

Fisheries

Spawning biomass of Sardine, *Sardinops sagax*, in waters off South Australia in 2024



Grammer, G. L., Ivey, A. R. and Cheesman, C.

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PO Box 120 Henley Beach SA 5022

November 2024

Report to PIRSA Fisheries and Aquaculture

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Drs Vittoria Cipriani and Adrian Linnane reviewed and provided comments on a draft of the report. The report was approved for publication by Dr Stephen Mayfield.

EXECUTIVE SUMMARY

This report provides an estimate of the spawning biomass of Sardine, *Sardinops sagax*, in waters off South Australia during 2024. The estimate of spawning biomass obtained using the Daily Egg Production Method (DEPM) is the key performance indicator for determining the status of the southern stock of Australian Sardine.

An ichthyoplankton survey was conducted during February to April 2024. The survey area included the new sites added in 2023 to the south-east of Kangaroo Island and extended transects in the central Great Australia Bight (GAB), as well as the additional sites added in 2020. The total survey area was 137,679 km². Live Sardine eggs were collected at 173 of 405 (42.7%) sites. The total spawning area (*A*) in 2024 was 61,471 km².

Mean daily egg production (P_0 , 95% CI) was 86.7 (78.7–95.5) eggs.day⁻¹.m⁻². P_0 was estimated using the linear version of the exponential mortality model and all data combined from 1998 to 2024.

Estimates of adult parameters (95% CI) calculated from all data obtained between 1998 and 2024 were: sex ratio (*R*): 0.53 (0.50–0.56); spawning fraction (*S*): 0.111 (0.100–0.122); and relative fecundity (F'): 308.4 (307.2–309.6) eggs.g⁻¹.

Sensitivity analyses showed the effects of inter-annual variability in parameters (i.e. P_0 , *R*, *S* and F') on the estimate of spawning biomass for 2024 and demonstrated the benefits of using parameter estimates obtained from combined current and historical data to estimate spawning biomass.

The estimate of spawning biomass (95% CI) of Sardine for 2024 was 291,731 (248,230–335,232) t, which was above the upper target reference point of 200,000 t set in the harvest strategy for the South Australian Sardine Fishery. On this basis, the southern stock of Australian Sardine is classified as **Sustainable**. This classification is consistent with the findings of the spawning biomass report for 2023, the stock assessment report for 2023 and the most recent report in the Status of Australian Fish Stocks (2024).

Keywords: Sardine, Spawning Biomass, South Australia, Daily Egg Production Method

1. INTRODUCTION

1.1. Daily Egg Production Method

The Daily Egg Production Method (DEPM) was developed for stock assessment of the Northern Anchovy (*Engraulis mordax*; Parker 1980, Lasker 1985), and has been applied to more than 20 species of small to medium-sized pelagic fishes (e.g. Stratoudakis et al. 2006, Dimmlich et al. 2009, Neira et al. 2009, Grammer et al. 2023). The method is widely used in coastal fisheries because it is often the most practical option available for assessment of pelagic species (Ward et al. 1998).

The DEPM relies on the premise that spawning biomass can be calculated by dividing the mean number of pelagic eggs produced per day throughout the spawning area (i.e. total daily egg production) by the mean number of eggs produced per unit mass of adult fish (i.e. mean daily fecundity, Parker 1980, Lasker 1985). Total daily egg production is the product of mean daily egg production (P_0) and total spawning area (A). Mean daily fecundity is the product of mean sex ratio (by weight, R), mean spawning fraction (proportion of mature females spawning each day/night, S) and mean relative fecundity (number of eggs produced per gram of total female weight (\hat{F}/W), F'). Spawning biomass (SB) is calculated according to the equation:

$$SB = P_0 * A / (R * S * F') \quad \text{Equation 1}$$

The DEPM, as applied to Sardine off South Australia, underwent a comprehensive review in 2021 (Ward et al. 2021). The review reanalysed data collected between 1995 and 2019 for South Australian Sardine and identified several ways to increase the precision of estimates of spawning biomass: 1) increase the precision of total daily egg production ($P_0 * A$) by using the estimate of P_0 obtained from all historical data rather than annual estimates of P_0 ; 2) continue to use the log-linear model to estimate P_0 for the southern stock of Australian Sardine; 3) increase the precision of mean daily fecundity ($R * S * F'$) by using the estimates of sex ratio (R), spawning fraction (S) and relative fecundity (F') obtained from all historical data rather than annual estimates; 4) combine batch fecundity (F) and female weight (W) into a single parameter: relative fecundity ($F' = \hat{F}/W$). These recommendations were implemented in 2022 and again for this report to ensure that estimates of spawning biomass are, and continue to be, as accurate and precise as possible.

1.2. Rationale, objective and approach

The DEPM has been used to estimate the spawning biomass of Sardine in South Australian waters since 1995 (Ward et al. 1998, 2011, 2021). The estimate of spawning biomass

obtained using the DEPM is the key performance indicator for determining the status of the southern stock of Australian Sardine (PIRSA 2023). The objective of this report is to estimate the spawning biomass of Sardine in waters off South Australia in 2024. Annual estimates of P_0 and A were obtained from an ichthyoplankton survey conducted in 2024. In 2024, dedicated sampling for adults occurred alongside the ichthyoplankton survey. Adult parameters were derived from all adult samples collected off South Australia between 1998 and 2024; an estimate of P_0 was also obtained from all current and historical data combined. Sensitivity analyses were undertaken to evaluate the effects of variability in estimates of individual parameters on the uncertainty associated with the estimate of spawning biomass for 2024.

2. METHODS

2.1. Study area and biophysical variables

2.1.1. Study area

An ichthyoplankton survey and sampling for adult Sardine were conducted from the *RV Ngerin* in shelf and gulf waters of South Australia during 2–13 February, 1–12 March and 31 March–6 April 2024 (Fig. 1). Plankton samples were collected at a total of 405 sites on 39 transects between Kingston and the Head of Bight (Fig. 1). The 405 sites sampled in 2024 included the new sites added in 2023 to the south-east of Kangaroo Island and extended the transects in the GAB, as well as the additional sites added in 2020 (Fig. 1). These additional sites were added in response to the expansion of the fishery into this region and recent observations that Sardine eggs had become more common in the area (Ward *et al.* 2020a; Fig. 1). Adult samples were collected opportunistically at selected sites throughout the survey area (Fig. 1).

An adaptive approach to egg sampling has been applied since 2014 to ensure that each survey covers as much of the spawning area as possible. Adaptive sampling was implemented in response to the incomplete coverage of the spawning area in 2013 (see Grammer *et al.* 2021). Under the protocol, extra samples are taken at sites located outside the area covered by the pre-determined sampling sites (Fig. 1). Decisions about whether (or not) to take extra samples are based on the presence/absence of eggs in samples taken using the Continuous Underway Fish Egg Sampler (CUFES) at sites located on the seaward end of transects. Sampling at additional sites continues until Sardine eggs are not present in the CUFES samples. In 2024, five extra sites were sampled on the seaward ends of four transects.

2.1.2. Water temperature and primary and secondary production

At each sampling site (Fig. 1), a *Sea-Bird* Conductivity-Temperature-Depth (CTD) recorder fitted with a fluorometer (attached to the bottom of the plankton sampling gear; see next section) was lowered to a depth of 70 m, or to 10 m from the seafloor in waters less than 80 m deep. Estimates of water temperature and fluorescence at the surface were extracted from each CTD profile. At sites where water temperature was not available, the average temperature of the adjacent stations was applied. Fluorescence is an indicator of primary production and gives an un-calibrated measure of chlorophyll-a concentration ($\mu\text{g}\cdot\text{L}^{-1}$). Spatial plots of sea surface temperature (SST), Salinity and chlorophyll-a concentration were prepared using minimum curvature algorithms in ArcGIS Pro® (Ver. 12).

Common taxa of zooplankton and phytoplankton were recorded for each sample and scored as absent, present, or abundant (i.e. a dominant taxon in sample) to better understand the distribution of these groups across the survey area relative to sardine eggs. These data were analysed and presented using a kernel density distribution in ArcGIS Pro®.

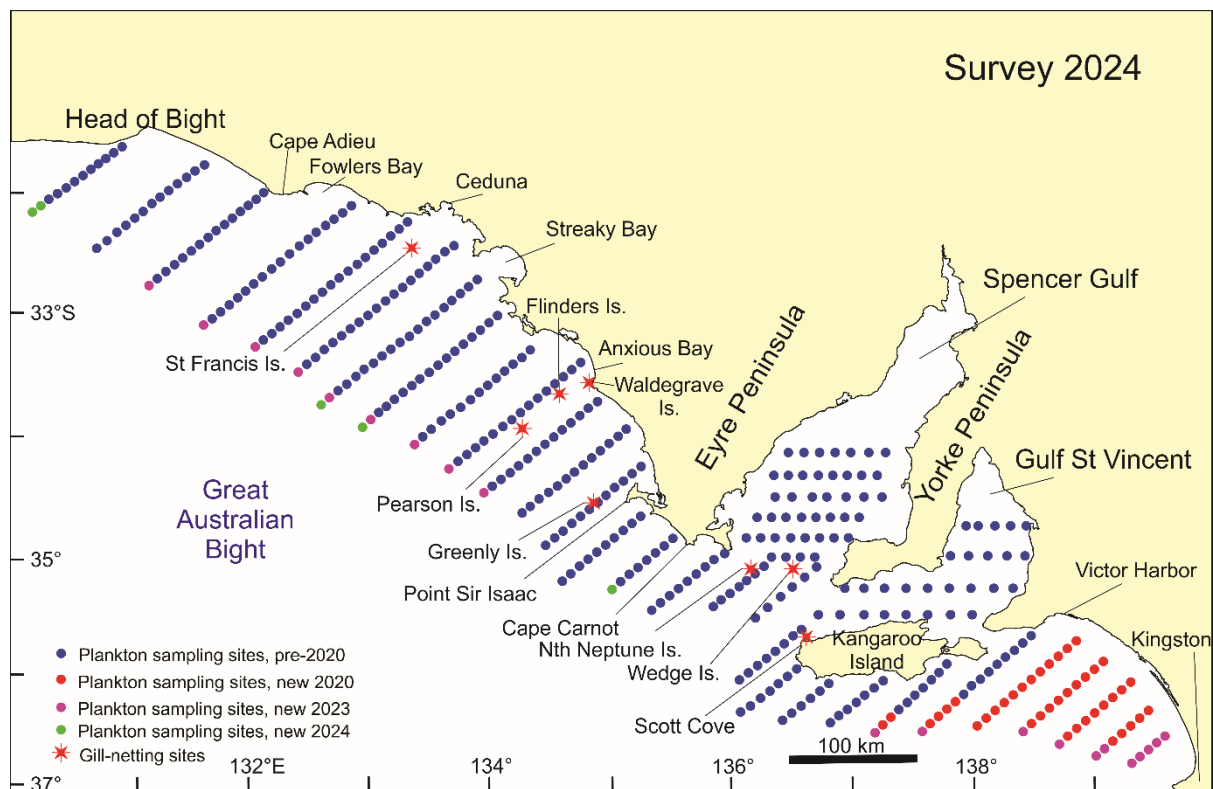


Figure 1. Map of South Australia showing sites where plankton samples were collected during 2024 and where adult samples were collected with a gillnet.

2.2. Mean daily egg production and spawning area

2.2.1. Plankton sampling

Plankton samples were collected at each site using paired Californian Vertical Egg Tow (CalVET) plankton nets. Each CalVET net had an internal diameter of 0.3 m, length of 1.8 m, 330 μm mesh and plastic removable cod-ends. The CTD recorder (see previous section) was attached below the cod-ends of the CalVET nets, and provided weight for the plankton sampling gear while collecting a CTD profile for the water column. During each tow the CalVET nets were deployed to a depth of 70 m or to 10 m of the seabed at depths <80 m. The nets were retrieved vertically at a speed of $\sim 1 \text{ m}\cdot\text{s}^{-1}$. *General Oceanics* 2030 flow-meters and factory calibration coefficients were used to estimate the distance travelled by the net during each tow. Where there was a discrepancy of more than 5% between flow-meters, the relationship between wire length and flow-meter units was used to determine which was correct and that value was used for both nets. Upon retrieval of the nets, the samples from the two cod-ends were rinsed with seawater, combined into a 1 L container, and fixed in 5% buffered formaldehyde and seawater solution.

2.2.2. Laboratory analysis

Sardine eggs and larvae were identified in each plankton sample using published descriptions (Neira *et al.* 1998, White and Fletcher 1998). Eggs were staged based on descriptions in White and Fletcher (1998). Total counts of eggs of each developmental stage in each sample were recorded. Eggs in the first and last stages were excluded from the statistical analyses as they can be under- and over-represented in samples, respectively (Ward *et al.* 2018).

2.2.3. Egg ageing and treatment of zero count egg samples

The development rate of Sardine eggs is dependent on ambient water temperature (Picquelle and Stauffer 1985, Pauly and Pullin 1988). Based on the temperature data from the CTD, egg samples were allocated to one of three temperature bins that covered the range of temperatures encountered during surveys (14–18°C, 18–22°C, and 22–26°C). The temperature bins were comparable to those used by Le Clus and Malan (1995) to describe the developmental rates of Sardine eggs. These published development rates were used to assign a mean age to each egg in each sample (Ward *et al.* 2018).

After each egg was assigned an age, the eggs in each sample were grouped into daily cohorts. This was done because a sample usually included eggs spawned on more than one night. The total number of eggs in each daily cohort was calculated by summing the number

of eggs of each stage assigned to a spawning day (i.e. day 0, day 1, day 2). The age of a daily cohort was calculated from the average age of each stage within the daily cohort, weighted by the number of eggs in each stage.

Samples with eggs could contain several possible combinations of daily cohorts depending on water temperature, spawning time (peak around 2:00 am) and sampling time. Zero counts were allocated for daily cohorts where the cohort was expected to be present but was not found within the sample (Ward *et al.* 2018). Samples with no eggs were excluded from the analyses and not considered part of the spawning area.

2.2.4. Egg density

The number of eggs of each day class under one square metre of water (P_t) was estimated at each site according to Equation 2:

$$P_t = \frac{C \cdot D}{V} \quad \text{Equation 2}$$

Where C is the number of eggs of each age in each sample, V is the volume filtered (m^3), and D is the depth (m) to which the net was deployed (Smith and Richardson 1977). Plots of egg distribution and abundance were prepared using ArcGIS Pro® (Ver. 10.8.1).

2.2.5. Spawning area (A)

The spawning area (A , Lasker 1985, Somarakis *et al.* 2004) was estimated using the Voronoi natural neighbour method (Watson 1981). The survey area was divided into a series of contiguous polygons approximately centred on each site using the *deldir* package in the statistical program R (Fig. 2; R Core Team 2024, Turner 2023). The area represented by each site (km^2) was calculated. A was defined as the total area of the polygons where live Sardine eggs were present in the plankton sample (see Fletcher *et al.* 1996).

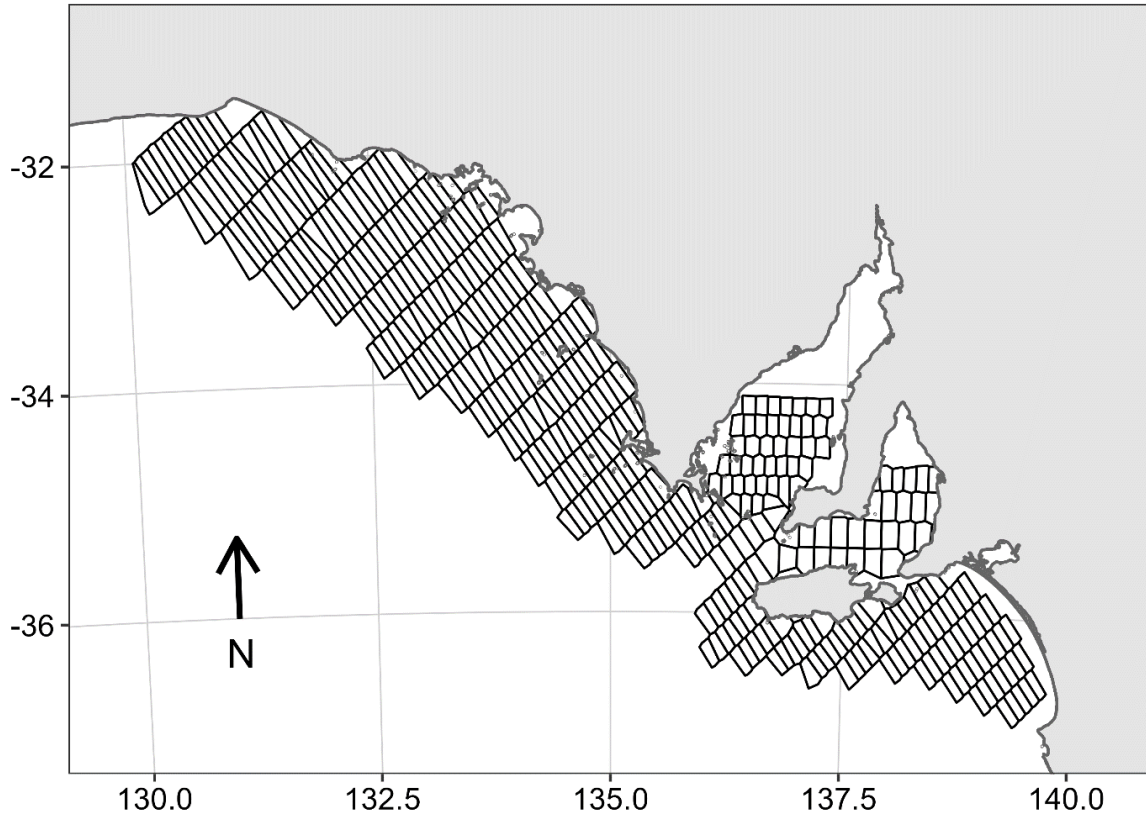


Figure 2. Voronoi nearest neighbour polygons used to estimate the total spawning area in 2024.

2.2.6. Mean daily egg production (P_0) and egg mortality (Z)

The underlying model used to calculate P_0 was the exponential egg mortality model (Equation 3) with a bias correction factor (Equation 4, the 'log-linear model'). The linear version of the exponential egg mortality model is:

$$\ln P_b = \ln(P_{i,t} + 1) - Zt, \quad \text{Equation 3}$$

where $P_{i,t}$ is the density of eggs of age t at site i and Z is the instantaneous rate of egg mortality.

Estimates of P_b obtained using the linear version of the exponential mortality model have a negative bias, therefore a bias correction factor was applied following the equation of Picquelle and Stauffer (1985):

$$P_0 = e^{(\ln P_b + \sigma^2/2)} - 1 \quad \text{Equation 4}$$

where, σ^2 is the variance of the estimate of biased mean daily egg production (P_b).

A generalised linear model (GLM) with a negative binomial error structure (NB1) was also used to estimate P_0 (Equation 5):

$$E[P_0] = g^{-1}(-zt + \varepsilon) \quad \text{Equation 5}$$

where $E[P_0]$ is the expected value of P_0 , g^{-1} is the inverse-link function, zt is the instantaneous rate of daily egg mortality at age t , and ε is the error term. The negative binomial error structure used is considered suitable for over-dispersed data, such as egg density by age (e.g. Ward *et al.* 2011, 2018, 2021). For NB1, variance increased linearly with the mean ($\sigma = \mu^*(1 + \mu + \varphi)$), where μ is the model estimate, σ is the model variance and φ is the over-dispersion parameter. The GLM used a log-link function (Wood 2006) and was fit using the *glmmTMB* package in R (Brooks *et al.* 2017).

Following the recommendations of Ward *et al.* (2021), the value of P_0 from the log-linear model was used to estimate spawning biomass for Sardine. P_0 was calculated using data collected solely in 2024, as well as with data from all years (combined) between 1998 and 2024. The all-years estimate of P_0 is considered more robust than the individual year estimate of P_0 , because sampling error within a year is greater than inter-annual variability of egg density and egg production (Ward *et al.* 2021).

2.3. Adult reproductive parameters

In 2024, dedicated sampling for adult Sardine occurred alongside the ichthyoplankton survey. Samples of adults were collected from the *RV Ngerin* opportunistically during the ichthyoplankton survey. Adult samples were also collected by the South Australian Sardine Industry Association (SASIA) from selected commercial vessels in their fleet during the same time period and sent to the South Australian Research and Development Institute (SARDI) Aquatic Sciences for processing and analyses.

Adult parameters used to estimate spawning biomass were derived from all adult samples of Sardine collected for DEPM surveys off South Australia between 1998 and 2018 (see Ward *et al.* 2021), combined with the samples collected in 2024 (both SARDI and commercial samples).

2.3.1. Sampling methods

From 1998 to 2024, fishery independent samples of mature Sardine were collected from sites located in the eastern Great Australian Bight, southern Spencer Gulf and Investigator Strait using a gillnet (Fig. 1). In the late afternoon, a dual frequency echo sounder (60 and 180 KHz) was used to search areas where schools of adult Sardine were known to aggregate. A gillnet comprised of three panels, each with a different multi-filament nylon

mesh size (*Double Diamond*: 210/4 ply meshes 25, 28 and 32 mm; Ward and McLeay 1998) was deployed from the port side of the *RV Ngerin* at protected locations where schools were encountered. Surface and sub-surface lights (150 W) were illuminated near the net after it was set. Net soak times varied from 15 minutes to 3 hours depending on the number of fish caught.

After the net was retrieved, fish were removed and dissected immediately. All Sardine collected were counted and sexed. Mature males and immature fish were frozen. Mature females were fixed in 10% buffered formaldehyde seawater solution.

Samples collected by SASIA in 2024 from commercial catches were taken from selected purse seine net-sets (i.e. where mature / spawning fish were likely to be encountered) during commercial fishing activity. The same sampling procedures were used as described above for the fishery independent samples, where the fish in each sample were dissected immediately, counted, sexed, and preserved or frozen. The samples were sent to SARDI Aquatic Sciences for all further processing and analyses.

2.3.2. Female weight (*W*) and Male weight

Mature females from each sample were removed from the formalin solution and weighed (± 0.01 g). Fixation in formalin has a negligible effect on fish weight (Lasker 1985). The mean weight of mature females in the population was calculated from the average of sample means weighted by proportional sample size:

$$W = \left[\overline{W}_i * \frac{n_i}{N} \right] \quad \text{Equation 5}$$

where, \overline{W}_i is the mean female weight of each sample i ; n is the number of fish in each sample and N is the total number of fish collected in all samples.

Mature males in each sample were thawed and weighed (± 0.01 g).

2.3.3. Sex ratio (*R*)

The mean sex ratio of mature individuals in the population was calculated from the average of sample means weighted by sample size:

$$R = \left[\overline{R}_i * \frac{n_i}{N} \right] \quad \text{Equation 6}$$

where, n is the number of fish in each sample, N is the total number of fish collected in all samples and \bar{R}_i is the mean sex ratio of each sample calculated from the equation:

$$\bar{R}_i = \frac{F}{(F + M)} \quad \text{Equation 7}$$

where, F and M are the respective total weights of mature females and males in each sample i .

2.3.4. Spawning fraction (S)

Ovaries of mature females were sectioned and stained with haematoxylin and eosin. Several sections from each ovary were examined to determine the presence/absence of post-ovulatory follicles (POFs). POFs were aged according to the criteria developed by Hunter and Goldberg (1980) and Hunter and Macewicz (1985). The spawning fraction of each sample was estimated as the mean proportion of females with hydrated oocytes plus day-0 POFs ($d0$) (assumed to be spawning or have spawned on the night of capture), day-1 POFs ($d1$) (assumed to have spawned the previous night) and day-2 POFs ($d2$) (assumed to have spawned two nights prior). The mean spawning fraction of the population was then calculated from the average of sample means weighted by proportional sample size:

$$S = \left[\bar{S}_i * \frac{n_i}{N} \right] \quad \text{Equation 8}$$

where, n is the number of fish in each sample, N is the total number of fish collected in all samples and \bar{S}_i is the mean spawning fraction of each sample calculated from the equation:

$$\bar{S}_i = \frac{[(d0 + d1 + d2POFs) / 3]}{n_i} \quad \text{Equation 9}$$

where, $d0$, $d1$ and $d2$ POFs are the number of mature females with POFs in each sample and n_i is the total number of females within a sample.

2.3.5. Batch fecundity (F)

Batch fecundity (F) was estimated from ovaries containing hydrated oocytes using the methods of Hunter and Macewicz (1985). Both ovaries were weighed and the number of hydrated oocytes in three weighed ovarian sub-sections counted. The total batch fecundity for each female was calculated by multiplying the mean number of oocytes per gram of

ovary segment by the total weight of the ovaries. Methods to estimate the batch fecundity for mature females without hydrated ovaries (\hat{F}) followed those outlined in Ward *et al.* (2021).

Relative Fecundity (F') was calculated by using the linear relationship of batch fecundity determined from all-years data (1998–2024) to estimate F and then dividing by the mean weight of all mature females collected (W).

2.4. Spawning biomass

Spawning biomass was calculated using the all-years estimate of P_0 (1998 to 2024) obtained from the log-linear model, spawning area (A) in 2024 and estimates of R , S and F' obtained from adult samples collected between 1998 and 2024.

The reliability of model fits, 95% confidence intervals (CIs) and coefficients of variation (CVs) for P_0 were estimated using bootstrap resampling methods with 10,000 iterations. Coefficients of variation and CIs for R , S and F' , were calculated from the all-years adult data. A ratio estimator was used calculate the variance for S , R , and F' (Rice 1995). The variance for the spawning biomass estimates were calculated by summing the squared CVs for each parameter and multiplying by the square of the estimate of spawning biomass (Parker 1985). Uncertainty estimates presented for all parameters are 95% CIs. Data analyses were done in the R programming environment (R Core Team 2024).

2.5. Sensitivity analysis

Sensitivity analyses were conducted to assess the effects of variations in the range of values obtained for each parameter in each year between 1998 and 2024 on the estimate of spawning biomass for 2024.

2.6. Quality assurance and quality control of data

All parameters used in the calculation of spawning biomass were computed independently in both the R programming environment and in Microsoft Excel. Physical and biological data were plotted and checked for inconsistencies and outliers. Discrepancies were corrected where necessary by checking against the datasheets recorded in the field and laboratory and re-examining the sample if required. All ichthyoplankton samples and histology slides are retained and archived at SARDI Aquatic Sciences.

3. RESULTS

3.1. Distribution and abundance of eggs

A total of 8,310 live Sardine eggs were collected at 173 of 405 sites (42.7%) on transects between Kingston and Head of Bight from February to April 2024 (Fig. 3). Sites with the highest egg densities were in southern Spencer Gulf, south of Head of Bight, and the inner GAB shelf off Ceduna. Eggs were also widespread throughout Investigator Strait and in the south and south-west region off Kangaroo Island.

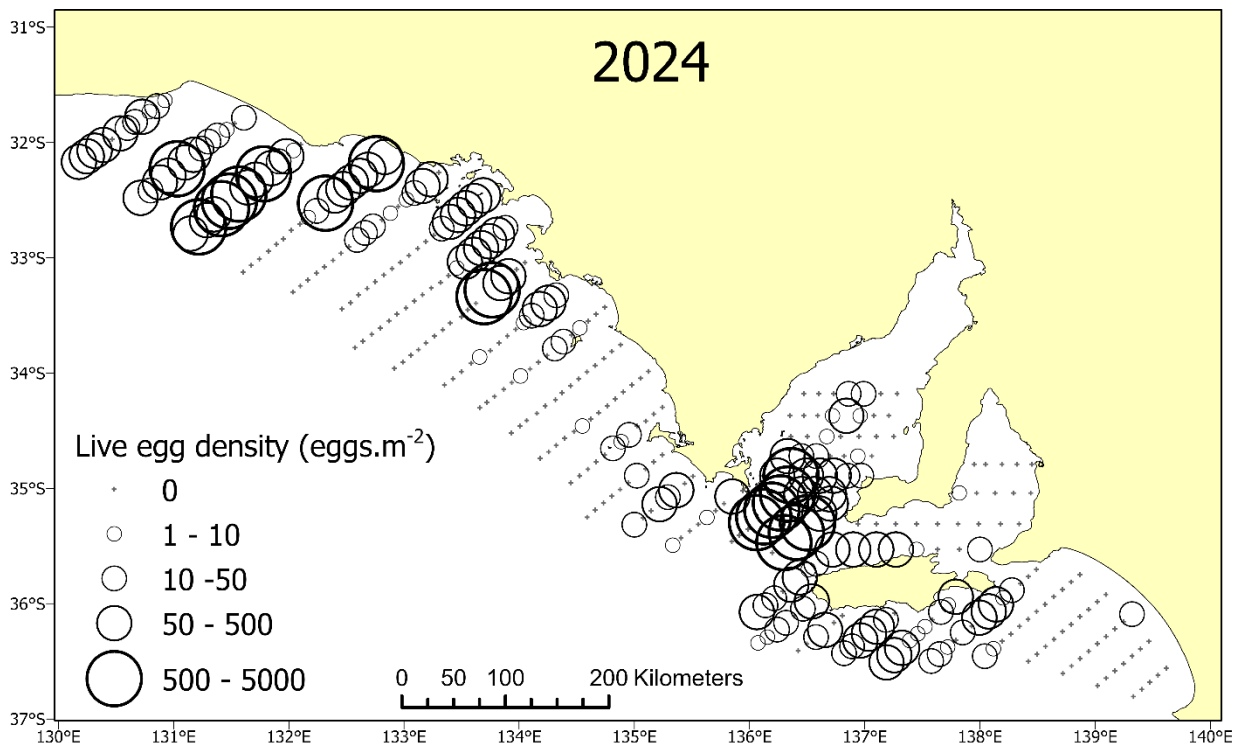


Figure 3. Densities of live Sardine eggs at sites sampled off South Australia from February to April 2024.

3.2. Biophysical variables

3.2.1. Sea surface temperature

Sea surface temperatures (SSTs) ranged from 13.1 to 22.5°C (Fig. 4) between February and April 2024. High SSTs (>20°C) were recorded in Spencer Gulf, Gulf St. Vincent and offshore in the central GAB. Cooler, upwelled water (<17°C) was widespread throughout the inner shelf region of the eastern GAB. Cooler water occurred south and west of Kangaroo Island but was less prevalent along the Bonney coast to the southeast of the survey area.

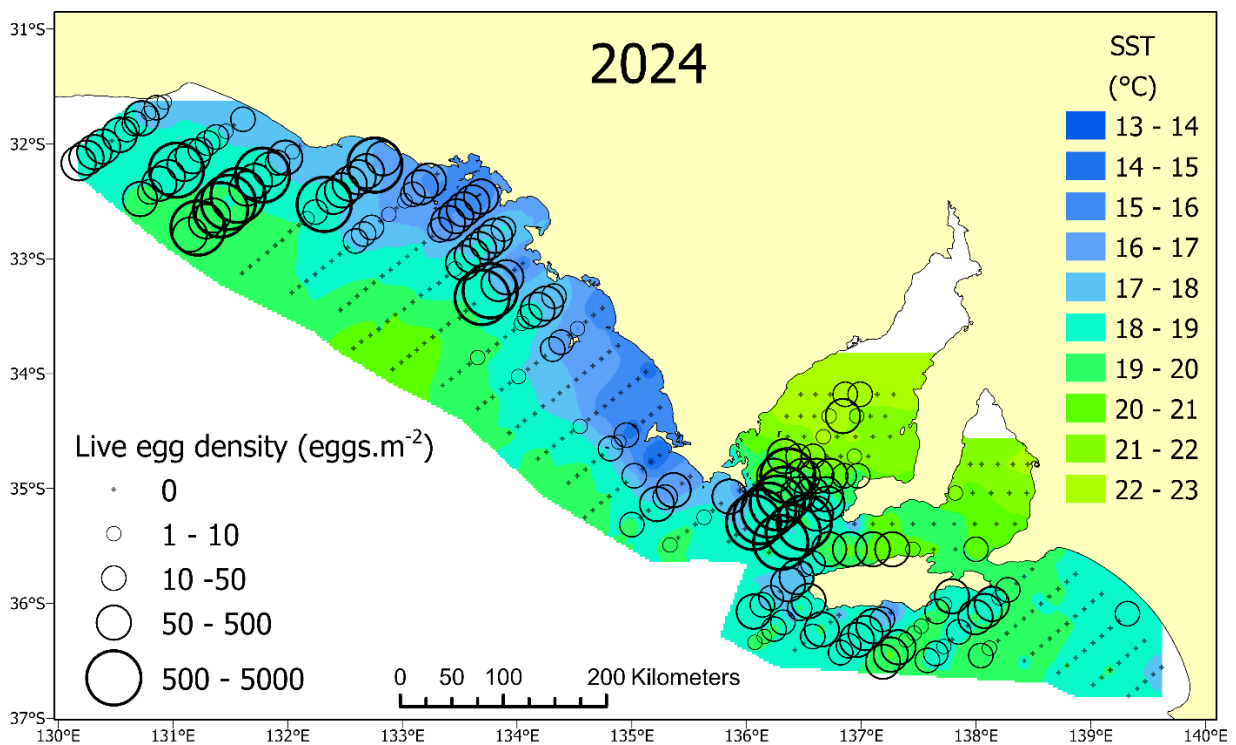


Figure 4. Sea surface temperatures overlaid with densities of live Sardine eggs at sites sampled off South Australia from February to April 2024.

3.2.2. Fluorescence

Surface chlorophyll-*a* concentration at each site ranged between 0 and $6.5 \mu\text{g.L}^{-1}$ (Fig. 5) between February and April 2024. The highest values were recorded in the coastal waters around Coffin Bay and extending northwest into the GAB. High fluorescence also occurred in waters around Streaky Bay, Ceduna and Vivonne Bay on Kangaroo Island. Relatively high fluorescence was also recorded in the near-shore waters of the central GAB, to the southwest of Kangaroo Island, and in the mouth of Spencer Gulf. The remainder of coastal and shelf waters mainly had chlorophyll-*a* concentrations $<1.0 \mu\text{g.L}^{-1}$.

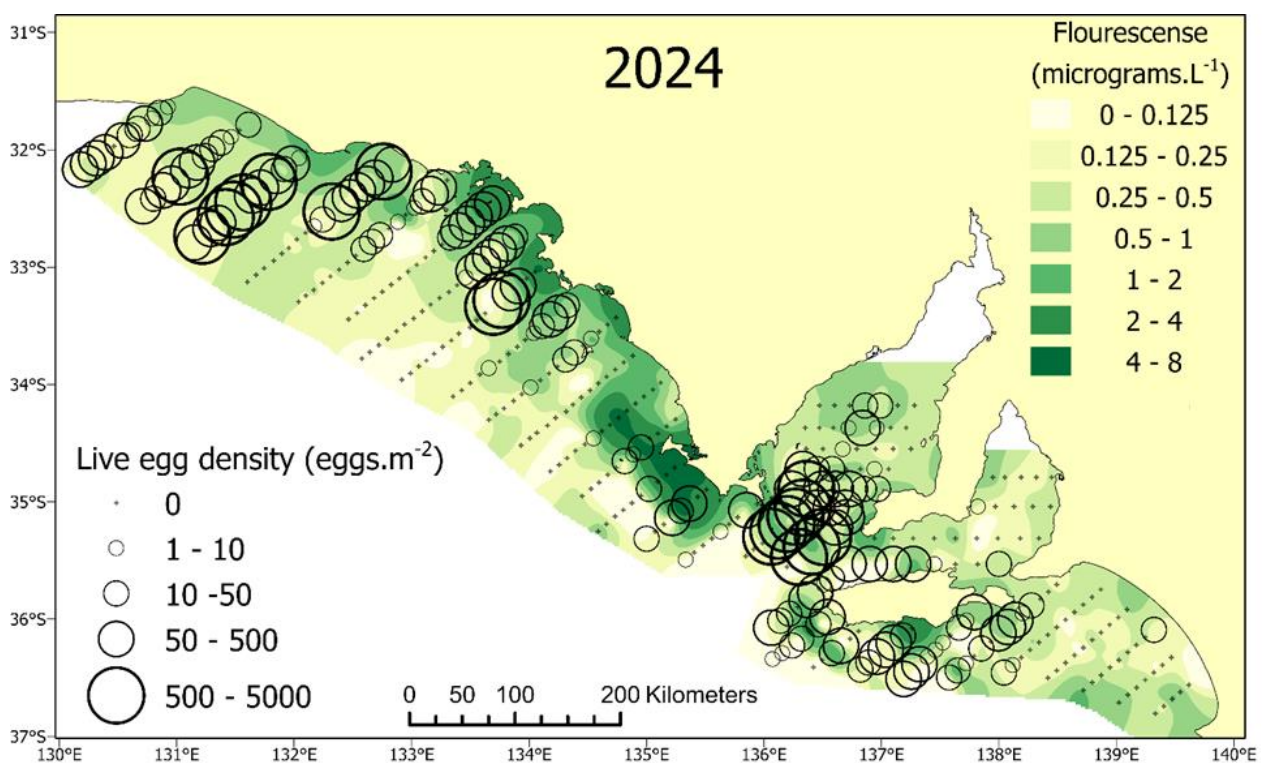


Figure 5. Surface concentration of chlorophyll-*a* overlaid with densities of live Sardine eggs at sites sampled from February to April 2024.

3.2.3. Distribution of common zooplankton and phytoplankton taxa

Common taxa of zooplankton and phytoplankton recorded from the survey area between February and April 2024 were copepods, salps, pteropods, cladocerans, diatoms and dinoflagellates (Fig. 6). Most taxa were abundant on the GAB shelf off the western Eyre Peninsula and in the mouth of Spencer Gulf. Copepods were also abundant southeast of Kangaroo Island. Salps were abundant on the GAB Shelf south of Ceduna and in the southeast of the survey near Kingston (Fig. 6).

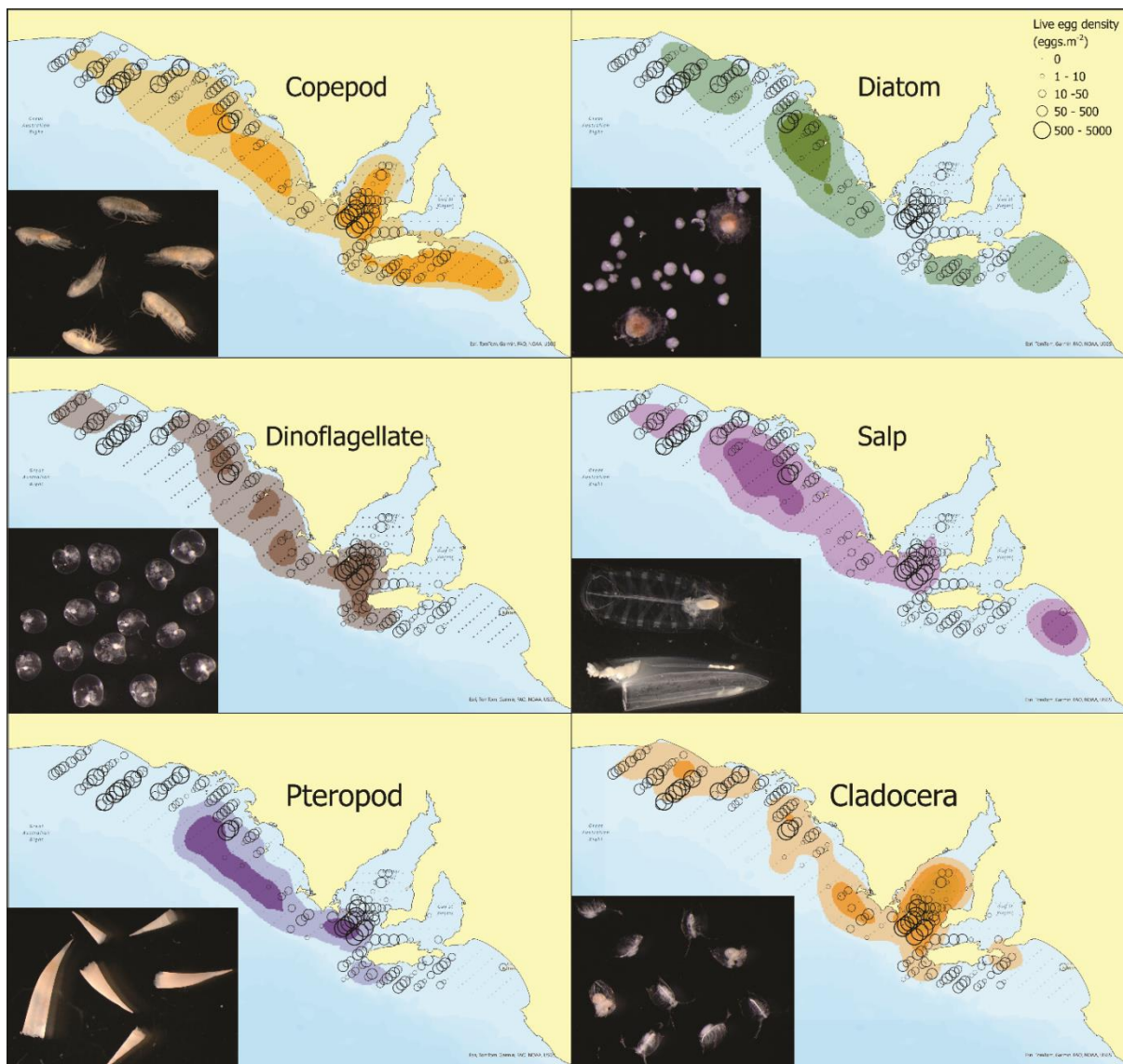


Figure 6. Distribution of common zooplankton and phytoplankton taxa overlaid with densities of live sardine eggs at sites sampled from February to April 2024. Coloured contours represent a kernel density distribution where the lighter colour represents presence and darker colour represents an abundance of the taxon.

3.2.4. Salinity

Surface salinity at each site ranged from 34.3 to 37.6 parts per thousand (Fig. 7). The highest salinities occurred in Spencer Gulf and Gulf St Vincent, while the lowest salinities were observed in the southeast region off Kingston and around the southern coast of Kangaroo Island. Low salinities also occurred along the western coast of the Eyre Peninsula from Coffin Bay to Baird Bay.

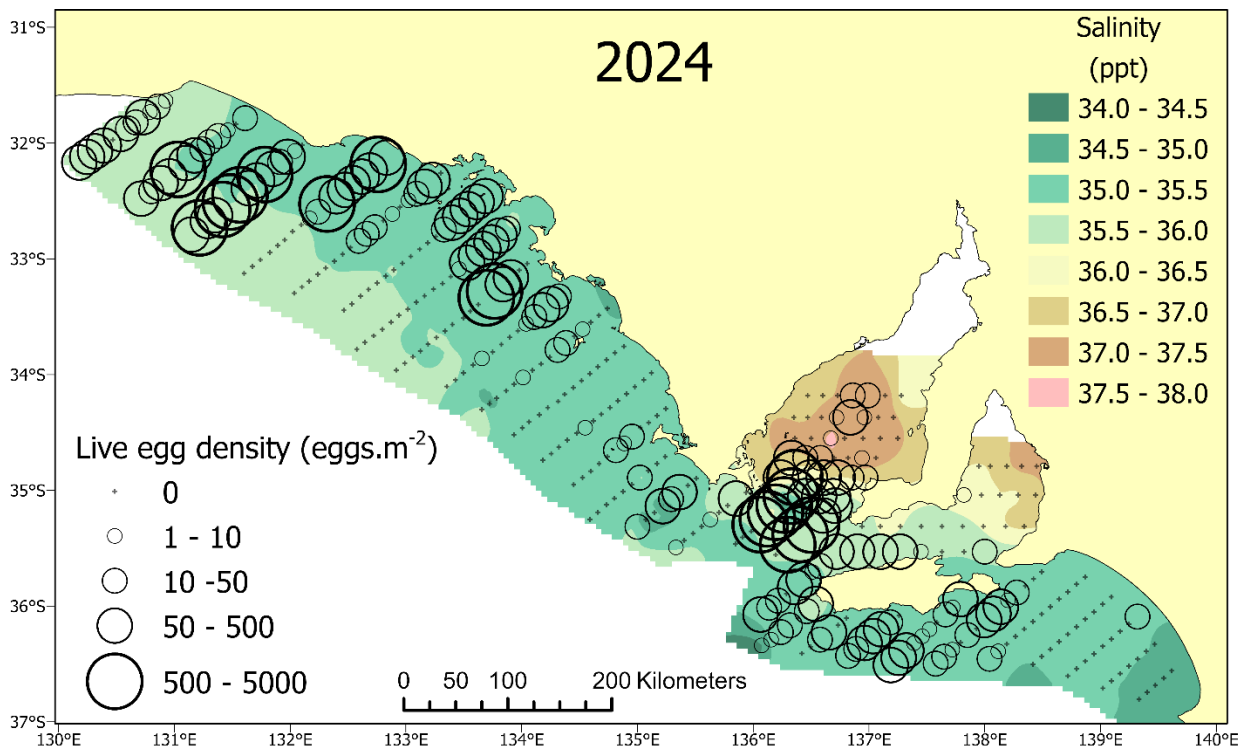


Figure 7. Surface salinity overlaid with densities of live Sardine eggs at sites sampled during February and April 2024.

3.3. Spawning area

The estimated spawning area was 61,471 km² and comprised 44.6% of the total area sampled (137,679 km²; Table 1, Fig. 2). If the additional stations added to the main survey since 2020 were not included, the spawning area would have been 58,855 km² (Figs. 1 and 8, Table 1).

Table 1. Total area surveyed and spawning area (A) estimated in 2024.

	Area sampled (km ²)	Spawning area, A (km ²)	Spawning area percentage
Pre-2020 survey	124,036	58,855	47.4%
With new stations	137,679	61,471	44.6%

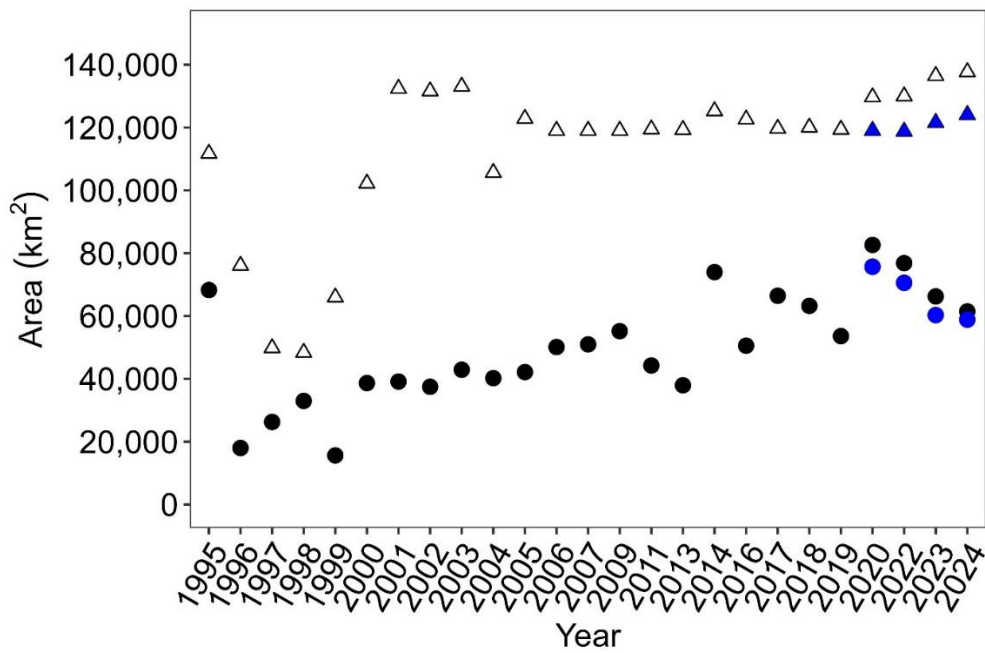


Figure 8. Sampling area (open triangles) and spawning area (closed circles) over the history of DEPM surveys in South Australia. For comparison: blue points exclude additional sites added since 2020.

3.4. Mean daily egg production (P_0)

The estimate of P_0 (95% CI) obtained by fitting the log-linear model (Eq. 3) to all data from 1998 to 2024 was 86.7 (78.7–95.5) eggs·day⁻¹·m⁻² (Table 2; Figs. 9 and 10A). The estimate of P_0 obtained by fitting the GLM NB1 (Eq. 5) to all data from 1998 to 2024 was 103.1 (89.3–120.5) eggs·day⁻¹·m⁻² (Table 2; Figs. 9 and 10A).

Table 2. Mean daily egg production (P_0) and instantaneous daily mortality (Z) estimated by fitting the log-linear model and GLM NB1 to all data collected from 1998 to 2024.

Model fit	P_0 (eggs·day ⁻¹ ·m ⁻²) (95% CI)	Z
Log-linear model	86.7 (78.7–95.5)	0.51 (0.43–0.58)
GLM, Negative Binomial	103.1 (89.3–120.5)	0.33 (0.28–0.39)

The estimate of P_0 (95% CI) obtained by fitting the log-linear model (Eq. 3) to data solely obtained in 2024 was 152.6 (99.6–227.8) eggs·day⁻¹·m⁻² (Table 3; Figs. 9 and 10A). The estimate of P_0 obtained by fitting the GLM NB1 (Eq. 5) to data solely obtained in 2024 was 146.7 (100.0–207.5) eggs·day⁻¹·m⁻² (Table 3; Fig. 9). Estimates of P_0 (log-linear model) for individual years between 1998 and 2024 have ranged from 39.0 in 2013 to 152.6 in 2024 (Fig. 10A; Appendix 1).

Table 3. Mean daily egg production (P_0) and instantaneous daily mortality (Z) estimated by fitting using the log-linear model and GLM NB1 to data solely collected in 2024.

Model fit	P_0 (eggs·day ⁻¹ ·m ⁻²) (95% CI)	Z
Log-linear model	152.6 (99.6–227.8)	0.52 (0.24–0.79)
GLM, Negative Binomial	146.7 (100.0–207.5)	0.24 (0.06–0.42)

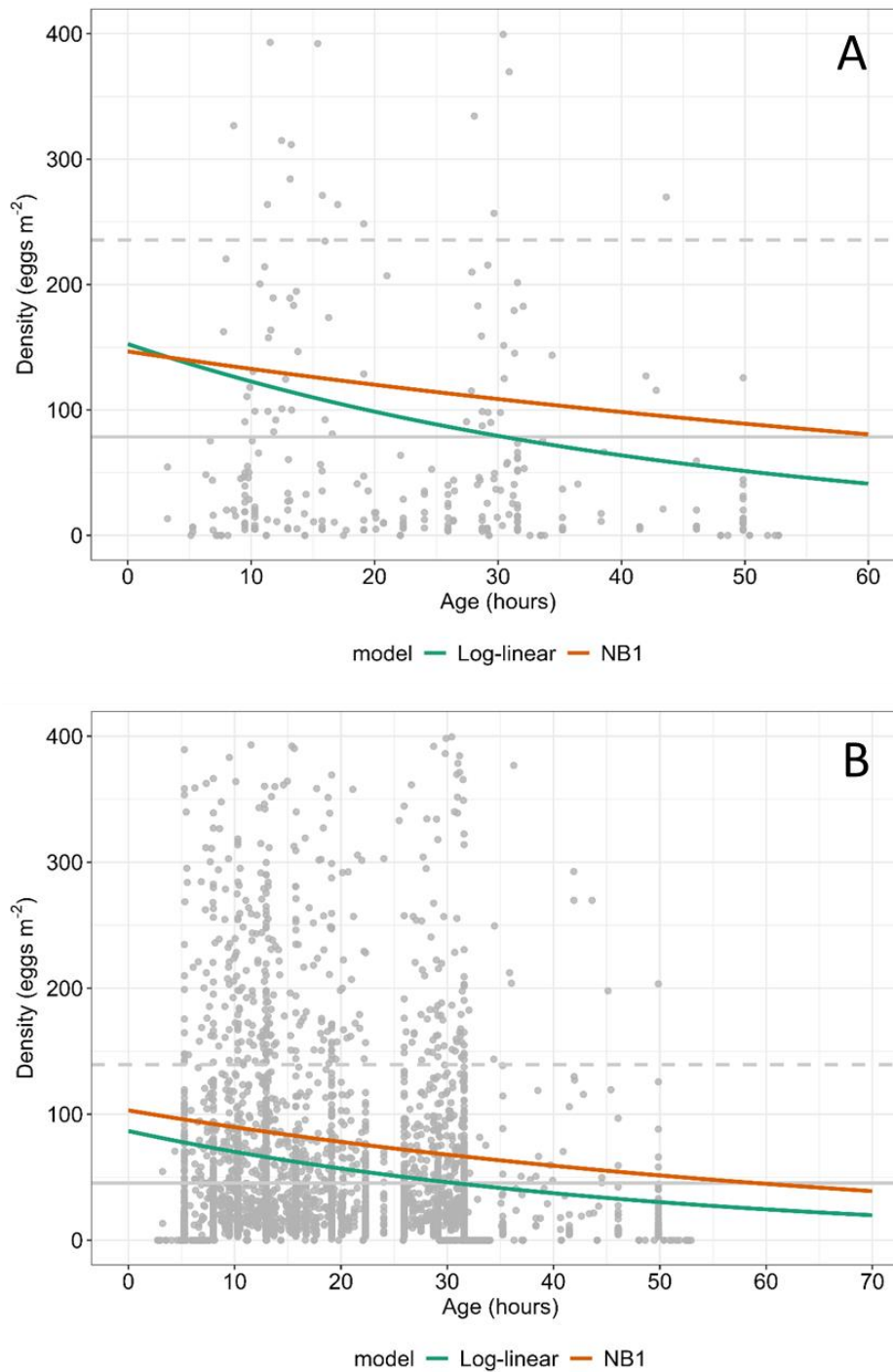


Figure 9. Models fitted to egg densities (eggs. m^{-2}) and egg age (hours) of Sardine cohorts in 2024 (**A**) and all years combined (1998 to 2024; **B**). Solid grey horizontal line: mean daily egg density, dashed grey horizontal line: mean total egg density.

3.5. Adult parameters

A total of 1,927 mature Sardine were collected from the *RV Ngerin* (fishery independent) and 1,933 were collected from commercial SASIA vessels (total adults combined: 3,860; Table 4). Six commercial samples were excluded from all analyses of adult parameters due to high rates of atresia in the ovaries (>30%), which indicated spawning was likely finished for the season) (Samples C4 to C9; Table 4). The fishery independent sample S5 was excluded due to the low number of fish collected, and S6 was only included in the calculation of F and W .

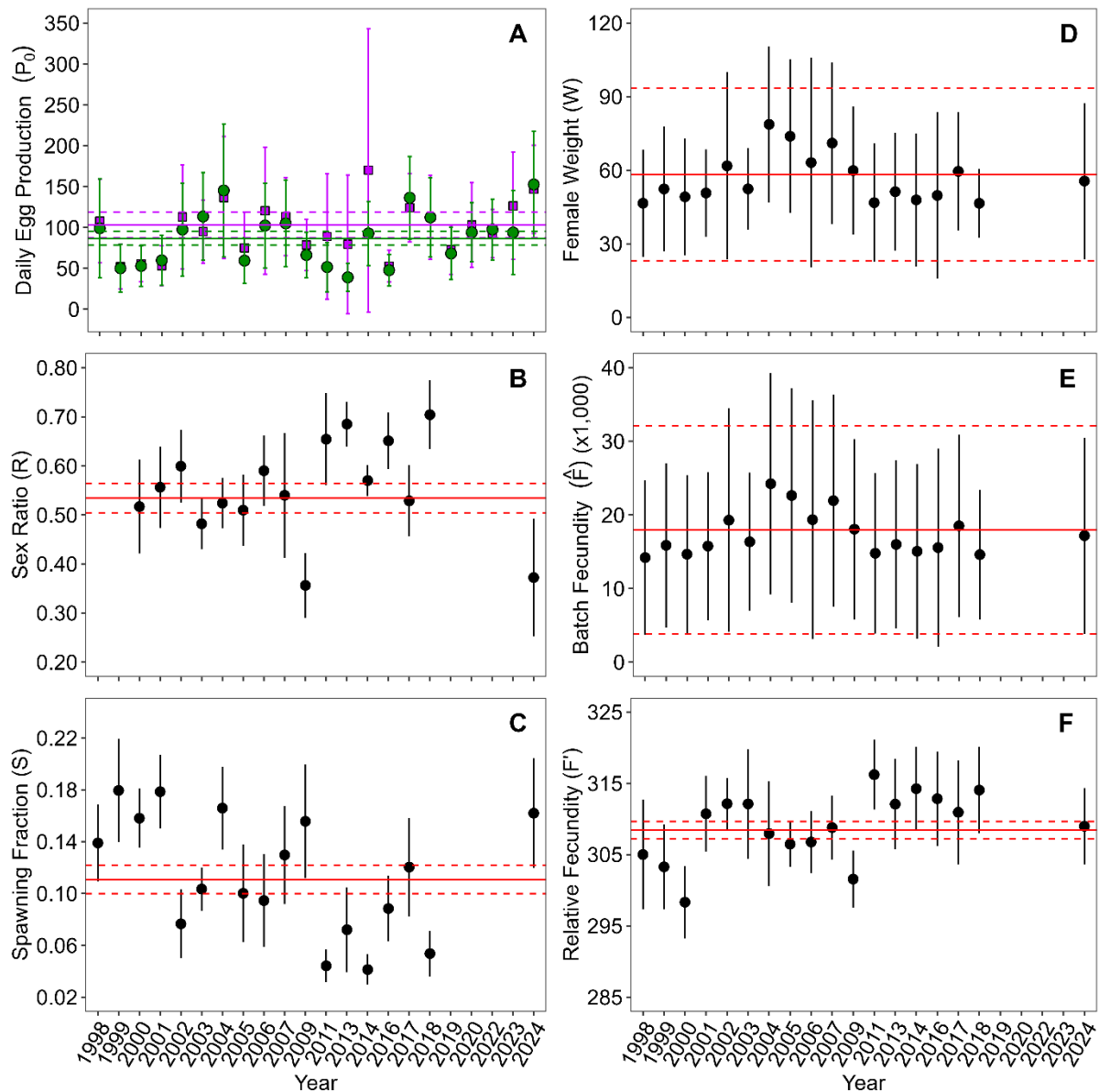


Figure 10. Annual estimates from 1998 to 2024 for **A**) Daily Egg Production (P_0): Log-linear model (circles) and GLM Negative Binomial (squares); **B**) Sex Ratio (R); **C**) Spawning Fraction (S); **D**) Female Weight (W); **E**) Batch Fecundity (\hat{F}); **F**) Relative Fecundity (F). Solid horizontal line: all years mean, dashed horizontal line and error bars 95% CI.

Table 4. Samples of Sardine collected in 2024 from commercial (C) and fishery independent (S) sampling (Is. = Island). Shown per sample are: number (n) of fish by sex; mean weight (grams) by sex; sex ratio (R; proportions of females by weight); number of fish with hydrated (H) ovaries and/or post ovulatory follicles (POF) aged Day 0, 1, or 2; number of ovaries with atresia present and percent atresia for sample; spawning fraction (S); and mean female fork length (mm FL). Shaded samples were excluded from analyses of adult parameters due to the presence of excessive atresia (>30%) or low numbers of fish in the sample. Bottom values are sums (*) and weighted means (#).

Sample ID	Location	Date	Time	Female (n)	Male (n)	Mean Female Weight (g)	Mean Male Weight (g)	R	H	POF 0	POF 1	POF 2	Atresia (n)	Atresia (%)	S	Mean Female FL (mm)
C 01	Thistle Is.	8/03/2024	4:00	92	117	39.3	34.4	0.47		24	16	14	12	13	0.20	153
C 02	Wedge Is.	16/03/2024	6:30	90	92	43.9	38.2	0.53		36	11	11	4	4	0.21	158
C 03	Thistle Is.	3/04/2024	2:30	81	142	37.7	34.7	0.38	1	2	8	14	23	28	0.10	154
C 04	Dangerous Reef	4/04/2024	1:00	89	56	35.4	30.5	0.65			1	6	50	56	0.03	148
C 05	Dangerous Reef	4/04/2024	3:00	90	80	34.9	30.8	0.56			1	6	58	64	0.03	149
C 06	Perforated Is.	6/04/2024	3:00	89	100	50.6	45.2	0.50		2	2	6	42	47	0.04	163
C 07	Perforated Is.	6/04/2024	4:20	90	102	44.3	36.6	0.52			1	6	57	63	0.03	158
C 08	Dangerous Reef	10/04/2024	6:30	87	82	37.5	34.4	0.54	1		6	8	33	38	0.06	153
C 09	Dangerous Reef	10/04/2024	19:40	88	81	36.6	32.9	0.55			3	4	55	63	0.03	152
C 10	Sth. of Kangaroo Is.	21/04/2024	1:00	91	63	66.0	62.3	0.60		2	1	14	12	13	0.06	180
C 11	Sth. of Kangaroo Is.	21/04/2024	2:45	90	41	71.3	63.3	0.71		3	6	13	10	11	0.08	184
S 01	Scotts Cove	2/02/2024	22:30	18	128	57.6	47.7	0.15	4		2	2	1	6	0.15	171
S 02	Scotts Cove	2/02/2024	23:00	27	45	58.8	47.8	0.43	2	8	2	3	1	4	0.19	175
S 03	Scotts Cove	2/02/2024	23:50	43	190	53.0	47.7	0.20		21	7	3	2	5	0.24	167
S 04	Snellings	9/02/2024	5:00	84	56	48.5	42.4	0.63	1	14	21	9	0	0	0.18	167
S 05	Scotts Cove	29/03/2024	~5:00	3	7	-	-	-	-	-	-	-				
S 06	St Francis Is.	5/04/2024	21:00	7	15	67.0	45.7	0.41	7				0	0		172
S 07	St Francis Is.	5/04/2024	22:30	76	133	63.4	48.0	0.43	27	3	7	6	6	8	0.19	174
S 08	St Francis Is.	5/04/2024	23:15	103	567	60.4	47.8	0.19	23	45	7	11	1	1	0.28	173
S 09	St Francis Is.	6/04/2024	21:30	26	58	63.3	50.6	0.36	11			2	2	8	0.17	172
S 10	St Francis Is.	6/04/2024	22:00	52	157	61.2	47.4	0.30	16	2		2	3	6	0.13	171
S 11	St Francis Is.	6/04/2024	22:30	51	81	65.9	47.5	0.47	3	5	3	2	1	2	0.08	176
				931*	1870*	55.6#		0.37#	88*	165*	105*	142*			0.16#	169#

3.5.1. Sex ratio

The mean sex ratio by weight (R , 95% CI) calculated from all fish collected between 1998 and 2024 was 0.53 (0.50–0.56) (Table 5; Fig. 10B). The estimate of R for samples collected in 2024 was 0.37 (0.25–0.49) (Table 4; Fig. 10B). Estimates of R for individual years ranged from 0.36 in 2009 to 0.70 in 2018 (Fig. 10B, Appendix 1).

Table 5. Parameter estimates used in the calculations of spawning biomass. Estimates of adult parameters (R , S , F') are calculated from all historical data from 1998 to 2024. CI: confidence interval; CV: coefficients of variation.

Parameter	All Years	95% CI	CV	2024 estimate (Range in previous years)
Egg Production (P_0 , eggs·day ⁻¹ ·m ⁻²)	86.7	78.7–95.5	0.049	152.6 (39.0–145.3)
Sex Ratio (R)	0.53	0.50–0.56	0.028	0.37 (0.36–0.70)
Spawning Fraction (S)	0.111	0.100–0.122	0.050	0.162 (0.041–0.179)
Relative Fecundity (F' , eggs·g ⁻¹)	308.4	307.2–309.6	0.002	309.0 (298.3–316.2)
Spawning Area (A , km ²)		-	-	61,471 (15,637–82,627)

3.5.2. Spawning fraction

The spawning fraction (S , 95% CI) calculated from all data collected between 1998 and 2024 was 0.111 (0.100–0.122) (Table 5; Fig. 10C). The estimate of S calculated for 2024 was 0.162 (0.120–0.204) (Table 4; Fig. 10C). Estimates of S for individual years ranged from 0.041 in 2014 to 0.179 in 2001 (Fig. 10C; Appendix 1).

Annual spawning fraction (S) was significantly correlated with sex ratio (R) (linear relationship: $S = -0.322R + 0.287$; $R^2 = 0.49$; $p < 0.01$) (Fig. 11). Estimates of spawning fraction are higher when the sex ratio is skewed towards males (i.e. sex ratio is lower) (Fig. 11).

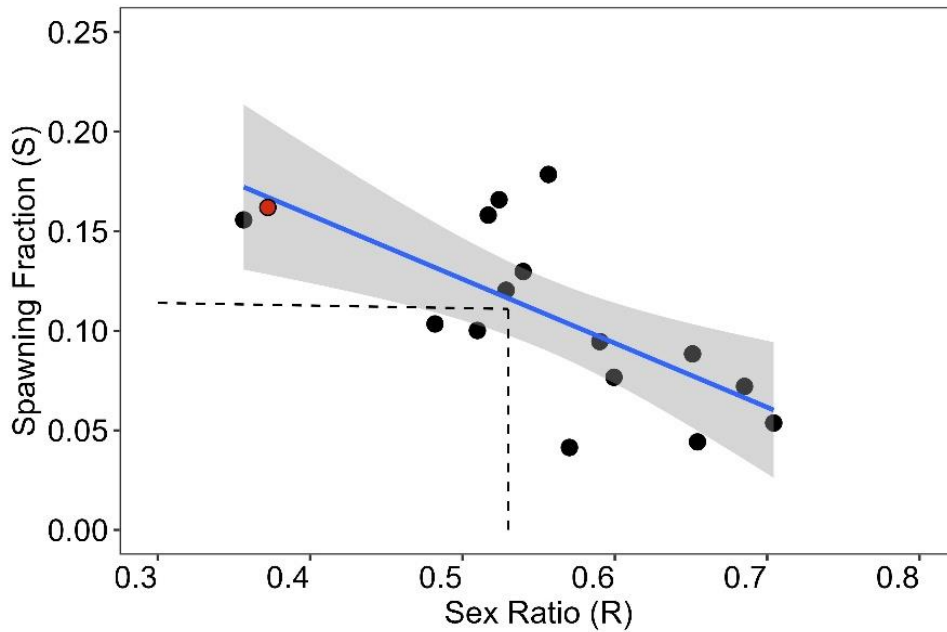


Figure 11. Relationship between annual estimates of spawning fraction (S) and sex ratio (R) for Sardine collected from 1998 to 2024. Blue: Linear relationship: $S = -0.322R + 0.287$ ($R^2 = 0.49$; $p < 0.01$); shading: 95% CI; dashed: all-years values for S (0.111) and R (0.53); red point: value for 2024.

3.5.3. Mean female weight

The mean weight of mature females (W , 95% CI) estimated from 930 fish in 15 samples collected in 2024 was 55.6 g (23.7–87.5) (Table 4; Fig. 10D).

The mean weight of mature females (W , 95% CI) estimated from 17,691 fish (271 samples) collected between 1998 and 2024 was 58.3 g (23.1–93.4) (Table 5; Fig. 10D). Estimates of W for individual years ranged between 46.5 g in 1998 and 78.7 g in 2004 (Fig. 10D, Appendix 1).

3.5.4. Batch fecundity

Between 1998 and 2018, 1,099 females with hydrated oocytes were collected (Ward et al. 2021), and 77 batch estimates were taken from samples collected in 2024. The fecundity-weight relationship estimated from all batch samples collected between 1998 and 2024 was: Batch Fecundity = $334 \times \text{Gonad Free Female Weight} - 558$ ($R^2 = 0.52$) (Fig. 12). Estimates of batch fecundity between 1998 and 2024 (based on fecundity-weight relationship estimated from all batch samples) ranged between 14,196 and 24,242 oocytes (Fig. 10E; Appendix 1). Mean gonad free female weight between 1998 and 2024 was 55.5 g and

ranged between 43.8 and 75.0 g (Appendix 1). Overall mean batch fecundity (\bar{F} , 95% CI) was 17,967 (3,802–32,131) oocytes (Fig. 10E; Appendix 1).

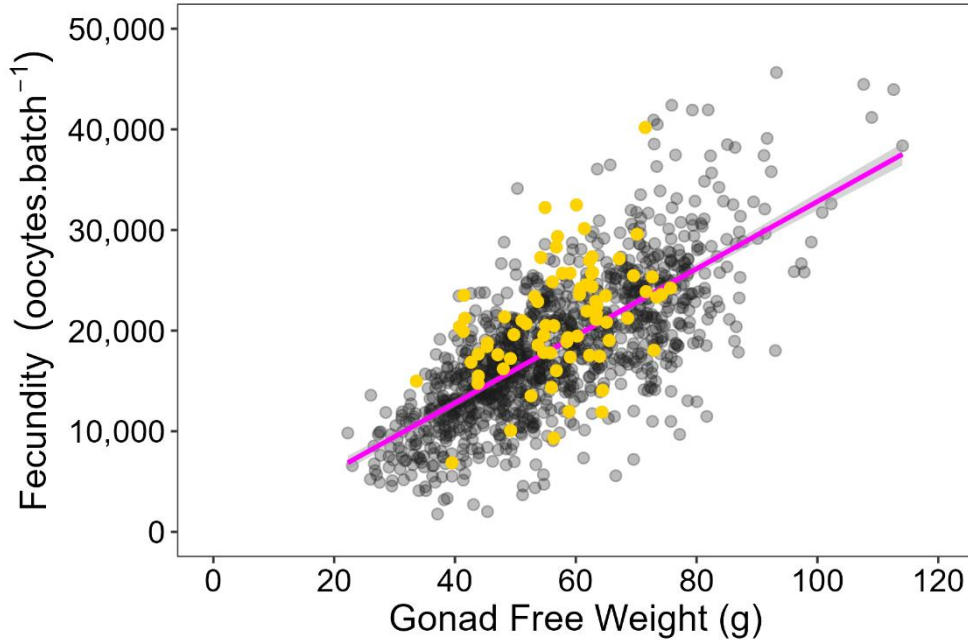


Figure 12. Relationships between gonad-free weight and batch fecundity for female Sardine with hydrated oocytes collected from 1998 to 2024 (data points added in 2024 shown in yellow). Regression line (magenta): Batch Fecundity = $334 \times \text{Gonad Free Female Weight} - 558$ ($R^2 = 0.52$).

3.5.5. Relative Fecundity (Eggs per gram of mature female weight (F'))

The estimate of relative fecundity (F' , 95% CI) calculated from all fish collected between 1998 and 2024 was 308.4 (307.2–309.6) (Table 5; Fig. 10F). The estimate of F' for samples collected in 2024 was 309.0 (303.6–314.3) eggs·g⁻¹ (Fig. 10F). Estimates of F' for individual years ranged from 298.3 eggs·g⁻¹ in 2000 to 316.2 eggs·g⁻¹ in 2011 (Appendix 1).

Relative fecundity (F') is almost constant across the range of weight (W) of mature females obtained in samples (Fig. 13). Fecundity increases approximately 308 eggs for every gram of increase in total female weight.

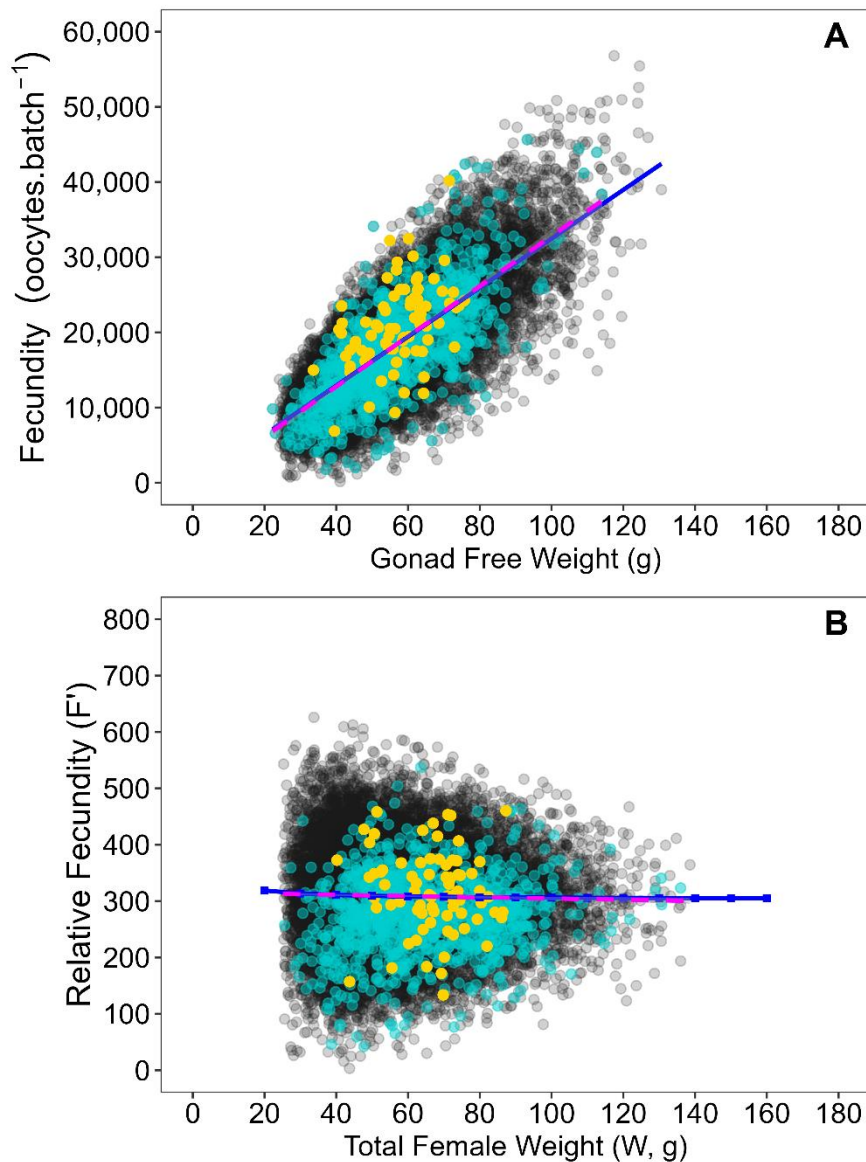


Figure 13. **A)** Batch fecundities measured for female Sardine with hydrated oocytes collected from 1998 to 2024 (cyan: 1998-2018; yellow: 2024) were used to estimate the fecundity of females without hydrated oocytes (black; $n = 16,515$). Batch fecundity relationship (magenta): $F = 334 \times \text{Gonad Free Female Weight} - 558$ ($R^2 = 0.52$). Blue: regression slope for predicted batch fecundities for comparison. **B)** Relationship (blue) between relative fecundity (F' , egg·g⁻¹) and female weight of sardine collected between 1998 and 2024. Fecundity estimates plotted in A are divided by female weight (W) and then regressed against W to show the relationship (blue) between F' and W . Cyan (1998-2018) and yellow (2024): measured F' values; Black: predicted F' values from estimates of \hat{F} produced in plot A divided by W . Shading around regression slopes are 95% CIs (narrow and difficult to see).

3.6. Spawning biomass

The estimate of spawning biomass (95% CI) calculated using the estimate of A obtained from the survey conducted in 2024, and the updated all-years estimates of P_0 (log-linear model), S , R , and F' was 291,731 t (248,230–335,232) (Fig. 14). The estimate calculated using the value of A without the additional stations added since 2020 was 279,315 t.

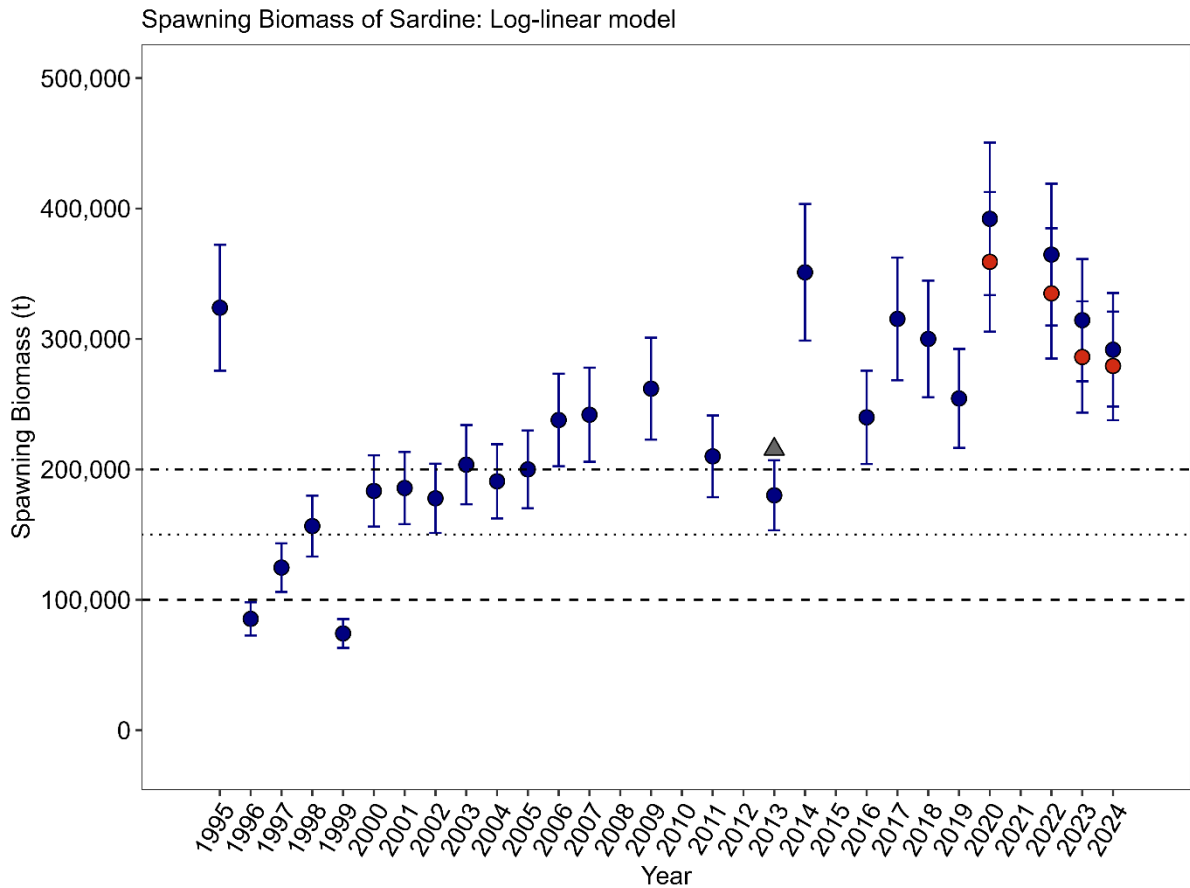


Figure 14. Estimates of spawning biomass (95% CI) for Sardine in South Australian waters from 1995 to 2024 using the log-linear egg production model and all-years data for all parameters, except for spawning area (A). The red circles for 2020 to 2024 are the estimate of spawning biomass obtained using the estimate of A without the additional stations added since 2020. The grey triangle for 2013 (when the survey did not cover the entire spawning area) is the estimate of spawning biomass using the mean A from 2002 to 2011 (45,406 km²). The horizontal lines indicate the 100,000 t (dash), 150,000 t (dotted) and 200,000 t (dash/dot) reference points in the Harvest Strategy (PIRSA 2023).

3.7. Sensitivity analysis

The sensitivity analysis shows the effects of inter-annual variability in parameters (i.e. P_0 , R , S and F') on the estimate of spawning biomass for 2024 (Table 5; Fig. 15; Appendix 1).

The high level of inter-annual variability in the estimates of P_0 reflects the high level of statistical uncertainty associated with annual estimates of this parameter (Fig. 10, Appendix 1) (see Ward *et al.* 2021). This range of variability had a strong influence on the estimate of spawning biomass. The estimate of spawning biomass obtained using the P_0 estimated from 2024 survey was higher than the estimate obtained using all-years data. The estimates of P_0 obtained for 2024 was the highest estimate for an individual year over the 26-year timeseries (Figs. 10 and 15; Table 3).

The estimates of R obtained in individual years were variable (Figs. 10 and 15; Appendix 1). The value of R obtained in 2024 of 0.37 was close to the historical minimum. The extreme values (i.e. 0.36 and 0.70) are likely due to the limitations of the adult sampling program rather than the relative abundance of sexes in the population (see Ward *et al.* 2021). The variations in R had a large influence on the estimate of spawning biomass for 2024 (i.e. >400,000 t).

The estimates of spawning fraction (S) obtained in individual years were also highly variable (i.e. ranging from 0.041 to 0.179) (Figs. 10 and 15; Appendix 1). The estimate of S for 2024 of 0.162 is higher than the historical average (Fig. 10; Appendix 1). This variation from the mean has strong negative influence on estimates of biomass. Similar to R , inter-annual variations in S are more likely to reflect the limitations of the adult sampling program than differences in the spawning rates occurring in the population (see Ward *et al.* 2021). Inter-annual variability in S had the strongest influence of all of the parameters on the estimate of spawning biomass (i.e. 185,000 to 800,000 t), which demonstrates the benefits of using all-years data to estimate this parameter.

The estimate of relative fecundity (F') was similar among years (Fig. 10; Appendix 1) and inter-annual variation in this combined parameter had a much smaller effect on spawning biomass (i.e. 300,000 to 317,000 t, Fig. 15). Inter-annual variations in W and F were large (see Fig. 10) and have a strong influence on the estimate of spawning biomass (Appendix 1; see Ward *et al.* 2021). Estimating F' as a single parameter, as done in the original formulation of the DEPM (Parker 1980), from all historical data greatly increases the precision of estimates of spawning biomass for Sardine (Ward *et al.* 2021).

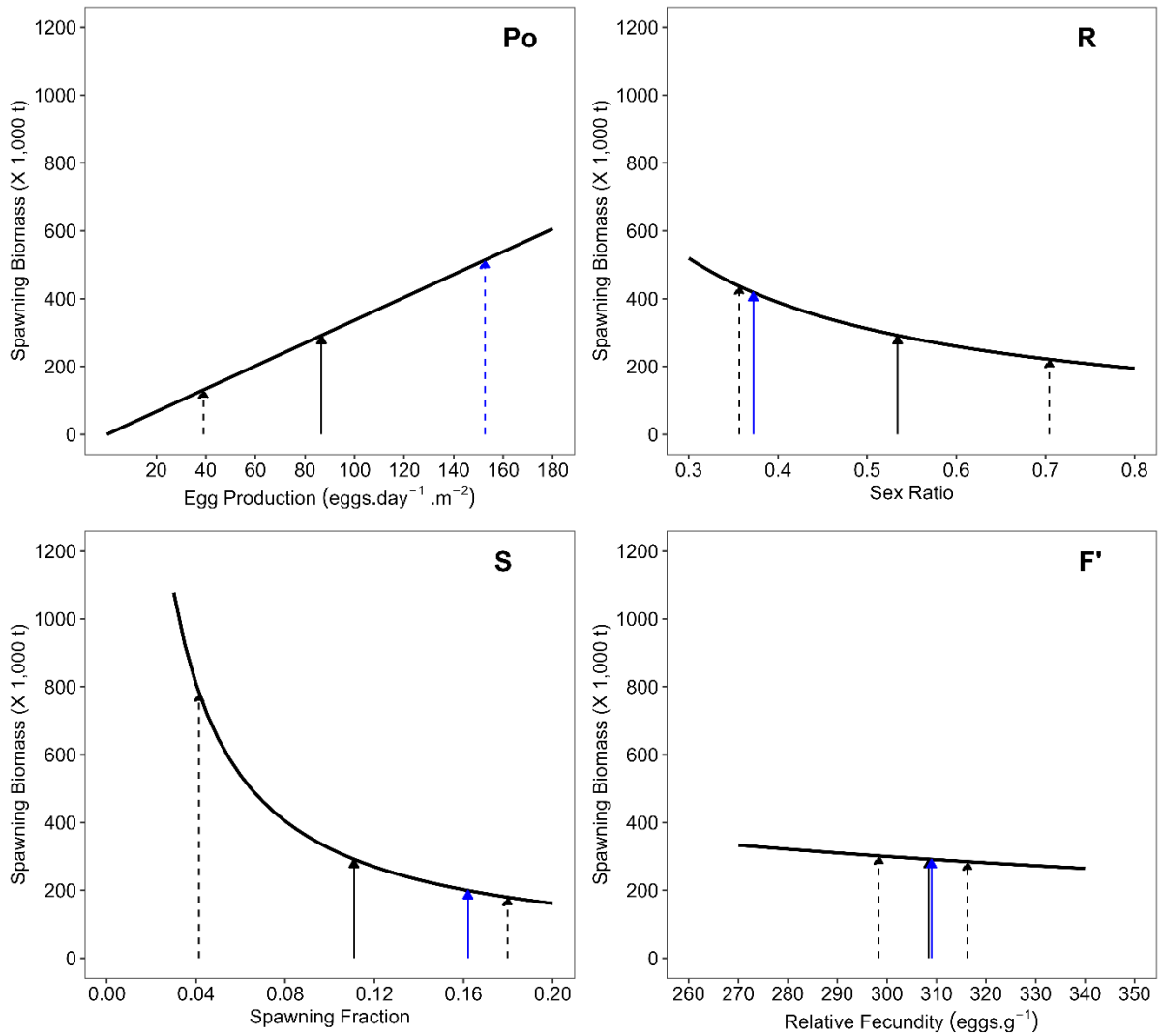


Figure 15. Sensitivity plots showing effects of variability in adult parameters and egg production on estimates of spawning biomass. Solid black arrows: parameter estimates for all years combined; Dashed arrows: range of values recorded between 1998 and 2024; Blue arrows: parameter estimates using only data collected in 2024.

4. DISCUSSION

4.1. Egg distribution and environmental factors

Plankton samples collected in 2024 contained a total of 8,310 live sardine eggs, which is the highest on record collected during a survey. The second highest number recorded was in 2017 when 7,955 live eggs were collected. Live sardine eggs were collected from 173 of the 405 survey stations (42.7%) which was lower than previous years. In 2023 for example, eggs were collected from 46% of sites, while in 2022 and 2020 eggs were found in 57.2% and 63.6% of sites, respectively (see Ward *et al.* 2020a, Grammer and Ivey 2022, 2023). These results show that the distribution of eggs in 2024 was not as widespread as in previous years, yet sardine eggs were abundant where they occurred.

While egg abundance was high, the general distribution of sardine eggs differed from that observed in recent years. In 2024, high densities of sardine egg were found off Head of Bight, on the inner GAB shelf off Ceduna, throughout Investigator Strait and in the region to the south and south-west of Kangaroo Island. Sardine eggs were absent from the outer sections of all transects between Point Sir Isaac (Eyre Peninsula) and west to Cape Adieu. This contrasts with egg distributions of recent years, where eggs were widely distributed throughout the continental shelf of the eastern GAB and abundant in the seaward sections of transects (e.g. Ward *et al.* 2020a, Grammer and Ivey 2022, 2023). Almost no eggs occurred in southeast region of the survey where they have been found in previous years (e.g. 2020, 2022 and 2023).

During the summer of 2023/24, a widespread upwelling event occurred in the eastern GAB along the western Eyre Peninsula, south-west of Kangaroo Island and along the Bonney Coast from December 2023 to March 2024. Average bottom temperatures recorded at the IMOS National Reference Station Kangaroo Island (NRSKAI) were $<12^{\circ}\text{C}$ from January to April 2024 and $<11^{\circ}\text{C}$ at the IMOS Bonny Coast Station (pers. comm. M. Doubell, SARDI). This was the strongest and most sustained upwelling event on record at the IMOS NRSKAI (pers. comm. M. Doubell, SARDI). Low SST ($<17^{\circ}\text{C}$) and elevated chlorophyll-*a* ($>6.49\ \mu\text{g}\cdot\text{L}^{-1}$) were recorded in inner-shelf waters off the western Eyre Peninsula during the 2024 survey; these values are indicative of strong upwelling in the region (Shute *et al.* 2022; Kämpf *et al.* 2023). Challenges during the 2024 survey occurred when attempting to locate spawning adult sardines at many of the historically productive, adult sampling sites, i.e. Pearson, Flinders, Neptune, Waldegrave and Greenly Islands. The survey team on the *RV Ngerin* reported encountering cold water (e.g. $\sim 14^{\circ}\text{C}$ SST at Waldegrave) and had unsuccessful nights of fishing with the gillnet being fouled with planktonic material at those sites (pers. comm. A. Ivey, SARDI). Successful collections of spawning adult fish were taken

at St Francis Island in April 2024 at the end of the survey, which coincides with the high densities of sardine egg off Head of Bight and Ceduna. Large schools of sardine were seen in the western GAB outside of the survey area when *RV Ngerin* travelled to Esperance, Western Australia immediately after the sardine survey (pers. comm. K. Pearson, *RV Ngerin* Crew, SARDI). This suggests a portion of the spawning biomass may have been outside of the survey area in warmer waters to the west.

The presence and/or absence of different zooplankton taxa are known to affect the distribution of eggs and adult sardine. For example, sardine eggs were largely distributed in areas with high copepod, cladoceran and dinoflagellate abundance, known primary food sources for adult sardine (Van der Lingen 2002). High densities of salps may explain the absence of eggs in the central GAB and in the southeast of the survey area. Salps are pelagic tunicates that can form intermittent swarms in suitable conditions and rapidly become dominant in the zooplankton assemblage. The lack of sardine eggs in this area could be due to: sardine avoidance as the salps' mucus nets could clog fishes' gills (Kashkina, 1986); salps, as highly efficient, non-selective suspension feeders (Vargas and Madin 2004, Gibbons and Richardson 2013), may consume fish eggs present in the area; and/or grazing salp swarms can quickly remove the daily primary production from an area (Dubischar and Bathmann 1997) leaving limited food for other planktivorous fish, such as sardine. Similar patterns of egg absence south of the Eyre Peninsula and Kangaroo Island have been seen in other years along with high densities of zooplankton (e.g. Ward *et al.* 2005, 2016; Grammer and Ivey 2023).

4.2. Spawning area and mean daily egg production

The spawning area in 2024 was estimated to be 61,471 km², which was lower than the spawning areas since 2020 (e.g. 82,627 km² in 2020; 66,248 km² in 2023) (Ward *et al.* 2020a, Grammer and Ivey 2022, 2023). However, these years have been amongst the highest spawning areas reported over the 29 years of DEPM surveys for sardine in South Australia, and the estimate for 2024 is above the average (8th highest out of 25 surveys). The additional survey area added to the southeast region in 2020 had minimal contribution to the spawning area in 2024 compared to previous years (see Ward *et al.* 2020a, Grammer and Ivey 2022, 2023). This was likely due to the exceptionally strong and sustained upwelling event in Summer 2023/24 along with a corresponding salp bloom encountered during the 2024 survey in the southeast region. Spawning area is strongly correlated with sardine abundance (Mangel and Smith 1990, Gaughan *et al.* 2004), and spawning area has been confirmed a good proxy for the abundance of adult sardine off South Australia (Ward *et al.* 2021). Although the spawning area was reduced in 2024 compared to previous years, the

spawning area observed in this study provides evidence that sardine were widespread and abundant off South Australia in 2024.

Using both historical and current data combined to estimate all DEPM parameters except spawning area means that fluctuations in estimates of spawning biomass are driven almost entirely by changes in the measure of spawning area. Adaptive sampling to improve the ability to collect plankton samples from the entire spawning area has been regularly applied since 2014 (Ward *et al.* 2013, 2014) and was continued in 2024. Future surveys must cover as much of the spawning area as possible and should continue to involve the adaptive approach to sampling.

Inter-annual variability in estimates of P_0 is low compared to statistical uncertainty (imprecision) for sardine off South Australia (Ward *et al.* 2021). The estimate for P_0 in 2024 of $152.6 \text{ eggs}\cdot\text{day}^{-1}\cdot\text{m}^{-2}$ (log-linear model) was the highest on record for an individual year. Total egg count (8,310) and mean total egg density ($236 \text{ eggs}\cdot\text{m}^{-2}$) was also the highest recorded since DEPM surveys have been applied in South Australia (Ward *et al.* 2020a, 2021, Grammer and Ivey 2022, 2023). The estimate of P_0 obtained by adding the 2024 data to all historical data was more precise (SD = 4.3) than the estimate obtained using data from 2024 only (SD = 33.2). Using historical data to estimate P_0 prevents large inter-annual fluctuations in estimates of spawning biomass driven by variations in the annual estimates of this parameter caused by statistical uncertainty.

The high estimate for P_0 in 2024 together with the reduction in spawning area may be an indication of spawning habitat becoming limited by environmental factors (i.e. strong upwelling), thus increasing the packing density (biomass per unit area) of adults in suitable spawning habitat (see Ward *et al.* 2021). In South Australia, spawning habitat for sardine has been characterised by mid-range SST (i.e. 19–20°C) and surface salinities (36.1–36.6 PSU) with intermediate phytoplankton biomass (chlorophyll-*a*: 0.4–0.9 $\mu\text{g}\cdot\text{L}^{-1}$) and the deep chlorophyll maxima between 60 to 90 m (Doubell *et al.* 2015). Due to the exceptional upwelling conditions in 2024, large portions of the survey area were well outside of these ranges. It is critical that P_0 continue to be monitored at a yearly timescale to look for changes in the parameter over time to reduce the risk of over- or under-estimating spawning biomass (Ward *et al.* 2021). In future applications of the DEPM, P_0 should continue to be estimated for sardine off South Australia using data obtained in all years since 1998, as well as within each year.

4.3. Adult reproductive parameters

In 2024, dedicated sampling for adult sardine occurred alongside the ichthyoplankton survey. These samples updated the historical adult reproductive parameters collected from 1998 to 2018. Samples of adult sardine were collected during the ichthyoplankton survey from both the *RV Ngerin* (fishery independent) and by SASIA staff from selected purse seine net-sets during commercial fishing activity (fishery dependent). Samples collected from commercial catches demonstrated that these were a viable source of adult reproductive samples to supplement the adult sampling program for the DEPM. The presence of POFs (particularly day-0 POFs) in fish collected from commercial catches demonstrated that these samples can be used for estimates of spawning fraction even if females with hydrated oocytes were not present in samples. The absence of females with hydrated oocytes was not unexpected given that most fish were collected from catches taken at dawn. Peak spawning time of sardine occurs around 2:00 am (Ward *et al.* 2021). The presence of day-0 POFs in the ovaries revealed that females that recently spawned were present in schools targeted by commercial fishers.

Estimates of adult parameters from samples collected in 2024 were within the range of the annual estimates from previous years. Re-analysis of all adult samples of sardine collected off South Australia since 1998 to include 2024 produced values that were very similar to the all-years values for each parameter reported in Ward *et al.* (2021). This continues to suggest that both individual parameters and mean daily fecundity are relatively stable among years, especially when inter-annual variability is evaluated within the context of potential sources of statistical uncertainty (i.e. precision and bias) (Ward *et al.* 2021). Large variations of the estimates of adult parameters among years are likely indicative of the limitations of adult sampling, rather than actual differences among years in the reproductive patterns of the population (Ward *et al.* 2021). For example in 2024, the estimate for sex ratio (R) was low (0.37, skewed towards males) and the estimate of spawning fraction (S) was high (0.16). Estimates of S and R are known to be correlated both in individual samples and annual estimates (Ward *et al.* 2016, 2020b). Samples obtained from actively spawning schools of sardine with high proportion of hydrated females (high spawning fraction) tended to have a sex ratio skewed towards males (low R) (e.g. sample S8: $R = 0.19$; $S = 0.28$; hydrated females = 23). Individual samples collected from non-spawning schools in commercial catches had sex ratios close to 0.5 or skewed towards females. Ganas *et al.* (2014) interpreted skewed sex ratios as an artefact of sampling spawning and non-spawning schools. The updated value of R using all data collected from 1998 to 2024 was 0.53 and the updated value of S was 0.111. This value of S corresponds to the global mean spawning fraction for sardine species of 0.11 (Ganas *et al.* 2014). Therefore, in the foreseeable future,

adult parameters used to calculate the spawning biomass of sardine off South Australia should continue to be estimated from data obtained in all adult surveys since 1998.

Detecting changes in the adult population of sardine over time due to environmental conditions (e.g. intensity/duration of upwelling) or density dependent effects is important. Adult reproductive parameters of sardine collected off South Australia from 1998 to 2024 were not correlated with spawning area; correlation would have suggested density dependent effects had occurred (Ward *et al.* 2021). Adult sampling is costly and logistically challenging, yet necessary. The ability to detect any changes in key adult parameters of sardine, such as spawning fraction, is critical since errors when estimating these parameters have major implications for estimates of spawning biomass (see Ward *et al.* 2021). The dedicated adult sampling program conducted in 2024 strengthened our understanding of key adult reproductive parameters. As demonstrated, samples collected from commercial catches in 2024, with their associated histological preparations of ovaries, were valuable additions to the adult reproductive dataset. This program should continue to be repeated every 5 years to determine if changes to adult parameters have occurred.

4.4. Spawning biomass

The estimate of spawning biomass for 2024 of 291,731 t (248,230–335,232) is above the upper target reference point of 200,000 t in the harvest strategy for the South Australian Sardine Fishery (PIRSA 2023). On this basis, the southern stock of Australian sardine is classified as **Sustainable**. This classification is consistent with recent assessments provided in the spawning biomass report for 2023 (Grammer *et al.* 2023), the stock assessment report for 2023 (Grammer *et al.* 2024) and the most recent report on the Status of Australian Fish Stocks (Roelofs *et al.* 2024).

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APPENDIX 1: ANNUAL AND ALL-YEARS PARAMETERS FOR ESTIMATES OF SPAWNING BIOMASS

Annual and all-years parameters used to calculate estimates of Spawning Biomass. Total A : total area sampled (km²), A : spawning area (km²); P_0 : mean daily egg production (egg·m⁻²·day⁻¹); S : spawning fraction; R : sex ratio; W : mean female weight (g); \hat{F} : batch fecundity (oocytes·batch⁻¹); F' : Fecundity / Female Weight. Errors around the estimates are standard deviation (SD). N : number of samples; n : number of individuals. F' was calculated using the all-years \hat{F}

Time	Total A	A	P_0	P_0 SD	N. P_0	S	S SD	N.S	n.S	R	R SD	N.R	n.R	W	W SD	N.W	n.W	\hat{F}	\hat{F} SD	N. \hat{F}	n. \hat{F}	F'	F' SD
All Years	-	-	86.7	4.3	7240	0.111	0.006	251	17210	0.53	0.02	226	30713	58.3	17.9	271	17691	17967	7227	271	17691	308.4	0.6
1998	48379	32980	99.0	30.8	164	0.139	0.015	12	530	-	-	-	-	46.5	11.2	11	461	14196	5365	11	461	305.0	3.9
1999	65956	15637	50.0	14.9	213	0.179	0.020	16	715	-	-	-	-	52.4	13.0	17	738	15879	5692	17	738	303.3	3.1
2000	102198	38658	52.9	12.7	290	0.158	0.012	15	1012	0.52	0.05	15	2179	49.2	12.2	16	1032	14664	5484	16	1032	298.3	2.6
2001	132382	39131	59.7	15.6	316	0.179	0.014	10	743	0.56	0.04	10	1397	50.7	9.1	11	1002	15765	5138	11	1002	310.7	2.7
2002	131574	37462	97.4	29.1	319	0.077	0.014	23	1631	0.60	0.04	23	2932	61.8	19.5	22	1836	19289	7749	22	1836	312.1	1.8
2003	133058	42905	113.5	27.4	320	0.103	0.009	8	435	0.48	0.03	8	986	52.4	8.5	8	435	16348	4796	8	435	312.1	3.9
2004	105621	40219	145.3	41.3	284	0.166	0.016	10	412	0.52	0.03	10	879	78.7	16.2	10	413	24242	7673	10	413	308.0	3.7
2005	122831	42142	59.5	14.3	334	0.100	0.019	33	2223	0.51	0.04	33	4827	73.9	16.0	33	2228	22642	7435	33	2228	306.5	1.6
2006	119038	50121	102.4	26.5	341	0.095	0.018	20	1332	0.59	0.04	20	2445	63.1	21.8	21	1335	19362	8285	21	1335	306.8	2.2
2007	119036	50972	104.9	27.1	341	0.130	0.019	20	1084	0.54	0.06	20	2244	71.1	16.8	21	1084	21940	7342	21	1084	308.8	2.3
2009	119031	55179	66.3	14.1	340	0.156	0.022	19	1537	0.36	0.03	9	2425	59.9	13.3	19	1536	18059	6251	19	1536	301.6	2.0
2011	119449	44245	51.5	15.4	340	0.044	0.006	14	1169	0.65	0.05	13	1798	46.8	12.3	15	1171	14793	5570	15	1171	316.2	2.5
2013	119297	37953	39.0	8.7	340	0.072	0.017	9	703	0.69	0.02	9	1089	51.3	12.3	9	721	15995	5836	9	721	312.1	3.2
2014	125249	73981	92.7	20.0	355	0.041	0.006	16	886	0.57	0.02	16	1574	47.9	13.9	16	861	15046	6065	16	861	314.3	3.0
2016	122598	50551	47.7	9.9	350	0.088	0.013	9	656	0.65	0.03	9	1088	49.7	17.3	9	679	15561	6863	9	679	312.8	3.4
2017	119661	66453	136.3	25.8	343	0.120	0.019	8	504	0.53	0.04	8	1030	59.6	12.3	9	511	18518	6321	9	511	310.9	3.7
2018	120043	63215	112.4	24.6	343	0.054	0.009	9	714	0.70	0.04	9	1026	46.5	7.2	9	718	14610	4500	9	718	314.1	3.1
2019	119369	53600	68.1	16.3	339	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2020	129700	82627	94.0	18.4	379	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2022	129982	76842	97.6	19.0	381	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2023	136471	66248	93.8	26.1	403	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2024	137679	61471	152.6	33.2	405	0.162	0.022	14	924	0.37	0.06	14	2794	55.6	16.3	15	930	17178	6800	15	930	309.0	2.7

relationship with W from that year. Data sources for table: Ward *et al.* (2021), Grammer *et al.* (2023).