Iberoamerican fisheries
and fish reproductive ecology
N. Bahamon, R. Domínguez-Petit, J. Paramo,
F. Saborido-Rey and A. Acero P. (eds)

Scientia Marina 86(4)
December 2022, e050, Barcelona (Spain)
ISSN: 0214-8358
https://doi.org/10.3989/scimar.05305.050

Influence of maternal effects and temperature on fecundity of *Sebastes fasciatus* on the Flemish Cap

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Summary: The conservation of a sufficient reproductive potential of an exploited stock is one of the goals of fisheries management, as it ensures sustainable productivity. However, there is evidence that spawning stock biomass (SSB) does not represent well the variation in stock reproductive potential, often leading to impaired stock-recruitment relationships. In this study we show that fecundity of *Sebastes fasciatus* on Flemish Cap is not proportional to SSB and shows temporal fluctuation influenced by maternal effects. Females were collected in 23 research surveys between 1996 and 2020. An autodiametric calibration model was developed for *S. fasciatus* for the first time to estimate fecundity. Mean potential fecundity was estimated as 36000 oocytes and mean relative fecundity as 79 oocytes g^{-1}. Potential fecundity varied significantly with female length, age, condition index, gonadosomatic index and environmental variability. Mixed-effect linear models were fitted to assess the effect of maternal traits and bottom temperature on fecundity. Fecundity increased significantly with condition factor and sea bottom temperature. Relative fecundity also increased significantly with length, age and gonadosomatic index, indicating that older, larger and better-conditioned females produce more eggs per female gram. This suggests that SSB is not a good proxy to stock reproductive potential so it is unsuitable for use in stock assessment and scientific advice. Considering that *S. fasciatus* is a viviparous species, future research should focus on maternal effects on offspring and on building time series of reproductive potential indexes that take into account maternal effects.

Keywords: reproductive potential; fish condition; life history; autodiametric method.

Influencia de los efectos maternales y la temperatura en la fecundidad de *Sebastes fasciatus* en Flemish Cap

Resumen: La conservación de un potencial reproductivo suficiente de una población explotada es uno de los objetivos de la gestión pesquera, ya que garantiza la consecución de una productividad sostenible. El establecimiento de relaciones fiables stock-reclutamiento es esencial para lograr este objetivo, pero la biomasa reproductora (SSB) se utiliza a menudo como índice poblacional, mientras que hay evidencias de que no representa bien la variación del potencial reproductivo de la población, lo que da lugar a relaciones stock-reclutamiento deficientes. En este estudio mostramos que la fecundidad de *Sebastes fasciatus* en Flemish Cap no es proporcional a la SSB y que tiene una fluctuación temporal influida por los efectos maternales. Se recogieron hembras en 23 campañas oceanográficas realizadas entre 1996 y 2020. Por primera vez, se desarrolló un modelo autodiamétrico para *S. fasciatus* para estimar la fecundidad. La fecundidad potencial media se estimó en 36000 ovocitos y la fecundidad relativa en 79 oovcitos g^{-1}. La fecundidad potencial varió significativamente con la talla de la hembra, la edad, el factor de condición, el índice gonadosomático y la variabilidad ambiental. Se ajustaron modelos lineales mixtos para evaluar los efectos de los rasgos maternos y la temperatura del fondo marino sobre la fecundidad. Los resultados mostraron que la fecundidad aumentó significativamente con el factor de condición y la temperatura del fondo. La fecundidad relativa también incrementó significativamente con la talla, la edad y el GSI, lo que indica que las hembras más longevas, más grandes y con mejor condición producen más huevos por gramo de hembra. Esto implica que la biomasa de la población reproductora (SSB) no es un buen indicador del potencial reproductivo de la población, lo que pone en peligro su uso en la evaluación de la población y el asesoramiento científico. Teniendo en cuenta que *S. fasciatus* es una especie vivípara, la investigación futura debería centrarse en los efectos maternos sobre las crías y en la creación de series temporales de índices de potencial reproductivo que tengan en cuenta los efectos maternales.

Palabras clave: potencial reproductivo; condición; historia vital; método autodiamétrico.

Citation/Como citar este artículo: González-Carrión F., Saborido-Rey F. 2022. Influence of maternal effects and temperature on fecundity of *Sebastes fasciatus* on the Flemish Cap. Sci. Mar. 86(4): e050. https://doi.org/10.3989/scimar.05305.050

Editor: N. Bahamon.

Received: June 3, 2022. **Accepted:** September 12, 2022. **Published:** November 3, 2022.

INTRODUCTION

Changes in spawning dynamics, size or age at maturity, size structure and poor condition can increase the variability of recruitment (Marteinsdottir and Thorarinsson 1998, Blanchard et al. 2003, Anderson et al. 2008), reduce the resilience and capacity of populations to dampen environmental changes (Hsieh et al. 2006) and increase the impact of climate change (Cheung et al. 2009). Fisheries management will considerably benefit from a better understanding of how maternal features affect offspring phenotypes (the so-called maternal effect) and hence of how stock reproductive potential determines population productivity and recruitment.

Consequently, fecundity studies are critical for understanding the reproductive potential of fish populations (Tomkiewicz et al. 2003, Lambert et al. 2003, Saborido-Rey and Trippel 2013) and how maternal effects can interact with fecundity (Thorsen and Kjesbu 2006). Fecundity is a highly temporal and geographically sensitive variable that changes drastically with attributes of the individual spawners, including length, age and condition factor (Murua and Saborido-Rey 2003, Rideout and Morgan 2010). In consequence, the population's egg production is highly dependent on adult stock demography and factors affecting demography, such as growth, maturation schedules, fishing pressure, environmental conditions and disease (McElroy et al. 2013, Chang et al. 2021). Moreover, in many teleosts, significant differences have revealed disproportionally positive relationships between potential fecundity and fish length (Stafford et al. 2014, Love et al. 2002), age and condition (Thorsen et al. 2006, Lambert 2008), highlighting the importance of maternal effects. Several studies have shown that in Pacific rockfish species maternal effects are determined by release offspring date and seasonal changes in the productivity of the California current, so offspring quality is directly affected (Fisher et al. 2007).

Monitoring of fecundity, as reported in the literature, can be used in stock assessment and fisheries management (Yoneda and Wright 2004, Lambert 2008, McElroy et al. 2013), especially under the climate change scenario in species with a strong maternal influence, such as those showing viviparity. However, long time series of fecundity are usually not available, as reported by Tomkiewicz et al. (2003), and the situation has not improved over time. The difficulty of estimating fecundity is likely the main hindrance to regular and routine estimation. In this regard, the autodiametric method developed by Thorsen and Kjesbu (2001) must facilitate fecundity estimations.

In this study, for the first time we applied the autodiametric method to estimate fecundity in *S. fasciatus* on the Flemish Cap bank to build a unique long time series of fecundity data of 20 years from 1996 to 2020. We analysed the maternal influence on several reproductive traits and tested whether water temperature influences fecundity. Our overall aim was to improve our understanding of the effects of maternal influence and climate variability on the productivity of *S. fasciatus*, following the hypothesis that spawning stock biomass (SSB) and other stock indexes do not represent well the variation in stock reproductive potential, often leading to impaired stock-recruitment relationships. Our results highlight the importance of building time series of reproductive potential variables other than SSB, such as fecundity.

MATERIALS AND METHODS

Study area

The study was carried out on the Flemish Cap in the northwest Atlantic, between 46°N and 49°N and 44°W and 46°W (Fig. 1). It is separated from the Newfoundland shelf by the Flemish Pass, a channel with depths in excess of 1100 m, which hinders the migration to and from the Grand Bank for most of the fish species inhabiting the Flemish Cap, including *S. fasciatus*. The Flemish Cap is a dome-shaped, deep-water mountain, with a total area of 17.000 square miles up to 1460 m and 10.555 square miles up to 730 m, with the shallowest part of the bank (120 m depth) located in the southeastern quadrant.

Data collection, histology and ovarian processing

Ovaries of *S. fasciatus* were collected from the EU Flemish Cap survey conducted annually in June/July since 1988 as part of the European Union sampling programme with the participation of Spain and Portugal. For each fish, fork length (FK), total weight (TW), gutted weight (GW) and maturity stage were recorded on board. Otoliths were removed for further age determination.

Ovaries were preserved in 4% buffered formaldehyde and then weighed in the laboratory. Ovary sections of 0.5 cm thickness from the central portion of the gonad were embedded in paraffin based on conventional histological processing. Sections of 3 µm were stained with haematoxylin and eosin protocol. The ovarian developmental phase, as described in Brown-Peterson et al. (2011), was determined under a microscope.

Bottom temperature was obtained from the Copernicus Marine Environment Monitoring service (https://doi.org/10.48670/moi-00021) for the Flemish Cap area (between 45°N to 49°N and 47°W to 43°W) for July within the period 1996-2020 and for sampling depths between 300 and 600 m.

Fecundity estimation and image analyses

Fecundity was estimated in ovaries with the presence of advanced vitellogenic oocytes and no signs of postovulatory follicles and/or fertilization. Because *Sebastes* species are group-synchronous with a determinate oocyte recruitment mode, this single leading cohort of oocytes is considered representative of the potential fecundity (Murua and Saborido-Rey 2003). A total of 281 ovaries were selected according to the above criteria between 1996 and 2020 (Table 1). Ovary weight was recorded and subsamples

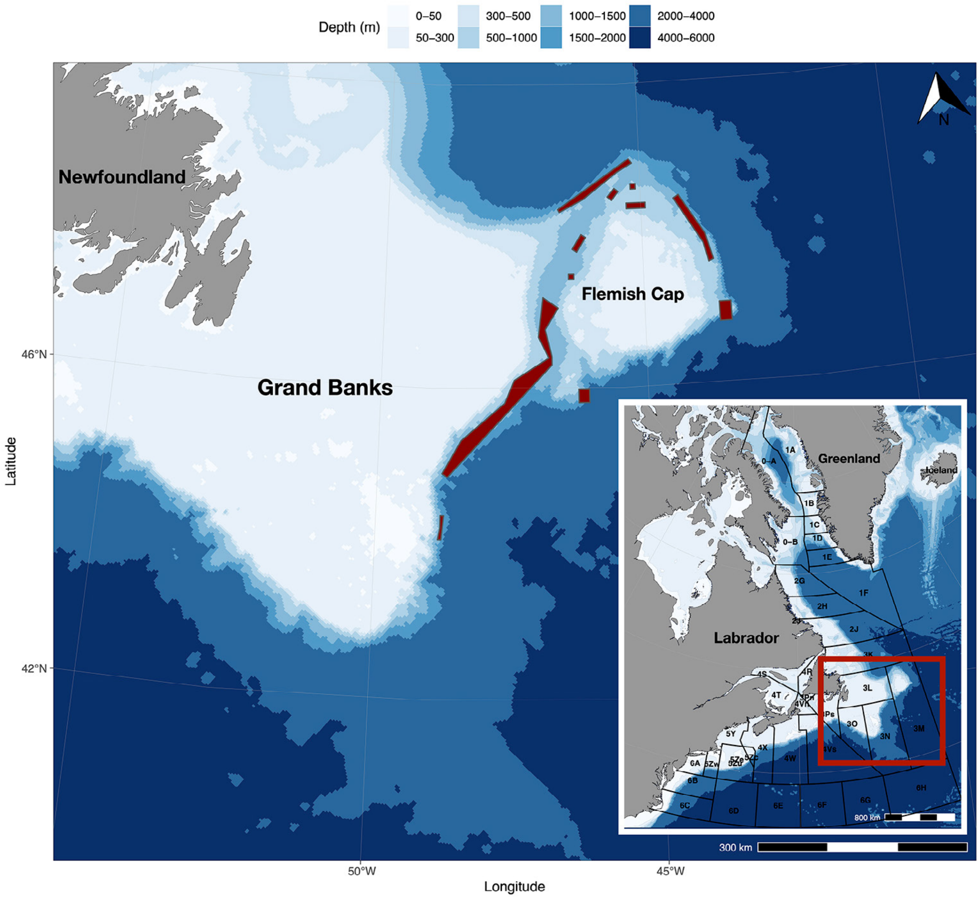

Fig. 1. – Map of the location of Flemish Cap in the Northwest Atlantic. Lines indicated isobath depth. The inset shows in detail the area of the red square: straight lines and codes indicate Northwest Atlantic Fisheries Organization (NAFO) management divisions around the Flemish Cap (3M). Red polygons indicate sponge closure areas.

of about 0.15 g were taken from the central ovary section. Several studies have shown no significant differences in mean follicle diameter and abundance between and within ovaries (Nichol and Acuna 2001, Kennedy et al. 2007, McElroy et al. 2013). Then, oocytes of each subsample were washed and separated from the connective tissue throughout sieving (150 µm, 300 µm and 600 µm).

Potential fecundity was estimated using the autodiametric method (Thorsen and Kjesbu 2001). This method relies on a relationship between mean vitellogenic oocyte diameter (OD) and oocyte packing density (OPD). Once this relationship is attained, fecundity is obtained by estimating the mean OD of an ovarian subsample and then converted to OPD to scale up to the weight of the ovary.

To build the autodiametric calibration curve, 115 ovaries were used. Oocyte counts and measurements were carried out using the software Leica LAS and the images were taken with a Leica Z6 APOA macroscope using a Leica DFC 490 camera. Each subsample was divided into 2 to 3 portions, and each one was analysed separately to facilitate the image analysis. The oocytes were counted and measured using a macro developed by Lucia Sánchez-Ruiloba (IIM-CSIC) in Image J software (https://imagej.nih.gov/ij/). Oocytes departing from sphericity were not considered for estimating average OD in each ovary, but they were counted to determine the final oocyte density (number of oocytes/g of ovary tissue) in each ovary.

The autodiametric calibration curve is based on the principle that OPD is inversely proportional to OD with a power relationship (Thorsen and Kjesbu 2001):

$$\mathrm{OPD} = a\ \mathrm{OD}^{b} \qquad (1)$$

where a and b are equation constants.

To improve the fit of the autodiametric calibration curve, OPD and OD data of *S. mentella* and *S. norvegicus* collected in the Irminger Sea and Iceland (Witthames et al. 2009, Saborido-Rey et al. 2015) were also used, and results among species were compared before the data were merged. Finally, the potential fecundity of 281 *S. fasciatus* females on the Flemish Cap was estimated by obtaining the OD of each ovary using the image analysis described above and applying the autodiametric calibration curve:

$$\mathrm{Fecundity} = \mathrm{OPD} \times \mathrm{OW} \qquad (2)$$

where OW () is the ovary weight (g) of each female analysed.

Table 1. – Summary statistics of the female S. fasciatus maternal traits: age, fork length, gutted weight (GW) and condition factor. Numbers indicate the average ± standard deviation, with ranges shown in parentheses. Years with merged data required to increase sampling size are indicated with asterisks and correspond to the year label used in the figures.

Year	n	Age (years)	Length (cm)	GW (g)	Condition factor
1996	14	8.43±2.53	29.29±2.53	381.54±169.99	1.43±0.08
		(6-14)	(25-39)	(240-820)	(1.3-1.57)
1997	12	11.36±3.93	30±3.3	428.75±133.04	1.53±0.06
		(7-21)	(25-35)	(220-640)	(1.41-1.61)
1998	5	8.4	25.8	269	1.56
		(7-10)	(24-28)	(235-340)	(1.45-1.7)
1999	10	11.7±4	30.6±4.97	436.1±168.62	1.45±0.18
		(6-16)	(21-36)	(140-659)	(1.27-1.78)
2000	16	12.88±2.22	32.44±2.9	503.44±112.68	1.46±0.1
		(10-17)	(27-37)	(320-720)	(1.28-1.63)
2001	29	11.23±3.28	28.9±2.81	351.14±97.17	1.42±0.11
		(6-16)	(22-35)	(140-610)	(1.23-1.74)
2002	4	11.75±3.86	28.25±3.1	328.25±109.59	1.41±0.06
		(6-14)	(24-31)	(188-445)	(1.36-1.49)
2004 (2003-2004)*	13	12.44±2.92	30.31±2.14	399.08±77.77	1.43±0.14
		(7-17)	(27-33)	(291-580)	(1.22-1.61)
2005	32	12.31±3.45	29.28±2.45	364.12±91.35	1.43±0.12
		(6-19)	(24-34)	(230-530)	(1.07-1.67)
2006	12	11.08±3.48	28.83±2.37	354.58±95.38	1.44±0.11
		(7-16)	(24-32)	(180-500)	(1.3-1.63)
2008	5	12±4.47	30.8±3.7	384±110.59	1.3±0.14
		(6-18)	(26-36)	(240-510)	(1.09-1.48)
2010 (2009-2010)*	7	10.86±2.79	31.14±2.97	431.29±116.45	1.4±0.13
		(7-16)	(26-34)	(260-580)	(1.25-1.61)
2011	3	12.33±3.79	32.67±4.51	523±213.19	1.44±0.12
		(8-15)	(28-37)	(293-714)	(1.33-1.56)
2013	13	14.85±6.03	32.77±4.9	565.08±219.82	1.55±0.16
		(7-25)	(26-40)	(272-975)	(1.32-1.81)
2014	12	13.92±3.12	32.58±2.84	508.92±117.7	1.45±0.14
		(9-20)	(28-36)	(325-653)	(1.25-1.66)
2015	8	15.25±7.15	35±6.85	672±352.8	1.46±0.2
		(6-24)	(22-44)	(198-1190)	(1.13-1.86)
2016	21	14.13±4.12	31.75±1.96	432.43±85.97	1.3±0.09
		(9-25)	(29-35)	(270-560)	(1.11-1.44)
2018 (2017-2018)*	35	14.76±4.02	33.06±3.34	518.09±148.81	1.41±0.16
		(8-28)	(27-41)	(316-950)	(1.22-2.05)
2019	15	16.73±3.2	35.27±3.53	675.13±172.18	1.52±0.13
		(10-22)	(28-40)	(360-940)	(1.3-1.83)
2020	15	14.4±4	34.07±4.77	630.47±259.34	1.53±0.13
		(8-20)	(27-44)	(323-1230)	(1.25-1.81)
Total	281	271	280	280	280

Maternal traits

The Fulton condition index (K) and the gonadosomatic index (GSI) were calculated as follows:

$$K = \left(\frac{GW}{FL^3}\right) \text{X}\, 100 \qquad (3)$$

$$GSI = \left(\frac{OW}{GW}\right) \text{X}\, 100 \qquad (4)$$

where GW represents gutted weight (g) and FL is fork length (cm) recorded for each female. Age (yr) and GW (g) were also recorded for each female for further analyses as an explanatory variable in the models and to estimate relative fecundity.

Statistical analysis

Generalized linear models (GLM) were fitted to examine the relationships between the reproductive investment (absolute and relative potential fecundity) and maternal traits (length, age and fish condition).

When bottom water temperature was included, generalized linear mixed models (GLMM) were used to analyse the effect of female traits on their reproductive output. Models were fitted using length, age, K and GSI as fixed effects, haul as a random effect and water temperature as a random slope to allow the relationship with bottom temperature to differ by year. Water temperature data were unavailable for numerous coordinate-year combinations, hindering possible water bottom temperature effects on potential fecundity relationships. However, a dataset covering 15 years was obtained. The reproductive output was analysed as follows:

$$\text{Reproductive output}_{t,i} = \alpha + \text{FL or A} + \text{K} + \text{GSI} + \text{TBTM} + a_i + \varepsilon_{t,i}$$

where reproductive output is the absolute and relative potential fecundity in year $_t$ and haul $_i$, α is the intercept, FL is the fork length, A is age, K is Fulton's condition factor, GSI is the gonadosomatic index, TBTM is the bottom temperature at deep habitat range (300-600 m), a_i is the random intercept allowing for variation between years, and b_i is the random intercept allowing for variation between hauls. The residuals εt,i are a normally distributed random error with mean 0 representing the within-year and haul variation.

To avoid collinearity due to fish length and age correlation, they were used in separate models: the models were fitted for absolute and relative fecundity using age and length separately. Haul and Year were included as random effects to correct for the non-independence of reproductive output from the same year and haul. Thus, we evaluated the effects of how these maternal traits and water bottom temperature affect potential fecundity. GLMM were fitted using negative binomial mean variance with a "log" link function. Diagnostic plots testing residual homogeneity, independence and normality and the Akaike information criterion (AIC) were used for model validation (Supplementary material, Tables S1, S2). We avoided transforming the response variable as long as possible using a negative binomial distribution. First, Poisson distribution was used in all the models because of the nature of the response variable (count data). However, high overdispersion values were obtained, so negative binomial distribution was used to avoid overdispersion problems (Zuur and Ieno 2013). Variance inflation factor was calculated in each model to test for collinearity between independent covariates. All statistical analyses were performed with the statistical software R4.0.1 (R Core Team 2020) and using the glmmTMB package (Brooks et al. 2017).

RESULTS

The autodiametric method

The estimated autodiametric relationship between *S. fasciatus* oocyte density (n/g) and mean OD was significant ($p<0.001$, $r^2=0.80$, $n=108$). No significant difference was detected ($df=255$, $P=0.133$) between the autodiametric curves of *S. fasciatus* on the Flemish Cap, *S. norvegicus* in Iceland and *S. mentella* in Iceland and the Irminger Sea (Fig. 2). The autodiametric curve with all species combined ($p<0.001$, $r^2=0.88$, $n=256$) was the following:

$$\text{Oocyte density (n/g)} = \exp\,(1.068\times 10 - (3.234\ 10^{-3})\times \text{OD}\ (\mu\text{m}) \qquad (5)$$

We then used this curve to estimate the potential fecundity from OD and ovary weight for *S. fasciatus* on the Flemish Cap.

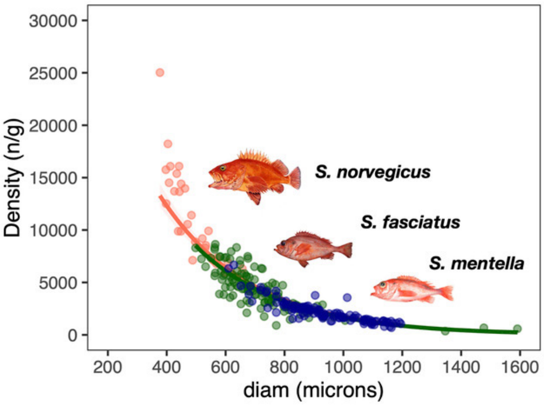

Fig. 2. – Relationship between oocyte diameter and oocyte density (number of oocytes/g) for species of the genus *Sebastes* sampled on the Flemish Cap bank (*S. fasciatus* with green dots) and in the Irminger Sea and Iceland (*S. norvegicus* and *S. mentella* with coral and blue dots, respectively). No significant differences were observed between areas.

Potential fecundity

Influence of female traits on fecundity

Four maternal traits (fork length, age, GSI and K) were used to study their influence on fecundity. To avoid using age and length together, two separate models were built. The resulting two GLM models explained 75% and 62% of potential fecundity (Table 2) using length and age, respectively. In the case of relative fecundity, the two models explained 47% and 50% of the variation (Table 2). Our results show that potential fecundity increased significantly with age and size. Interestingly, relative fecundity also increased with those female traits, indicating a disproportionally higher fecundity at larger sizes and older ages (Fig. 3).

Females with higher K and constant GSI (1.58, the average value of the time series) had a higher potential fecundity than fish with lower K (Fig. 3). For example, for a length of 34 cm (the average of the mature stock), the potential fecundity varied between 33707 oocytes with a K=1.2 compared with 47512 oocytes with a K=1.6 and 56409 oocytes with a K=1.8, i.e. an increase of 41% and 67%, respectively (Fig. 3A). Similarly, for a female at 15 years old, the predicted potential fecundity for all three scenarios of K was 34544 oocytes for K=1.2, 40739 oocytes for K=1.6 and 44242 oocytes for K=1.8 (Fig. 3B). Thus, potential fecundity of females in poorer condition was notably lower.

However, relative fecundity did not increase significantly with condition. For a fixed length of 34 cm, the relative fecundity was 71 oocytes g^{-1} body weight for K=1.2, 76 oocytes g^{-1} body weight for K=1.6 and 79 oocytes g^{-1} body weight for K=1.8, i.e. a difference of 7% and 11%, respectively. Moreover, for a fixed age of 15 years, relative fecundity was 72 oocytes g^{-1} body weight for K=1.2, 76 oocytes g^{-1} body weight for K=1.6 and 78 oocytes g^{-1} body weight for K=1.8, i.e. a difference of barely 5% and 8% (Fig. 3C and D).

Interannual variation of fecundity

Interannual variation in potential fecundity was examined by comparing potential relationships between fecundity and maternal traits between 1996 and 2020 (Fig. 4). Fork length and age showed a significant effect on potential fecundity in all years analysed ($p<0.001$), and the optimal model showed a significant year effect ($p<0.001$). However, the post hoc Tukey test showed that the fecundity variation between years was caused by only a few years (Tables S3, S4), mostly 2010, a year with a low sample size.

Figure 5 shows the fecundity variation for a 34 cm female. Potential fecundity showed generally higher values at the beginning of the time series, an average of 48500 oocytes between 1996 and 2001 and four years with fecundity above 50 thousand oocytes. Later, fecundity decreased to an average of 42000 oocytes for the rest of the times series (except 2010). During this period, fecundity was below 45000 oocytes in all years except 2010, with particularly low values in the latest years (2015-2019). The year with the highest (2000) fecundity for a fixed size of 34 cm and age of 15 years showed 1.8-fold greater fecundity rates on average than the year with the lowest fecundity (2015) (not considering 2010).

The analyses with relative fecundity yielded similar results to those with absolute potential fecundity. Optimal models included length, age and year, which explained 22% and 34%, respectively (Supplementary Table 5 and Supplementary Table 6). For a 34 cm female, relative fecundity ranged between 62 and 139 oocytes g^{-1}, showing a very similar pattern to potential fecundity, with higher values before 2002 (mostly above 90 oocytes g^{-1}) and lower values thereafter (mostly below 80 oocytes g^{-1}).

Table 2. – Summary of GLM negative binomial models fitted to estimate the effect on potential and relative fecundity of the maternal traits fork length, age, condition factor (K) and gonadosomatic index (GSI) of *S. fasciatus* on the Flemish Cap.

Models	Response variable	n	R^2	Variable	Coeffs	SE	z value	Pr(>|z|)
1	Potential fecundity	252	0.75	α	4.862	0.278	17.491	**<0.001**
				Length	0.113	0.005	22.216	**<0.001**
				K	0.858	0.142	6.028	**<0.001**
				GSI	0.445	0.033	13.654	**<0.001**
2	Potential fecundity	252	0.62	α	7.917	0.276	28.732	**<0.001**
				Age	0.093	0.006	14.852	**<0.001**
				K	0.424	0.175	2.421	**<0.05**
				GSI	0.405	0.042	9.767	<0.001
3	Relative fecundity	252	0.47	α	2.905	0.251	11.588	<0.001
				Length	0.016	0.005	3.367	<0.001
				K	0.096	0.112	0.857	0.39138
				GSI	0.436	0.031	14.187	<0.001
4	Relative fecundity	244	0.50	α	3.257	0.188	17.301	<0.001
				Age	0.023	0.005	4.685	<0.001
				K	0.042	0.108	0.391	0.696
				GSI	0.413	0.038	13.437	<0.001

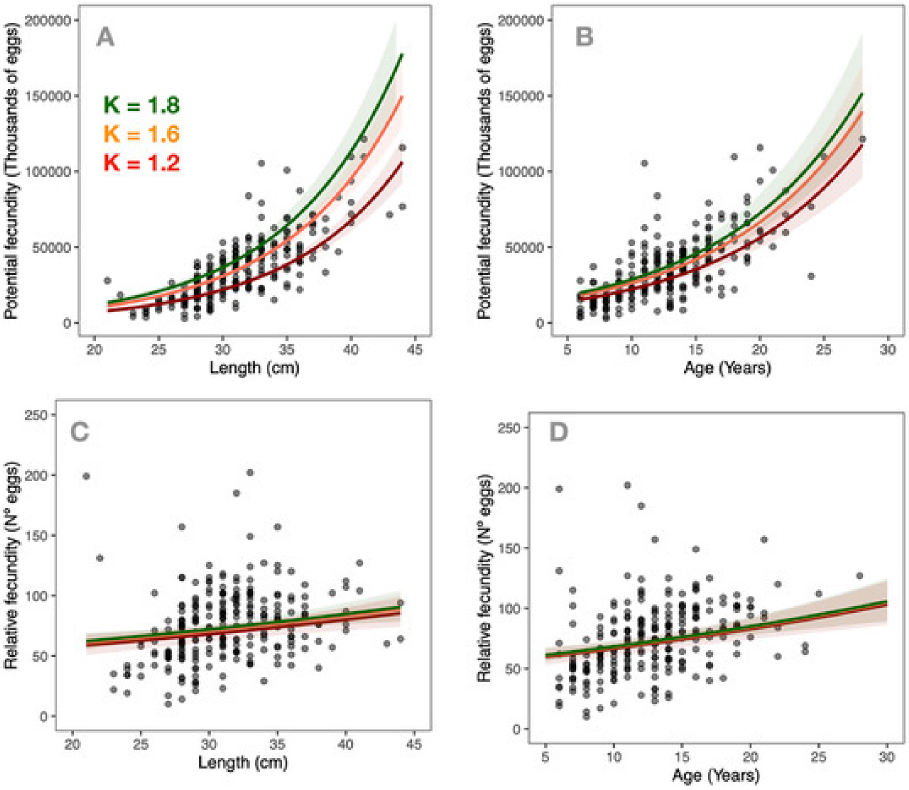

Fig. 3. – Relationship and fitted curves between potential fecundity by length (A) and age (B), and between relative fecundity by length (C) and age (D) of *S. fasciatus* on the Flemish Cap between 1996 and 2020. Data were fitted for three different values of condition factor (K=1.2, K=1.6 and K=1.8)

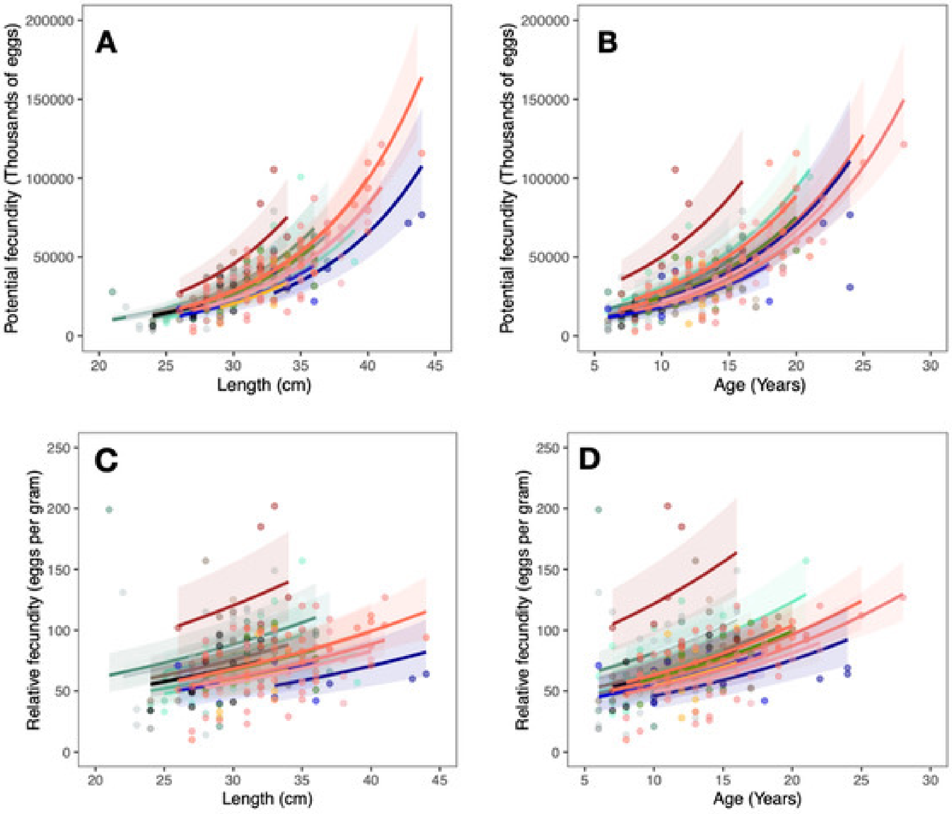

Fig. 4. – Interannual variation of the relationships between potential fecundity by length (A) and age (B), and between relative fecundity by length (C) and age (D) of *S. fasciatus* on the Flemish Cap between 1996 and 2020.

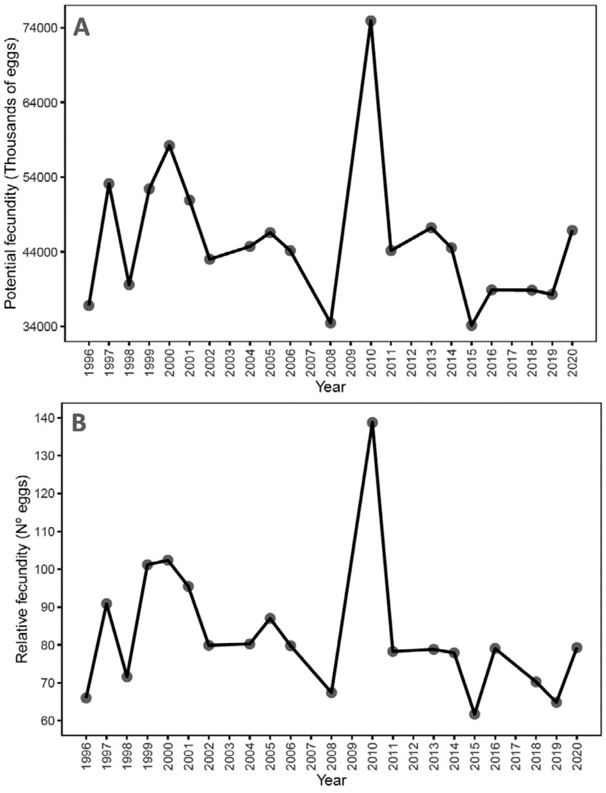

Fig. 5. – Temporal variation in potential fecundity (A) and relative fecundity (B) between 1996 and 2020 for a 34 cm *S. fasciatus* female.

The role of bottom water temperature in fecundity

The range of bottom temperature in which females were sampled varied between 3°C and 5°C, with the highest frequencies in a narrow range between 3.5°C and 4°C, i.e. 70% of females were sampled in a range of 0.5°C (Fig. 6). Because samples were randomly taken during the survey, this result likely reflects the distribution of females in advanced stage of vitellogenesis.

The potential and relative fecundity increased per degree of bottom temperature water (Fig. 6 A, B). The median of potential fecundity increased from 30743 oocytes in 3°C to 45000 oocytes in 4.5°C, i.e. by 31%. Similarly, relative fecundity increased from 64 oocytes g^{-1} body weight at 3ºC to 85 oocytes g^{-1} body weight at 4°C, i.e. an increase of 24%. The two GLMMs fitted (using length and age) showed that fecundity-at-length and at-age increased with temperature (Fig. 6C, D). However, only the model using age showed a significant positive relationship between bottom temperature and potential fecundity in the age model (Table 3 and Table 4).

DISCUSSION

Our findings provide empirical evidence of autodiametric curve stability, indicating that the autodiametric method for estimating fecundity originally developed in cod (Thorsen and Kjesbu 2001) can be applied in North Atlantic *Sebastes* species.

This study demonstrated no significant differences in autodiametric curves between three species of *Sebastes* on the Flemish Cap, in Iceland and in the Irminger Sea. Likewise, no significant differences were obtained between autodiametric curves from different stocks in the northeast Arctic, the northern Gulf of St. Lawrence and Georges Bank (Thorsen and Kjesbu 2001, Lambert 2008, Alonso-Fernández et al. 2009). For example, for a fixed diameter size of 800 µm, the oocyte density varied between 3174 oocytes in the Flemish Cap autodiametric curve and 3303 oocytes in the Irminger Sea autodiametric curve, a difference of 4%. Lambert (2008) found a similar difference of less

Table 3. – Parameters of the optimal GLMM using potential fecundity as the response variable and including length, condition factor (K), gonadosomatic index (GSI) and bottom temperature from 21 years (N=280 observations) as explanatory variables. SD, standard deviation; SE, standard error. R2LMM(m) describes the proportion of variance explained by fixed effects alone and R2LMM(c) describes the proportion of variance explained by fixed and random effects combined.

Fixed effects	Parameter estimate	SE	z value	Pr(>lzl)
Intercept	3.764875	0.490177	7.68	**<0.001**
Length	0.125494	0.007794	16.10	**<0.001**
K	0.971214	0.188958	5.14	**<0.001**
GSI	0.526113	0.05054	10.41	**<0.001**
Sea bottom temperature	0.107033	0.07218	1.48	0.138
Random effects (SD)				
Year	0.00971			
Haul	0.01133			
Metric				
$R^2_{LMM(m)}$	0.813			
$R^2_{LMM(c)}$	0.858			

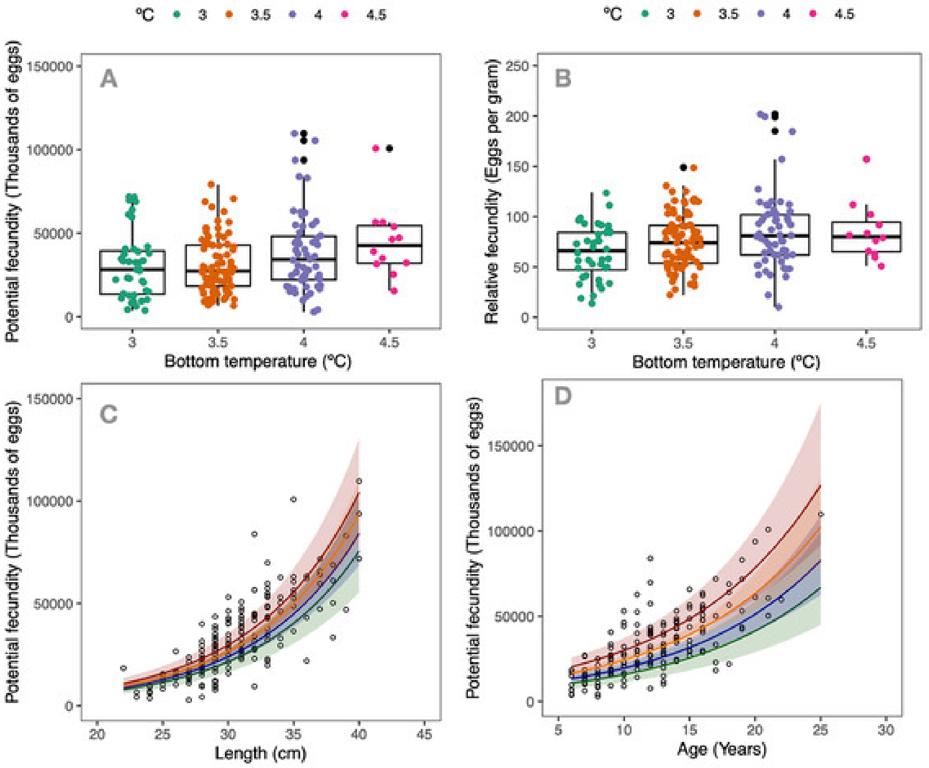

Fig. 6. – Boxplots displaying the relationship of sea bottom temperature with potential fecundity (A) and relative fecundity (B) of *S. fasciatus* on the Flemish Cap. The relationships of potential fecundity at four different temperatures are shown in C) for length and in D) for age.

Table 4. – Parameters of the optimal GLMM using potential fecundity as the response variable and including age, condition factor (K), gonadosomatic index (GSI) and bottom temperature from 21 years (n=280 observations) as explanatory variables. SD, standard deviation; SE, standard error. R2LMM(m) describes the proportion of variance explained by fixed effects alone and R2LMM(c) describes the proportion of variance explained by fixed and random effects combined.

Fixed effects	Parameter estimate	SE	z value	Pr(>lzl)
Intercept	7.413802	0.439226	16.879	**<0.001**
Age	0.090452	0.007516	12.035	**<0.001**
K	0.334705	0.200544	1.669	0.135
GSI	0.418751	0.057942	7.227	**<0.001**
Sea bottom temperature	0.166456	0.082827	2.010	**<0.05**
Tandom effects (SD)				
Year	0.009952			
Haul	0.026120			
Metric				
$R^2_{LMM(m)}$	0.677			
$R^2_{LMM(c)}$	0.778			

than 6.5% in oocyte density estimated with different calibration curves for two cod stocks, concluding that they were essentially the same curve.

The use of OPD and the success of the autodiametric method could vary between areas, stocks and species (Dominguez-Petit et al. 2018)spatial differences in the autodiametric calibration curve were observed in the Northwest Atlantic, but did not translate into differences in fecundity at length. This is the first time that spatial differences between ACCs of the same species have been reported, what could be the result of (i, for reasons such as energy allocation and preservation techniques (Friedland et al. 2005).Thus, fecundity estimations could be inaccurate when published calibration curves not estimated for the species or a stock of interest are used (Witthames et al. 2009).

In this paper, we have studied the fecundity of *S. fasciatus* on the Flemish Cap for the first time, building a twenty-year time series between1996 and 2020; such long time series in fecundity are rarely seen in the literature. Mean potential fecundity and mean relative fecundity were 36000 oocytes per female and 78.17 oocytes/gram female respectively. These results are in accordance with the fecundity reported for *S. mentella* in the Irminger Sea (Saborido-Rey et al. 2015). Our study shows annual changes in potential fecundity between several years of the time series, as other reported in species of the genus *Sebastes* (Beyer et al. 2015).

We have shown that larger, older and better-conditioned fish produced more offspring in both absolute and relative terms than smaller individuals. Therefore, SSB may not be an accurate metric for the reproductive potential of stocks with a different demographic composition. The relative fecundity-age relationship suggests that there is a significant effect of repeat spawners in *S. fasciatus* stocks and highlights the importance of maintaining a strong length/age population structure. Similar results have been reported in several species, such as cod (Blanchard et al. 2003, Yoneda and Wrigth. 2004, Mion et al. 2018). We have also shown significant variation in fecundity between years. It is well known that fecundity, like many other life-history traits, is highly variable between stocks, geographic areas and/or years (Kraus et al. 2000, Marteinsdottir and Begg 2002, McElroy et al. 2013). Nevertheless, fecundity is still mostly ignored in the monitoring programmes. As a consequence, population egg production is rarely estimated for assessment purposes, or if estimated a constant fecundity-at-length or at-age relationship is used.

An increase in potential fecundity with female size was observed in other *Sebastes* species, including *Sebastes melanops, S. goodei, S. entomelas, S. flavidus* and *S. atrovirens* (Berkeley et al. 2004, Sogard et al. 2008, Dick 2009). However, our results show an increase in reproductive potential with size and age and the importance of using indexes other than SSB to measure stock reproductive potential. This finding has ben reported in *S. mentella* and *S. norvegicus* (Saborido-Rey et al 2015), where the exponent of the fecundity-length power function differed significantly from 3. It is important to highlight that we used females with ovaries showing advanced vitellogenic stages, as down-regulation of fecundity has been shown to drastically modify fecundity during the course of vitellogenesis (Saborido-Rey et al 2015). This process is likely driven by fish condition and environment factors (Murua et al. 2003, Armstrong and Witthames 2012).

In line with length and age, Fulton's condition factor and the GSI were only significantly related to potential but not to relative fecundity in our study. In addition, other studies have demonstrated that fish condition has a high influence on potential fecundity, with the result that fish in better nutritional status had a higher fecundity than fish in poorer conditions (Thorsen et al. 2006, Kennedy et al. 2007, Lambert 2008).

In this paper, explained variance of fecundity was high when K and GSI were included. The GLM model using fish length, condition factor and GSI as a dependent variable explained 75% of the variability in fecundity, in agreement with an earlier study carried out in cod (Lambert et al. 2008). Considering that the effect of the condition factor can be related to the fact that it intervenes in the final part of oocyte recruitment, i.e. during this phase fish will feed and therefore the condition factor will be a key maternal trait determining fish fecundity. However, a recent study (Beyer et al. 2015) showed that the hepatosomatic index (HSI) was significantly related in four studied species, whereas K was significant in one species. This finding suggests that a more accurate index of fish condition, such as HSI, lipid concentration or muscle water content and prey availability index (Kraus et al. 2002), should be included in future research into maternal effects on fecundity.

In this study, we found a positive relation between potential fecundity and bottom water temperature. Several studies have described water temperature as an important factor that can play a direct or indirect key role in fecundity variation in fish (Kjesbu et al. 1998, Kraus et al. 2000, Lambert et al. 2008). Moreover, bottom temperature, which has been increasing on the Flemish Cap since the 1990s (Colbourne et al. 2018), could generate changes in the way in which *S. fasciatus* allocates energy to reproduction during the whole time series. For example, Yoneda and Wright (2004) describe spatial and temporal fecundity variation as changes in energy allocation that influence maternal condition. The increasing temperature reported on the Flemish Cap may be one of the causes of the sharp increase in *S. fasciatus* abundance after several strong year-classes in 2002-2006 (González-Troncoso et al. 2022). Although recruitment was poor thereafter, it produced a shift in dominance on the Flemish Cap, where the traditionally more abundant *S. mentella* declined in favour of *S. fasciatus*, traditionally considerably less abundant. It is important to highlight that *S. mentella* has a distribution towards more northern and colder waters than *S. fasciatus*. Reproduction of other aquatic species can also be affected by variability of environmental factors such as sea surface temperature, which plays an important role in regulating brooding activity in crustaceans (Chang et al. 2021) and barnacles (Román et al. 2022) through the primary productivity.

Potential implications and future directions

Firstly, our findings provide for the first time an autodiametric calibration curve between oocyte mean diameter and ovarian oocyte density in *S. fasciatus*, which can be applied to estimate potential fecundity in North Atlantic for species of the genus *Sebastes*. Secondly, our study shows that potential fecundity varies interannually in *S. fasciatus*, probably a response of maternal effects of individual females to varying combinations of biological and environmental factors. Because maternal effects have been reported in a number of exploited species, we suggest that annual variations in fecundity should be monitored regularly. This would improve stock reproductive indexes and increase our understanding of the processes affecting reproductive success. Our results suggest that developing a better understanding of how maternal effects impact on offspring quality may help to understand recruitment processes, enhance stock assessment models, and ultimately improve our capacity to achieve a sustainable fisheries management.

ACKNOWLEDGEMENTS

This study was funded by grant IN606A 2017/4 funded by the Regional Government of Galicia (Xunta de Galicia), Spain and by the EU Data Collection Framework (European Maritime and Fisheries Fund). The authors would like to thank the editor and reviewers for their comments. We thank our colleagues at the IIM and the IEO who collaborated in the biological sampling onboard research vessels from 1996 and especially in 2016.

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SUPPLEMENTARY MATERIAL

Table S1. – Selection of random effects for GLMM fitted with potential fecundity as a dependent variable. First, optimal random effects were tested. The covariates in all models (i.e. fixed structure) are the maternal traits length/age, , condition factor (K), gonadosomatic index (GSI) and sea bottom temperature.

Model	Fixed effects	Random effects	AIC	BIC	logLik	P-value
1	Length, K, GSI, Btm temperature	Year	3860.1	3882.6	–1923.0	0.2532
2	Length, K, GSI, Btm temperature	Year and Haul	3860.8	3886.6	–1922.4	
3	Age, K, GSI, Btm temperature	Year	3769.4	3791.7	–1877.7	
4	Age, K, GSI, Btm temperature	Year and Haul	3761.4	3786.9	–1872.7	<0.001

Table S2. – Selection of random effects with potential fecundity as a dependent variable. First, optimal random effects were tested AIC, Akaike information criterion. Note: The covariates in all these models (i.e. the fixed structure) are the fork length, condition factor (K), gonadosomatic index (GSI) and bottom temperature. The ΔAIC of random intercept and slope model is lower compared with random intercepts. However, the likelihood ratio test was performed to compare models.

Model	Random effects	Correlation	Parameters	AIC	ΔAIC
1	Year intercept and bottom temperature slope by year	None	10	3852.178	0
2	Intercept varying between Year and Haul	None	8	3916.77	71.72

Table S3. Summary of the multiple regression models for potential fecundity against length and interannual variation (years) of *S. fasciatus* on the Flemish Cap bank. GLM NB, negative binomial generalized linear.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(>lzl)	Post hoc Tukey HSD test																		
GLM NB Potential fecundity	**α**	**0.62**	6.340897	0.222047	28.557	**<0.001**		1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019
	Length		0.122727	0.006775	18.116	**<0.001**	1996																			
	1997		0.366615	0.14684	2.497	**<0.05**	1997	0.5864																		
	1998		0.073197	0.195804	0.374	0.708533	1998	1	0.9964																	
	1999		0.353864	0.154717	2.287	**<0.05**	1999	0.7438	1	0.9986																
	2000		0.458608	0.138183	3.319	**<0.001**	2000	0.1001	1	0.9175	1															
	2001		0.324362	0.121439	2.671	**<0.01**	2001	0.45	1	0.9983	1	0.9999														
	2002		0.155521	0.211627	0.735	0.46241	2002	1	1	1	1	0.9971	1													
	2004		0.194977	0.143856	1.355	0.175303	2004	0.9987	0.9999	1	1	0.9431	1	1												
	2005		0.235417	0.119544	1.969	**<0.05**	2005	0.9151	1	1	1	0.9317	1	1	1											
	2006		0.181792	0.146795	1.238	0.215567	2006	0.9996	0.9997	1	1	0.9335	0.9999	1	1	1										
	2008		-0.065257	0.194633	-0.335	0.737413	2008	1	0.8166	1	0.8812	0.4011	0.8297	1	0.999	0.9827	0.9996									
	2010		0.710836	0.173143	4.105	**<0.001**	2010	**<0.01**	0.926	0.3023	0.9249	0.9955	0.624	0.6866	0.2605	0.2081	0.2477	**<0.05**								
	2011		0.1821	0.238438	0.764	0.445034	2011	1	1	1	1	0.9998	1	1	1	1	1	1	0.8806							
	2013		0.24921	0.145613	1.711	0.086997	2013	0.9779	1	1	1	0.995	1	1	1	1	1	0.9896	0.4781	1						
	2014		0.190639	0.148449	1.284	0.19907	2014	0.9994	0.9999	1	1	0.9435	1	1	1	1	1	0.9993	0.2726	1	1					
	2015		-0.075086	0.169813	-0.442	0.65837	2015	1	0.5489	1	0.6688	0.1103	0.5179	1	0.9907	0.8878	0.9963	1	**<0.01**	1	0.9298	0.9925				
	2016		0.055175	0.129799	0.425	0.670775	2016	1	0.7361	1	0.867	0.1195	0.6011	1	1	0.9796	1	1	**<0.01**	1	0.9961	1	1			
	2018		0.054424	0.120708	0.451	0.652079	2018	1	0.609	1	0.7875	**<0.05**	0.3842	1	0.9999	0.9351	1	1	**<0.01**	1	0.9889	0.9999	1	1		
	2019		0.039704	0.144431	0.275	0.783391	2019	1	0.8029	1	0.895	0.1845	0.7658	1	1	0.9906	1	1	**<0.05**	1	0.9961	1	1	1	1	
	2020		0.241787	0.142364	1.698	0.089438	2020	0.9796	1	1	1	0.9886	1	1	1	1	1	0.9907	0.4066	1	1	1	0.9258	0.9962	0.9875	0.9958

Table S4. Summary of the multiple regression models for potential fecundity against age and interannual variation (years) of *S. fasciatus* on the Flemish Cap bank. GLM NB, negative binomial generalized linear model.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(>|z|)	**Post hoc Test TukeyHSD**																			
GLM NB Potential fecundity	**α**	**0.61**	8.999869	0.114758	78.425	<0.001		1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019
	Age		0.111031	0.006379	17.407	<0.001	1996																			
	1997		0.232985	0.153979	1.513	0.1303	1997	0.9946																		
	1998		-0.342318	0.197644	-1.732	0.0833	1998	0.9749	0.3556																	
	1999		0.096701	0.158439	0.61	0.5416	1999	1	1	0.8563																
	2000		0.35734	0.141687	2.522	<0.05	2000	0.5665	1	0.0472	0.9791															
	2001		-0.065619	0.127014	-0.517	0.6054	2001	1	0.8079	0.9956	0.9999	0.0583														
	2002		-0.357145	0.216111	-1.653	0.0984	2002	0.9849	0.4551	1	0.894	0.0868	0.9973													
	2004		-0.127733	0.164081	-0.778	0.4363	2004	1	0.8501	1	0.9993	0.1961	1	1												
	2005		-0.205216	0.124054	-1.654	0.0981	2005	0.9847	0.1052	1	0.8033	<0.001	0.9981	1	1											
	2006		-0.193367	0.150191	-1.287	0.1979	2006	0.9993	0.4337	1	0.9658	<0.05	1	1	1	1										
	2008		-0.280005	0.198942	-1.407	0.1593	2008	0.9978	0.5785	1	0.9602	0.1126	0.9999	1	1	1	1									
	2010		0.71477	0.176272	4.055	<0.001	2010	<0.01	0.4841	<0.001	0.1042	0.8706	<0.001	<0.001	<0.01	<.0001	<0.001	<0.01								
	2011		0.13418	0.24261	0.553	0.5802	2011	1	1	0.9777	1	1	1	0.98	1	0.9958	0.9989	0.9953	0.7905							
	2013		-0.023449	0.151732	-0.155	0.8772	2013	1	0.9867	0.9919	1	0.4446	1	0.9937	1	0.9969	0.9999	0.9994	<0.01	1						
	2014		0.007224	0.153278	0.047	0.9624	2014	1	0.9976	0.9787	1	0.6505	1	0.9841	1	0.9852	0.9993	0.9975	0.0143	1	1					
	2015		-0.068408	0.17366	-0.394	0.6936	2015	1	0.9803	0.9996	1	0.5198	1	0.9996	1	1	1	1	0.0118	1	1	1				
	2016		-0.26184	0.145587	-1.799	0.0721	2016	0.9632	0.1171	1	0.7322	<0.001	0.9911	1	1	1	1	1	<.0001	0.9852	0.9843	0.9561	0.9998			
	2018		-0.195491	0.12706	-1.539	0.1239	2018	0.9933	0.1348	1	0.8472	<0.001	0.9994	1	1	1	1	1	<.0001	0.9971	0.9981	0.9902	1	1		
	2019		-0.149036	0.150588	-0.99	0.3223	2019	1	0.6043	1	0.9925	<0.05	1	1	1	1	1	1	<0.001	0.9998	1	1	1	1	1	
	2020		0.170095	0.146018	1.165	0.2441	2020	0.9998	1	0.5308	1	0.9985	0.9407	0.6135	0.95	0.1628	0.624	0.7413	0.1765	1	0.9988	0.9999	0.9972	0.1732	0.1774	0.7412

Table S5. – Summary of the multiple regression models for relative fecundity against length and interannual variation (years) of S. fasciatus in Flemish Cap bank. GLM NB, negative binomial generalized linear model.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(>|z|)		Post hoc Tukey HSD test																		
GLM NB Relative fecundity	*α*	**0.22**	3.004153	0.216123	13.9	<0.001		1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019
	Length		0.034865	0.006489	5.373	**<0.001**	1996																			
	1997		0.32001	0.142844	2.24	**<0.05**	1997	0.7753																		
	1998		0.081475	0.191604	0.425	0.67067	1998	1	0.9996																	
	1999		0.42751	0.149608	2.858	**<0.01**	1999	0.3167	1	0.9734																
	2000		0.439153	0.134197	3.272	**<0.01**	2000	0.1143	1	0.9397	1															
	2001		0.3693	0.119615	3.087	**<0.01**	2001	0.1872	1	0.9862	1	1														
	2002		0.191255	0.204729	0.934	0.35021	2002	1	1	1	0.9999	0.9996	1													
	2004		0.195788	0.14048	1.394	0.1634	2004	0.9981	1	1	0.9921	0.9549	0.9964	1												
	2005		0.276552	0.117999	2.344	**<0.05**	2005	0.7036	1	0.9999	0.9998	0.9957	1	1	1											
	2006		0.19001	0.143549	1.324	0.18562	2006	0.999	1	1	0.9919	0.9593	0.9962	1	1	1										
	2008		0.02129	0.18925	0.112	0.91043	2008	1	0.9915	1	0.8667	0.7468	0.9022	1	1	0.9959	1									
	2010		0.743227	0.165104	4.502	**<0.001**	2010	**<0.001**	0.5465	0.1649	0.9545	0.9294	0.5517	0.596	0.0946	0.1384	0.1033	0.0603								
	2011		0.170889	0.228625	0.747	0.45478	2011	1	1	1	0.9999	0.9997	1	1	1	1	1	1	0.6958							
	2013		0.177755	0.141809	1.253	0.21003	2013	0.9995	1	1	0.9822	0.9084	0.9905	1	1	1	1	1	0.0682	1						
	2014		0.165809	0.144438	1.148	0.25099	2014	0.9999	1	1	0.9757	0.8904	0.9858	1	1	1	1	1	0.0636	1	1					
	2015		-0.067009	0.165361	-0.405	0.68531	2015	1	0.7113	1	0.293	0.1153	0.2624	0.9999	0.9889	0.6994	0.9939	1	**<0.001**	1	0.9942	0.9975				
	2016		0.180599	0.13871	1.302	0.19292	2016	0.9992	1	1	0.9809	0.9012	0.9885	1	1	1	1	1	0.0617	1	1	1	0.9925			
	2018		0.062649	0.118983	0.527	0.59851	2018	1	0.8342	1	0.311	**<0.05**	0.107	1	0.9999	0.6855	1	1	**<0.001**	1	1	1	1	1		
	2019		-0.017752	0.140948	-0.126	0.89977	2019	1	0.6719	1	0.2193	**<0.05**	0.1335	1	0.9933	0.5875	0.9971	1	0.0005	1	0.997	0.999	1	0.9957	1	
	2020		0.183641	0.138597	1.325	0.18517	2020	0.999	1	1	0.9823	0.8973	0.9907	1	1	1	1	1	0.0612	1	1	1	0.989	1	0.9999	0.9926

Table S6. – Summary of the multiple regression models for relative fecundity against age and interannual variation (years) of *S. fasciatus* on the Flemish Cap bank. GLM NB, negative binomial generalized linear model.

Response variable	Variable	R2	Parameter estimate	SE	z value	Pr(>|z|)	Post hoc Test TukeyHSD																			
GLM NB Relative fecundity	**α**	**0.34**	3.609169	0.1034872	34.875	**<0.001**		1996	1997	1998	1999	2000	2001	2002	2004	2005	2006	2008	2010	2011	2013	2014	2015	2016	2018	2019
	Age		0.0493357	0.0054966	8.976	**<0.001**	1996																			
	1997		0.2150357	0.1351951	1.591	0.11171	1997	0.9902																		
	1998		-0.0407179	0.1752052	-0.232	0.81623	1998	1	0.9973																	
	1999		0.2960636	0.1384885	2.138	**<0.05**	1999	0.8373	1	0.9503																
	2000		0.3222687	0.1243912	2.591	**<0.01**	2000	0.5122	1	0.8457	1															
	2001		0.2021966	0.1129256	1.791	0.07337	2001	0.9648	1	0.9954	1	0.9998														
	2002		-0.0319896	0.1893652	-0.169	0.86585	2002	1	0.9993	1	0.98	0.9271	0.999													
	2004		0.0848131	0.1439403	0.589	0.55571	2004	1	1	1	0.9976	0.9705	1	1												
	2005		0.072853	0.1106353	0.658	0.51022	2005	1	0.9995	1	0.9364	0.5641	0.995	1	1											
	2006		0.027246	0.1329194	0.205	0.83759	2006	1	0.9983	1	0.9285	0.6846	0.9937	1	1	1										
	2008		-0.0910626	0.1751269	-0.52	0.60308	2008	1	0.9755	1	0.8263	0.6161	0.958	1	1	1	1									
	2010		0.6991852	0.151583	4.613	**<0.001**	2010	**<0.001**	0.1671	**<0.05**	0.5345	0.4987	**<0.05**	**<0.05**	**<0.05**	**<0.001**	**<0.001**	<0.001								
	2011		0.0835729	0.2104391	0.397	0.69127	2011	1	1	1	1	0.9998	1	1	1	1	1	1	0.3842							
	2013		-0.0265995	0.133847	-0.199	0.84247	2013	1	0.9639	1	0.7002	0.3061	0.8885	1	1	1	1	1	**<0.001**	1						
	2014		-0.0008873	0.1349319	-0.007	0.99475	2014	1	0.9907	1	0.8399	0.4958	0.968	1	1	1	1	1	**<0.001**	1	1					
	2015		-0.1920493	0.1533378	-1.252	0.2104	2015	0.9995	0.4671	1	0.1697	**<0.05**	0.2738	1	0.9753	0.8946	0.997	1	**<0.001**	0.9996	0.9999	0.9994				
	2016		-0.0404102	0.1310346	-0.308	0.75778	2016	1	0.9274	1	0.5898	0.2039	0.7903	1	1	1	1	1	**<0.001**	1	1	1	1			
	2018		-0.1300531	0.1132962	-1.148	0.25101	2018	0.9999	0.2212	1	**<0.05**	**<0.001**	**<0.05**	1	0.9724	0.5959	0.9979	1	**<0.001**	0.9999	1	0.9998	1	1		
	2019		-0.2279436	0.1329839	-1.714	0.08652	2019	0.9775	0.0939	1	**<0.05**	**<0.001**	**<0.05**	1	0.7757	0.316	0.9216	1	**<0.001**	0.9951	0.9878	0.9666	1	0.9935	1	
	2020		0.0453156	0.1286718	0.352	0.7247	2020	1	0.9992	1	0.9414	0.6756	0.9962	1	1	1	1	1	**<0.01**	1	1	1	0.9848	1	0.9741	0.7477