test was carried out instead of a nested ANOVA to compare observations between egg groups. The males omitted from the ANOVA were included here since Welch’s \(T\)-tests do not admit nesting effects. Welch’s \(T\)-test disregards variation among the males, by lumping all data and using an average value per male.

Detailed recording of behavioural events

Descriptive accounts of some complex behaviours are given, as they could not be adequately represented quantitatively. These included clearing the nest of invertebrates, courtship and spawning events, a multiple male aggressive bout, and a sneaker male event.

Eggs and larvae

During each dive all nests were inspected for eggs. Upon the appearance of eggs on the site, eggs were sampled from 19 nests using small vials. Eggs were collected from the same nests on consecutive days. The maximum number of consecutive days eggs were captured from the same nest was 5 days, and the average was 3 days. Eggs were collected by gently scraping the surface of the nest using a small spoon and guiding the eggs into a plastic vial. The vials were 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. The photographs were used to capture the progression of 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.

Results

Nesting site description

The nests were scattered on and between outcrops of Cape Peninsula granite. Six nest clusters, labelled A to F (Fig. 2; see Fig. S1 for additional cluster images), ranged in size from 8 to 39 \(m^2\). Each cluster was within 5 to 10 m from another cluster. The density of nests in each cluster ranged from 0.6 to 1.3 nests \(m^{-2}\). Four of the clusters (A to D) were on the sandy bottom, while the remaining two clusters (E and F) were on separate granite outcrops. The maximum number of nests observed on the site across all clusters was 83. The average nest size was 0.3 \(m^2\) \((SD = 0.12 m^2, n = 39)\), and ranged from 0.04 to 1.0 \(m^2\). The nests were directly bordered by sand and calcareous debris, mainly comprised of mollusc shells. At a distance beyond 30 cm from the nest borders, the seafloor was covered with a variety of ophiuroids, crinoids, holothuroids, sponges, sea fans, and soft corals. It was immediately clear that the fish kept the invertebrates off the nests.
Water temperature on the nests rose from 11 °C on the 27th of August to 16 °C on the 9th of September but stabilised thereafter between 13 and 17 °C (Fig. 3). A 2 °C dip in temperature occurred on the 20th of September and a near 4 °C drop between the 3rd and 5th of October (Fig. 3). These temperature drops were both preceded by a few days of south-easterly gales (Fig. 3). Throughout the nesting period, southerly winds dominated, punctuated by northerly winds associated with coastal lows and fronts. On one occasion, we documented the destruction of nests following a south-easterly gale. Multiple nests had disappeared, and many were covered in sand. In the following days after this event, most of the nests were rebuilt.

Nests were inspected for eggs from the 28th of August, yet no eggs were observed on any nests until the 3rd of September (Fig. 3). The number of nests with eggs then steadily increased from the 3rd of September until reaching a maximum of 58 nests with eggs on the 24th of October, out of a total of 83 nests. Thereafter, the number of nests with eggs decreased to reach zero on the 5th of November with no further evidence of egg-laying. 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 that a nest held eggs ranged from 2 to 9 days.

Fifty-one days elapsed from the first to the last record of eggs on any nest, which represents the

Fig. 3 North south wind vectors, for which a southerly wind is positive (top), in situ temperature on the nesting site (middle) and percentage of nests with eggs on the nest (bottom). Red circles identify south-easterly gale events, and red arrows identify temperature drops. The last south-easterly event (C) was accompanied by a sudden drop in percentage of nests with eggs. The red line denotes the logistic equation model used to model the percentage of nests with eggs over time. The black cross denotes the date at which 50% of the nests on the site had eggs. The outlier on the 15/10/2019 was omitted from the model. A south-easterly gale had recently occurred, and it was too difficult to tell by looking at the nests if the eggs had been swept away or if they were simply covered with sand.
length of the spawning season. Halfway into the spawning season, the percentage of nests with eggs remained below 16%. Thereafter, the percentage of nests with eggs increased rapidly to reach a maximum of 72.5%. The spawning season ended (when no nests held eggs) within 12 days of this peak. On the assumption that nesting began on the date of our discovery of the first nests and that it ended on the first day after peak spawning on which no eggs were observed on any nest, it is estimated that the average male spent 77% of the 67-day nesting period engaged in nest-preparation and courtship, and that the remaining 23% was spent on paternal care (Fig. 3).

Behavioural effect of egg absence or presence on the nest

Once a camera was placed and turned on, it took males a mean time of 4 min 28 s (SD = 2 min 59 s, N = 72) to return to the nest. There was no significant effect of video length on the percentage of time each male spent on the nest (mean = 79.4, p = 0.45, R² = 0.01, df = 70, N = 72).

Five out of 15 behavioural variables were omitted from the nested analysis of variance (ANOVA) due to heteroscedasticity (p < 0.05) (Table S2).

Males remained active throughout nesting and carried out multiple behaviours. The nested ANOVAs revealed that most of the behaviours that were tested decreased in frequency and duration (Table 2) in the presence of eggs. Mean event time for nest departures and time out of frame also decreased in the presence of eggs (Table 2). Results for the ANOVA tests and Welch’s T-tests can be seen in Tables S3 and S4 respectively.

In the presence of eggs, males decrease their territorial and aggressive behaviours. They dropped the frequency and duration (Table 2) of aggressive bouts and the frequency of chases towards conspecifics (Table 2). These conspecific chases decreased in frequency towards other males but not towards other females (Table 2; Fig. S3). The frequency of conspecific males swimming over nesting males also decreased on nests with eggs (Table 2; Fig. S4).

Courtship displays decreased in frequency in the presence of eggs, occurring on average 9 counts h⁻¹ on empty nests compared to 6 counts h⁻¹ when guarding eggs (Table 2). Nevertheless, courtship display was the behaviour which took up the most total time for males guarding eggs (2.42 min h⁻¹) and the second most time for males on empty nests (0.93 min h⁻¹) (Table 2). Females visited empty male nests more frequently than they visited nests with eggs (Table 2), but the total duration of these visits as well as the average event time per visit remained the same irrespective of egg presence (Table 2).

Some behaviours such as clearing the nest and fanning did not change in frequency before or after eggs. Fanning was the most frequent of all behaviours irrespective of egg presence (82 counts h⁻¹) and was also the most frequent behaviour for males guarding eggs (86 counts h⁻¹) (Table 2). The frequency of cleaning the nest however was the most frequent behaviour for males on empty nests (84 counts h⁻¹) but dropped significantly for males guarding eggs (8 counts h⁻¹) (Table 2). On the 30th of August, one male cleaned his nest by picking at algae growing on the surface at a frequency of 196 counts h⁻¹.

Detailed behavioural descriptions

Clearing the nest

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.

The clearing of unwanted items or organisms from the nest was one of the more captivating behaviours observed. As males cleared their nests by depositing unwanted intruders throughout the site, they often dropped the item into the nest of another male. The most common item cleared was intact gastropod shells. It is highly likely that most of these shells were occupied by hermit crabs, as almost all shells inspected during dives were occupied by hermit crabs, but this was not possible to confirm from the footage. Gastropod shells were the only item cleared significantly more in the presence of eggs ($p=0.05$, $df=14.9$, $t=-2.11$).

### Courtship and spawning

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 (Fig. 6). Once the female was on the nest and inspecting the nest surface, the male repeatedly swam up and down around her and frequently nuzzled...
Fig. 4  Boxplot depicting the percentage of time spent on the nest by *Spondylosoma emarginatum* males in the absence and presence of eggs on the nest. Significant value reflects the result from the nested analysis of variance (ANOVA). *$p<0.05$, **$p<0.01$, ***$p<0.001$*

Fig. 5  Boxplots depicting the frequency of *Spondylosoma emarginatum* male behaviours in the absence and presence of eggs on the nest. Significant values reflect results from the nested analysis of variance (ANOVA). *$p<0.05$, **$p<0.01$, ***$p<0.001$*
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 (Fig. 6).

Spawning was captured on three separate nests (Table 3). Two events occurred around 13:00 (male 010 and male 009) on the 7th and 14th of September, whereas the other event happened around 10:30 (male 017) on the 2nd of October. For male 010 and 017, each spawning occurred with a single female who released her eggs in batches. She stayed on the nest for the entire video (56 min). 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 the frame between spawnings and she had no physical features strong enough to confirm identity.

**Multiple male aggression**

One 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 (Fig. S5). 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.

**Sneaker male**

A sneaker male was observed on the 7th of September between 12:00 and 13:00. A male attempted to sneak into a paired spawning event between a nesting male courting a female from his nest (Fig. 7). As the nesting male is courting the 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, and the nesting male attacks 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.

**Eggs and larvae**

Eggs were laid in dense layers over the nests and were mostly directly attached to the nest surface but

### Table 3 Details for observed Spondylosoma emarginatum spawning events during the study

| Date       | Male already guarding eggs from prior spawning? | Number of successive spawnings | Time of event   | Temperature (°C) |
|------------|-----------------------------------------------|-------------------------------|-----------------|-----------------|
| 07/09/2019 | Yes                                           | 5                             | 13:05–13:16     | 15.89           |
| 14/09/2019 | Yes                                           | 8                             | 13:04–13:29     | 14.67           |
| 02/10/2019 | Yes                                           | 3                             | 10:32–10:35     | 16.57           |
in some cases, the eggs were also attached to algae growing on or bordering the nest surface. The following egg developmental stages were observed (Fig. S6): blastula, gastrula, and an early and late embryo stages in which the yolk sac was greatly reduced. None of the larvae sampled were in preflexion phase, which is commonly characterised by full absorption of the yolk sac and flexion of the notochord. Eggs of different developmental stages were found on the same nest, with an egg in the blastula stage and another in an early larval stage.

Discussion

Male investment in reproduction

A variety of behaviours previously undescribed for Spondylisoma emarginatum were captured on a nesting site. The videos confirm that males excavate and defend nests and tend to their eggs until hatching. Nesting males limit their activities to nesting, courtship, and egg defence and only spend about 13 min per hour off their nest over the 67-day nesting period. This amount of time spent on the nest is similar to that allocated by nesting Chromis crusma (Valenciennes in Cuvier & Valenciennes 1833) (80%, Navarrete-Fernández et al. 2014) and Micropterus salmoides (Lacepede 1802) (97%, Maxwell et al. 2018).

S. emarginatum males build nests in close proximity to one another and form clusters. This can also be referred to as colonial nesting or fish spawning aggregations (Chérubin et al. 2020). Colonial nesting has been observed in the two other nesting Sparidae species: Spondylisoma cantharus (Collins and Mallinson 2012) and Spicara smaris (Harmelin and Harmelin-Vivien 1976). Colonial nesting is a common occurrence for nesting fish species (Drazen et al. 2003) and may be a result of predation risk or sexual selection. Aggregations can increase chances of brood survival, as it decreases the chances of any single nest being targeted. For example, in cooperatively breeding cichlids, Neolamprologus pulcher (Trewavas and Poll 1952), individuals invested less in antipredator defences (e.g., alarm calling and vigilance) at high densities (Jungwirth et al. 2015). Nesting aggregations also allow for increased mate-choice by females. S. emarginatum females often swam-by and visited nesting males without spawning and this could be part of a mate selection procedure. In colonial nesting grounds for shell-brooding cichlids, Lamprologus callipterus (Boulanger 1906), females preferred to breed with males surrounded by many neighbours (Schütz et al. 2016). Aggregations allow females to “window-shop” and choose the best males to spawn with. Female mate-choice in protogynous species has been shown to result in high levels of variance in reproductive success among males (Benvenuto et al. 2017).

The cost of reproduction to males is a combination of gonadal investment, energy-sapping nesting activities, lost feeding opportunity and the heightened risk of predation. Sperm production is not the major cost. For an average-sized ripe male (300 g) the GSI (1.8%) indicates that approximately 5.6 g mass is lost to sperm, whereas the total condition loss over the nesting period is in the order of 10% or 30 g body mass (Attwood and Ensair 2020). The video analysis suggests that spawning is infrequent, the number of females fertilised per male is limited to one or a few
and that there is no sperm competition, which collectively suggests that the male does not release much sperm.

Nesting activities were sufficiently lengthy and energy-demanding to account for the substantial loss of condition measured in males, a loss that occurs in the quarter after the condition loss in females (Attwood and Ensair 2020). The male’s activities recorded on the nest, and the limited time spent off the nest suggest that they do not feed during the 67-day nesting period. Seabreams typically use body fat for gametogenesis but continued feeding supplements gametogenesis during the spawning season (Aristizábal 2007). We did not observe any male *S. emarginatum* feed whilst on the nest in any of the videos. If, as we suspect, male *S. emarginatum* do not feed during nesting, they will have limited capacity to replace their sperm during the season. This hypothesis aligns with our interpretation that very little sperm is needed relative to broadcast spawners.

Ovarian development in most seabreams is asynchronous, and they are batch spawners, releasing small quantities of oocytes over 2 to 6 months (Brouwer and Griffiths 2005; Mann 2013). The spawning season of *S. emarginatum* (estimated at 51 days on this site in 2019) is considerably shorter than that of most seabreams. The trade-off is that the GSI of ripe females is high, suggesting that oocytes are accumulated and released over a short period. Spawning is more concentrated in *S. emarginatum* than in the broadcast spawning seabreams. *S. emarginatum* is closer to a capital spawner (McBride et al. 2015) than other seabreams.

Female *S. emarginatum* can feed unabated during the spawning season, but the season is probably truncated by the energetics of the male. The energy demand coupled with a lack of nutrition in the nesting male limits the spawning season. The bet-hedging strategy employed by other seabreams, which release their eggs pelagically over a long season, is likely traded off in *S. emarginatum* for the benefits of paternal care. We suspect that a drastic reduction in egg predation is achieved by keeping eggs in a nest, away from filter-feeders during the endogenous feeding phase, which could boost larval survivorship by orders of magnitude (Popiel et al. 1996; Tyler 1995).

Hatchlings leave the nest to commence exogenous feeding once the yolk sac has been absorbed. Hatchling takes between 7 and 10 days from fertilisation (Beckley 1989), which agrees with our longest observed consecutive run of eggs on a nest of 9 days. As we found eggs of different stages in a nest, it is possible that longer runs (>9 days) may have gone unobserved. The best fit of the logistic model suggests 15 days are spent on the care of eggs. The presence of different stages of eggs allows for the interpretation that *S. emarginatum* could be polygamous, as we suspect after witnessing several females visiting a nest with eggs in one video. Nevertheless, given that the longest run of eggs on a single nest did not exceed the hatching period, the number of females that mate with any given male is likely to be small.

The trade-off introduced by nesting involves not only the length of the spawning season, but also the number of years over which spawning can take place. Nesting exposes nest-bound males to predation. Although we did not witness predation, males were vigilant and temporarily fled their nest when danger presented. We speculate that the unusually short lifespan of *S. emarginatum* among seabreams is a consequence of heightened exposure to predation. This must be considered as a cost in Darwinian rather than direct energetic terms. The timing of the switch from female to male in protogynous seabreams is mediated by the adult mortality rate, to maintain an optimal sex ratio (Buxton and Garratt 1990; Kerwath et al. 2008). We hypothesise that predation on males has shortened the lifespan and reduced the ages at maturity and sex-change, in comparison to other seabreams.

**Activities on the nest**

While many behaviours decreased in frequency due to egg presence, they never completely stopped. Energetically demanding behaviours such as fanning and clearing (Jones and Reynolds 1999; van Iersel 1953) were continuous throughout the nesting period. 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). The fanning rate increases with brood size and correlates with weight loss in bluegill sunfish *Lepomis macrochirus* (Rafinesque 1819) (Coleman and Fischer 1991). Experiments on three-spined stickleback *Gasterosteus aculeatus* (Linnaeus 1758) 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). Fanning occurred at similar rates throughout the entire nesting period for S. emarginatum irrespective of egg presence suggests a large energetic expenditure throughout the nesting period and is likely to be an important limiting factor for brood size and recurrent fertilisations during a season. The uninterrupted rate of fanning throughout the nesting period also implies that fanning serves a dual purpose for S. emarginatum males. Prior to oviposition, fanning helps keep the nest clear of debris and invertebrates. Following oviposition fanning then helps keep the eggs ventilated and clear of debris.

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 suggest they may be an important egg predator at this site. No other invertebrate was removed more often in the presence of eggs; however, it is also possible that regular fanning is enough to keep lightweight predators off, such as red-chested sea cucumbers Pseudocnellina insolens, cask sea cucumbers Pseudocnella sykion, and serpent-skinned brittlestars Ophioderma wahlbergii. Some large invertebrate predators, notably the 20 cm diameter starfish Marthasterias glacialis (Clark Hubert Lyman 1923), required considerable effort for males to lift from the nest and move away.

On several instances, conspecifics swam over nest- ing males and even came to inspect the nest surface when the nesting male was gone. Conspecific predation also occurs in other nest-tending species (Gross and MacMillan 1981; Nakazono et al. 1989; Sikkel 1998). For example, in nesting Bluegill Sunfish L. macrourus, predation is mainly by conspecifics (Gross and MacMillan 1981). Predation pressures have helped explain the benefits of colonial nesting since larger numbers help alleviate the pressure of predation through collective defence or selfish herd effects (Gross and MacMillan 1981). Predation increases the necessity for males to remain on their nest to avoid brood predation and adds to the energetic costs spent during nesting. Predation pressures may also lead to females preferring to lay eggs on nests which already have eggs. All spawning events captured in this study were by a female laying her eggs with a male currently guarding some eggs. Female preference for laying eggs among other eggs has been documented in other species such as Hypsypops rubicundus (Girard 1854) (Sikkel 1989) and is thought to lead to increased egg survival (Jamieson 1995). Alternatively, it could also be that since the observed spawning events occurred towards the end of the spawning season, the majority of the nests already had eggs. An additional find about conspecifics swimming over nesting males is that the rate of swim-bys decreased towards the end of the nesting period. This coincided with fewer males chasing away conspecifics. It is likely that since the number of males busy guarding eggs increased as the nesting period progressed, fewer males remained swimming over the nesting site.

These energetic demands help explain sneaker males, 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 (Alonzo and Heckman 2010; DeWoody and Avise 2001). Until now, sneaker males in the Sparidae are mentioned only for the broadcast-spawning Australasian snapper Chrysophrys auratus (Forster 1801) (Smith 1986) and Santer seabream Cheimerius nufar (Valenciennes 1830) (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. These events are more appropriately described as sperm competition in a spawning aggregation, where males compete 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 seabream.

Life-history strategy

Despite the rarity of the combination, this nesting strategy is compatible with a protogynous life-history, since larger individuals will be more capable of excavating and guarding a nest and should be less prone to predation. Warner and Lejeune’s (1985) statement that nest-building, and paternal care limits the number of females that a large male can fertilise is relevant here, but we suggest that the size advantage lies not in the number of females that get fertilised, but rather the probability of maintaining a nest and defending eggs until hatching in a competitor- and predator-rich
setting. Importantly they will have greater stamina to prolong the nesting period. Nesting behaviour and paternal care may provide the size-advantage for males needed to meet Warner’s requirement for protogyny (Warner 1975).

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 (nests in this case), 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, S. smaris, has an identical female to male sex ratio of 4.1:1 (Dučić et al. 2003). We suspect that the sex-ratio is self-regulating in these protogynous seabreams (Buxton and Garratt 1990; Kerwath et al. 2008; Tunley et al. 2009) and that this asymmetrical ratio is optimal for this reproductive strategy, which requires less sperm than is the case in other seabreams.

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 species among South Africa’s 42 seabreams, and its success might be attributed to its ability to flourish in stochastic conditions and in a variety of ecosystem types. The short-term stochasticity of the environment was highlighted in this study when strong south-easterly gales led to the destruction of multiple nests. Despite being a benthic egg layer, the Spondyliosoma spp. complex is more widespread than other seabream genera, as it ranges from the North Atlantic off the western British Isles to Durban in the south-western Indian Ocean. In so doing it spans a massive range of habitat and biogeographic zones. This is very rare for a protogynous species, as a recent review stated that only 5% of protogynous species have adapted to temperate environments (Pla et al. 2021).

The opportunistic strategy is possibly what has allowed Spondyliosoma spp. to occupy widely divergent coastal environments, in both hemispheres, spanning 86 degrees of latitude. Whereas fish species resilience has frequently been linked to life-history combinations (King and McFarlane 2003), we contend that the natural ranges of fishes might be similarly affected. Indeed, life-history is a predictor of invasive potential (Capellini et al. 2015; Marchetti et al. 2004).

Conclusions

The size-advantage model (SAM) applies differently to S. emarginatum than it does to pelagic spawning seabreams. For this nest-building protogynous fish, the advantage of a large male is its increased stamina for nest-building, nest maintenance, and nest-guarding, yet they spawn with a limited number of females. In contrast, large protogynous pelagic spawners have the advantage of a greater access to females.

Spondyliosoma spp. differ from other seabreams in that they are short-lived opportunists. Predation may lead to short longevity, early maturation, and as a consequence small size. Their strategy hinges on reducing mortality in the younger stages (from eggs to hatching), thereby removing the necessity for extreme bet-hedging (high longevity, high life-time fecundity, long spawning seasons) in variable coastal environments.

The fact that these benthic egg-laying seabreams are more widely distributed than their pelagic broadcast-spawning counterparts is a paradox that might be explained by their opportunistic life-history and begs an investigation into a correlation of life-history characteristics and range restriction within the family.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All ethics were approved by the Science Faculty Animal Ethics committee (SFAEC) at the University of Cape Town, and the study was performed in accordance with the ethical standards as laid down in the 1964 Declaration of Helsinki and its later amendments.

Conflict of interest The authors declare no competing interests.

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