

Effects of elevated temperature on fish sperm quality: A meta-analysis



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Effects of elevated temperature on fish sperm quality: A meta-analysis

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Declaration

Effects of elevated temperature on fish sperm quality: A meta-analysis

The results presented in the thesis with the above mentioned title are entirely of the candidate's own investigations and no part of the results has been accepted for any degree nor it is being concurrently submitted for any degree.

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DEDICATED To

MyBELOVED **D**AUGHTER

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Abstract

Climate change particularly global warming poses a great threat to animal reproduction which is very sensitivity to increases in temperature. Studies revealed that elevated water temperature could hinder sperm production, damage sperm functioning across generations and reduce sperm competitiveness in many species. Following a systematic review of the literature, a meta-analysis was performed to explore how the elevated water temperature would influence some selected sperm traits such as sperm density, morphology, motility, survival rate, velocity and volume in different fish species. The PRISMA screening process was followed and 33 studies were finally eligible for the meta-analysis. The meta-analyses showed that sperm density, survival rate and velocity were significantly affected by the elevated water temperature, while sperm morphology, motility and volume were not significantly influenced by it. The sperm density data revealed a significant negative effect size because of elevated water temperature, whereas sperm survival rate and velocity showed a significant positive effect size. Overall, the findings suggest a clear evidence of profound influence of elevated water temperature on some sperm traits in different fish species that may affect fertilization success and offspring fitness of this species.



Chapter-1

1. Introduction

The reality of worldwide warming is presently irrefutable. Numerous sea-going environments are encountering dynamic increments in regular temperatures coupled with more extensive warm variety, and an expanded rate of extraordinary warm waves (Collins et al. 2019; Frolicher et al. 2018). The endless lion's share of fishes are ectotherms and these temperature changes are likely to have strong impacts on their physiology, with suggestions at the individual, populace, and species level, and hence on the fisheries they maintain (McKenzie et al. 2016). Three major wonders have been recorded as wide scale reactions by fishes to the continuous warming of their environments: (a) latitudinal shifts in species disseminations, with poleward developments by temperate and sub-tropical fishes (Hickling et al. 2006; Parmesan and Yohe 2003; Perry et al. 2005); (b) changes in phenology of major life-cycle occasions, for case the timing of migrations and bringing forth, or the length of regenerative seasons (Crozier and Hutchings 2014; Myers et al. 2017), and (c) a diminishment in normal body measure, connected to decreases in final grown-up measure and an expanded proportion of younger and littler individuals in populaces (Audzijonyte et al. 2020; Gardner et al. 2011).

Temperature is one of the foremost critical physicochemical factors that decide the overall functioning of aquatic communities (Miranda et al. 2013). All physiological forms inside an living being happen inside a restricted temperature run, which may vary depending on the atomic and cellular instruments related with each specific process (Miranda et al. 2013). The reproduction in 777fish, compared with other physiological forms, only happens in a bounded temperature extend (Pörtner and Farrell 2008) and thus, little changes in water temperature might essentially influence this process. In this context, abnormal water temperature conditions seem create a mismatch between propagation and ideal environmental conditions for offspring advancement (Durant et al. 2007). Other than, shortening or indeed total misfortune of the breeding season might too happen. It is vital to note that any of these possible scenarios may create a loss within the reproductive yield of a given population, alter its structure and may jeopardize its maintainability (Miranda et al., 2013).

A lot of studies are available about the impacts of worldwide warming on female fish reproductive frameworks. The quality of eggs, delay in ovulation, the decrease of egg size,

fertilization rate and embryos survival is adversely influenced when females spawned out of time due to raised temperature (Pankhurst and King 2010; Tveiten and Johnsen 1999). For case in *Anarhichas lupus*, low embryos survival was obtained from broodstocks raised at 12°C compared to 4°C and 12°C groups (Tveiten and Johnsen 1999). Similar finding was detailed in *Salmo salar* with a low fertilization rate. In pejerrey *Odontesthes bonariensis* females the impact of elevated temperature during vitellogenesis is more unfavorable at the conclusion of this regenerative stage (Pankhurst and Munday 2011). On the other hand, there are less numbers of studies conducted on the impacts of elevated temperature on male reproductive physiology. The decline of sperm quality at high temperatures may be associated with increased metabolic rates when submitted to high temperatures (Billard 1995). Duration of sperm motility can be increased at higher temperature (Sunitha and Jayaprakas 1997). Sperm density may be higher at lower temperature (Tate and Helfrich 1998). Higher temperature can increase sperm velocity compared to lower temperature (Pinherio et al. 2020). Exposure to warm temperature in male juveniles affects negatively not only survival, growth, and fecundity, but also the motility of spermatozoa and body formation (Butzge et al. 2021). The significant decrease in milt volume is likely due to spermatogonial apoptosis because of higher thermal treatment was performed at juvenile stage (Butzge et al. 2021). *Oncorhynchus mykiss* appeared that high temperature may have a negative impact on spermatogenesis, diminishing the gonadal steroids testosterone and 11-KT (Manning and Kime 1985). *Cyprinus carpio* showed that higher temperature may have negative impact on sperm motility duration than lower temperature (Dadras et al. 2016).

Although some studies are available about the effects of elevated temperature on fish sperm quality, no studies are found as a compilation of these findings systematically. Therefore, the present study has been designed to compile the findings of previous studies systematically using the meta-analysis and to analyze how the effects of elevated temperature on sperm quality were depicted on those studies.

Meta-analysis could be a statistical method that coordinating the comes about of a few independent studies considered to be “combinable” (Huque 1988). Meta-analysis ought to be seen as an observational study of the prove. Well conducted meta-analyses permit a more objective evaluation of the evidence than conventional account reviews, give a more exact estimate of a treatment impact, and may clarify heterogeneity between the results of individual studies, can produce new hypotheses (Egger et al. 1997).

Objectives of the study

- ❖ To evaluate the effects of elevated temperature on sperm quality in different fish species through meta-analysis,
- ❖ To analyze how the effects of temperature on sperm quality results were depicted in previous studies,
- ❖ To find out publication bias through the sensitivity analysis.

Chapter-2

2. Materials and Methods

A systematic literature search was carried out to obtain relevant studies testing the effects of elevated temperature on sperm quality in different fish species according to PRISMA guidelines (Page et al. 2021).

2.1 Review design and search strategy

An initial database search was conducted in Scopus and Web of Science using 20 different keyword strings (Figure 1) until 24/01/2022.

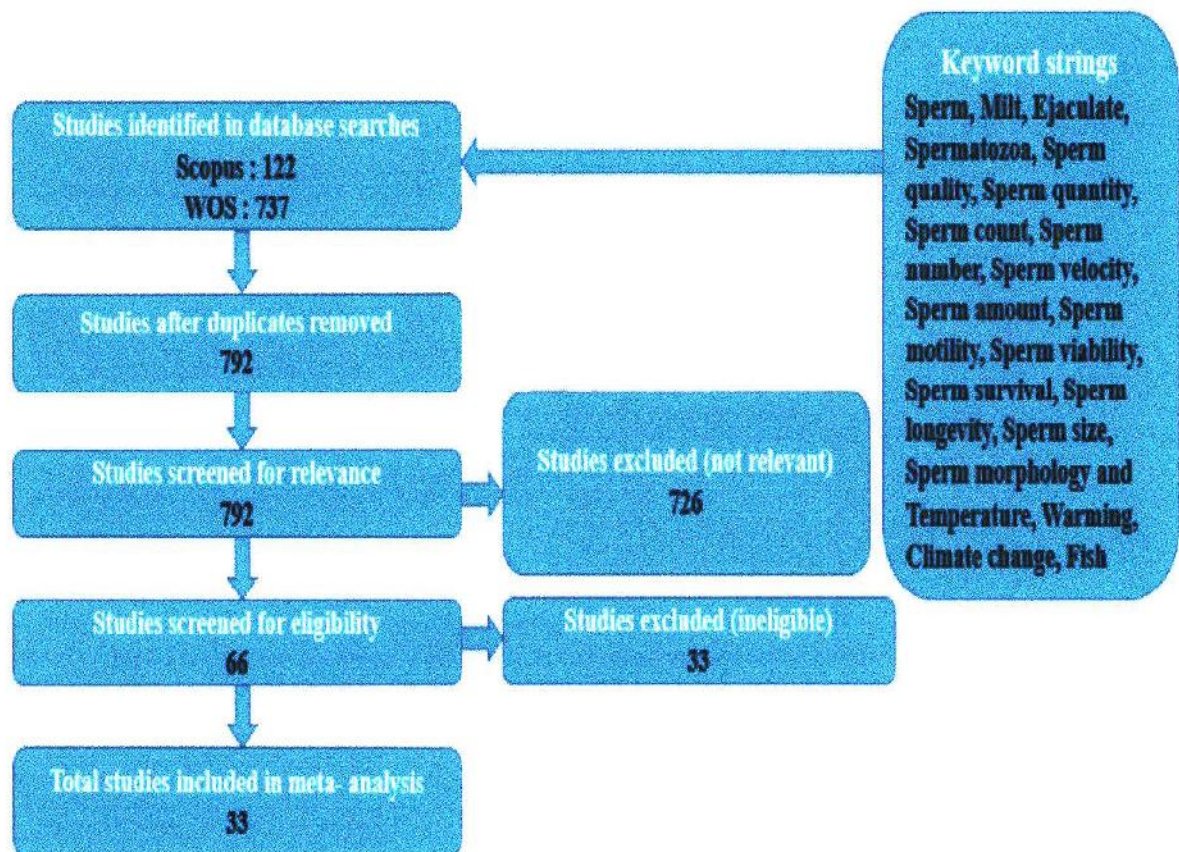


Figure 1. PRISMA flow diagram depicting the results of each step in the systematic literature search.

2.2 Study selection

Two reviewers independently (Md. Moshir Rahman & Shaikh Tareq Arafat) searched and selected the eligible studies. When there was any disagreement between the two reviewers, the suggestions of two other reviewers (Jannatul Ferdose and Sk. Mustafizur Rahman) were taken into account. The detailed search results for each stage of the PRISMA workflow are provided in Figure 1. Search results for each keyword string were exported as CSV files, formatted for consistency (i.e., with respect to columns and relevant information), and merged into a single Microsoft Excel file after which duplicates were removed.

For meta-analysis, input criteria to select the studies were as follows: (a) the studies tested the effects of elevated temperature on fish sperm, (b) the studies related to different sperm traits, and (d) the studies that had data as mean $\pm$ (SE or SD). After selecting the published articles following the input criteria, the abstracts were read carefully for evaluation. Each article was screened for relevance by reading the titles and abstracts and selecting only those studies that experimentally tested the effect of elevated temperature on different sperm traits such as sperm density/concentration, morphology, motility, survival rate/viability, velocity and volume. The term 'study' was used for any published article in which one or more experiments might be included, and each experiment retained the information about a control group and a treatment group. Some studies or experiments within studies were further excluded if the experimental temperature condition was not relevant to sperm traits, no mean, and standard deviation or standard error were mentioned. This selection process resulted in 33 studies eligible for the meta-analysis.

2.3 Data extraction and quality assessment

For each of the 33 studies (or their included experiments), we collected various qualitative and quantitative attributes. Specifically, we recorded general bibliographic data (authors, year published), the country or origin of species in where experiment was done, study location of species (from where sample were collected), name of the species tested, living state of species (freshwater or marine water), species maturity stage, fish group name, culture condition of species during experiment, type of the work (fieldwork or experiment), treatment and control type, unit of treatment and control ($^{\circ}\text{C}$ or $^{\circ}\text{F}$), interactive variable of treatment and control and its unit, response variable (sperm quality or quantity) and its unit. When any study reported for any sperm trait with a different unit, it could not be converted to a single unit, and therefore, this outcome with different

unit was excluded. For each eligible experiment, we also obtained the mean, sample size (n), and variance reported for the control and experimental treatment. These values were obtained directly from the text or tables within the article, from graphs within the article by using ImageJ software. We also added data source (exactly from where data were collected) and if there were any lack of information those were added in the comment section. All standard errors (SE) were converted to standard deviations (SD) prior to analysis. Where multiple stressors or factors were studied (e.g., temperature, oxygen, salinity, pH etc.), we only collected data for temperature effects under control treatment of the other variable to isolate temperature-only effects for between-study comparability.

2.4 Statistical analyses

The analysis calculated the standardized mean difference (SMD) as the effect size, Hedges' d using the following formula (Cohen 1988; Hedges and Olkin 1985):

$$SMD_i = \frac{\bar{X}_{2i} - \bar{X}_{1i}}{\sqrt{\frac{(n_{1i} - 1)SD_{1i}^2 + (n_{2i} - 1)SD_{2i}^2}{n_{1i} + n_{2i} - 2}}}, \quad (1)$$

$$Var(SMD_i) = \frac{n_{1i} + n_{2i}}{n_{1i}n_{2i}} + \frac{SMD_i^2}{2(n_{1i} + n_{2i})}, \quad (2)$$

where the i th effect size (SMD) and sampling variance (Var) are a function of the means ($\bar{X}$), standard deviations (SD of sample) and sample size (n) of the two groups (1 and 2); Equations 1 and 2 could be modified to add a small sample-size correction factor (Borenstein et al. 2009).

95% confidence interval (CI) was also calculated using a random effect model. The amount of heterogeneity (i.e., τ^2), was estimated using the restricted maximum-likelihood estimator (Viechtbauer 2005). In addition to the estimate of τ^2 , the Q-test for heterogeneity (Cochran 1954) and the I^2 statistic (Higgins and Thompson 2002) are reported. In case any amount of heterogeneity is detected (i.e., $\tau^2 > 0$, regardless of the results of the Q-test), a prediction interval for the true outcomes is also provided (Riley et al. 2011). Heterogeneity varies from 0% to 100% (Fallah et al. 2018). In this regard, $I^2 > 50\%$ indicates high heterogeneity (Higgins and Thompson

2002). Effect sizes and their variance for each experiment were calculated using the `escalc()` function in R version 4.0.5 (R Core Team 2020) and the `metafor` package version 3.4.0 (Viechtbauer 2010). We explored a subset of the qualitative and quantitative factors collected from each experiment as potential explainers of effect size variation such as study, year of publication, study environment, study location, study species, experimental temperature, etc.

Studentized residuals and Cook's distances are used to examine whether studies may be outliers and/or influential in the context of the model (Viechtbauer and Cheung 2010). Studies with a studentized residual larger than the $100 \times (1 - 0.05 / (2 \times k))$ th percentile of a standard normal distribution are considered potential outliers (i.e., using a Bonferroni correction with two-sided $\alpha = 0.05$ for k studies included in the meta-analysis). Studies with a Cook's distance larger than the median plus six times the interquartile range of the Cook's distances are considered to be influential. The rank correlation test (Begg and Mazumdar 1994) and the regression test (Sterne and Egger 2005), using the standard error of the observed outcomes as predictor, are used to check for funnel plot asymmetry.

The existence of publication bias was investigated by Egger method (Egger et al. 1997) and Begg's test (Begg and Mazumdar 1994) followed by funnel plots. Sensitivity analysis was performed to discover the sources of heterogeneity in the experiments to determine which experiments have affected the meta-analyses.

Chapter-3

3. Results

3.1 Overview of included studies

A total of 33 studies published between 1998 and 2021 that examined the effects of elevated temperature on different sperm traits of fish species were eligible for the meta-analysis database (Fig. 1). The studies were started searching on 17/01/2022 and finished on 24/01/2022. The review found only one eligible study in 1998, and after that the number was increased in very recent years (Fig. 2). The number of studies was greatest in Europe (21 studies), followed by South America (5 studies), and North America (4 studies) (Fig. 3a). The highest number of studies (6 publications) were conducted in the Czech Republic, followed by Brazil (4 publications), and Austria (3 publications) (Fig. 3b). The aggregation included 22 fish species in which the brown trout (*Salmo trutta*) was received the most interest (in 4 studies), followed by the common carp (*Cyprinus carpio*) (in 3 studies) (Fig. 4). During these studies, mostly the fish were reared under the laboratory conditions (in 21 studies), followed by tank (in 6 studies), pond (in 3 studies), and farming conditions (in 2 studies) (Fig. 5a). Out of 33 studies, the highest percentage of publication (54.55%) converged freshwater and marinewater species (42.42%), while only one study (3.03% of total fish habitat investigated) was done with a brackishwater species (*Sander lucioperca*) (Fig. 5b). The review revealed that 31 studies were conducted with mature fish, while only 2 studies selected juvenile fish during their experiments.

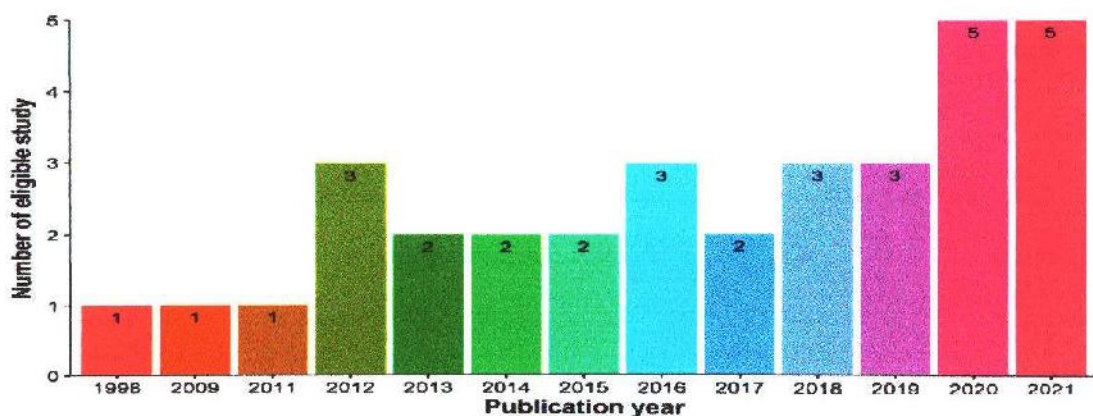


Figure 2. Number of eligible studies with their publication year.

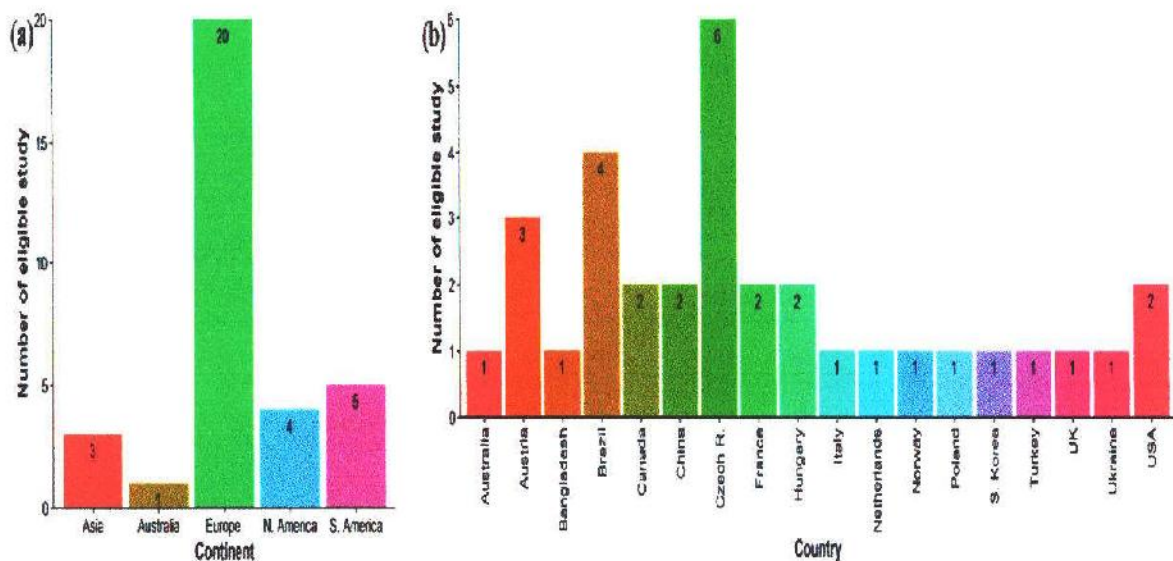


Figure 3. (a) Number of eligible studies according to continent, and (b) Number of eligible studies according to country.

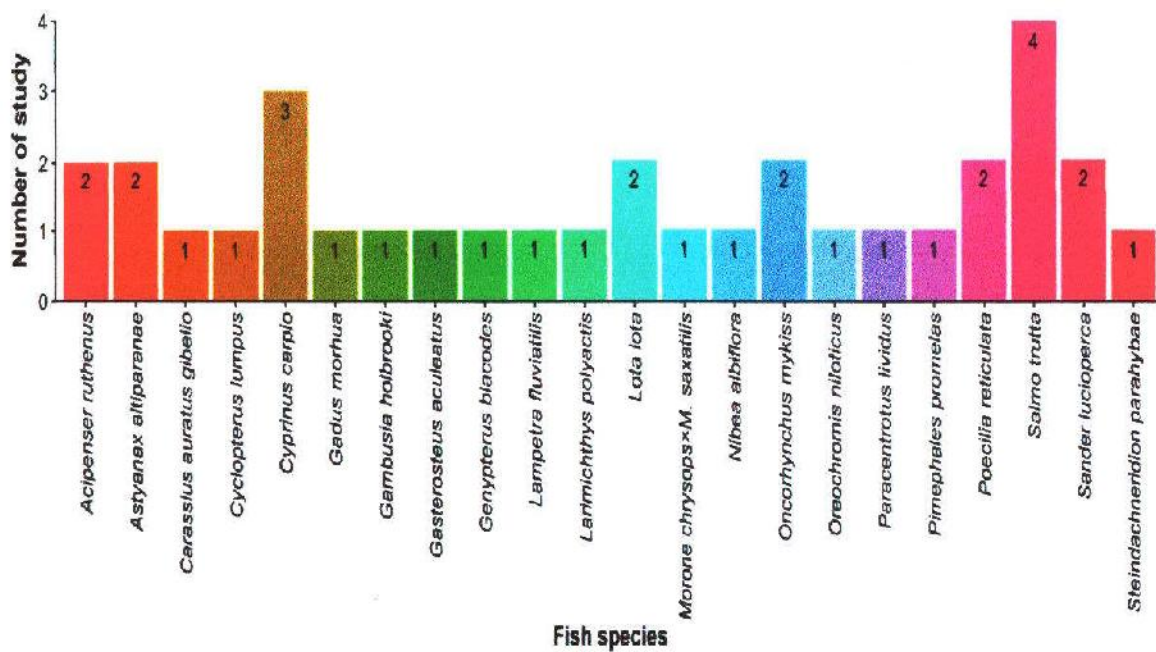


Figure 4. Number of eligible studies conducted with different fish species.

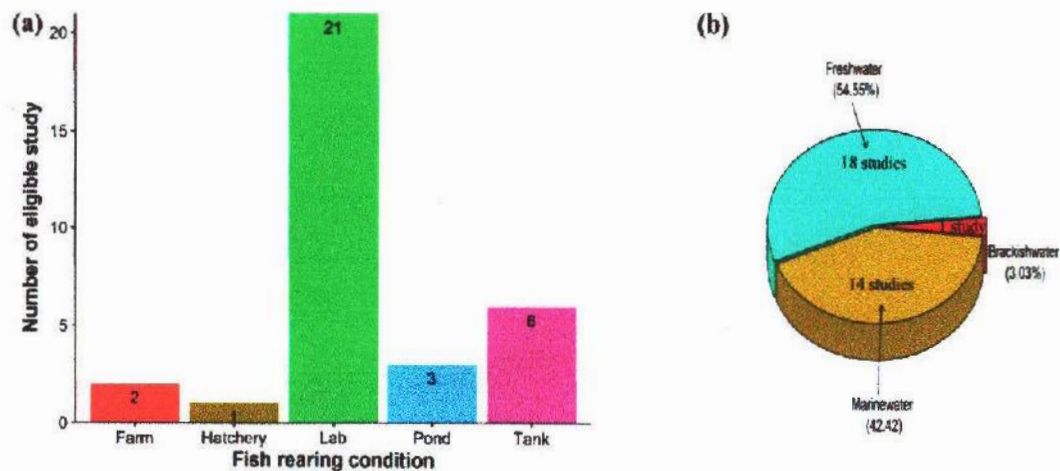


Figure 5. (a) Number of eligible studies carried out at different fish rearing conditions, and (b) Number of eligible studies according to different fish habitats.

3.2 Effects on sperm density

A total of 9 studies having 26 multilevel experiments tested the effects of elevated temperature on sperm density (Fig. 6). Mean effect sizes (Hedges' d) and 95% confidence interval (CI) for each study are depicted in Fig. 6.

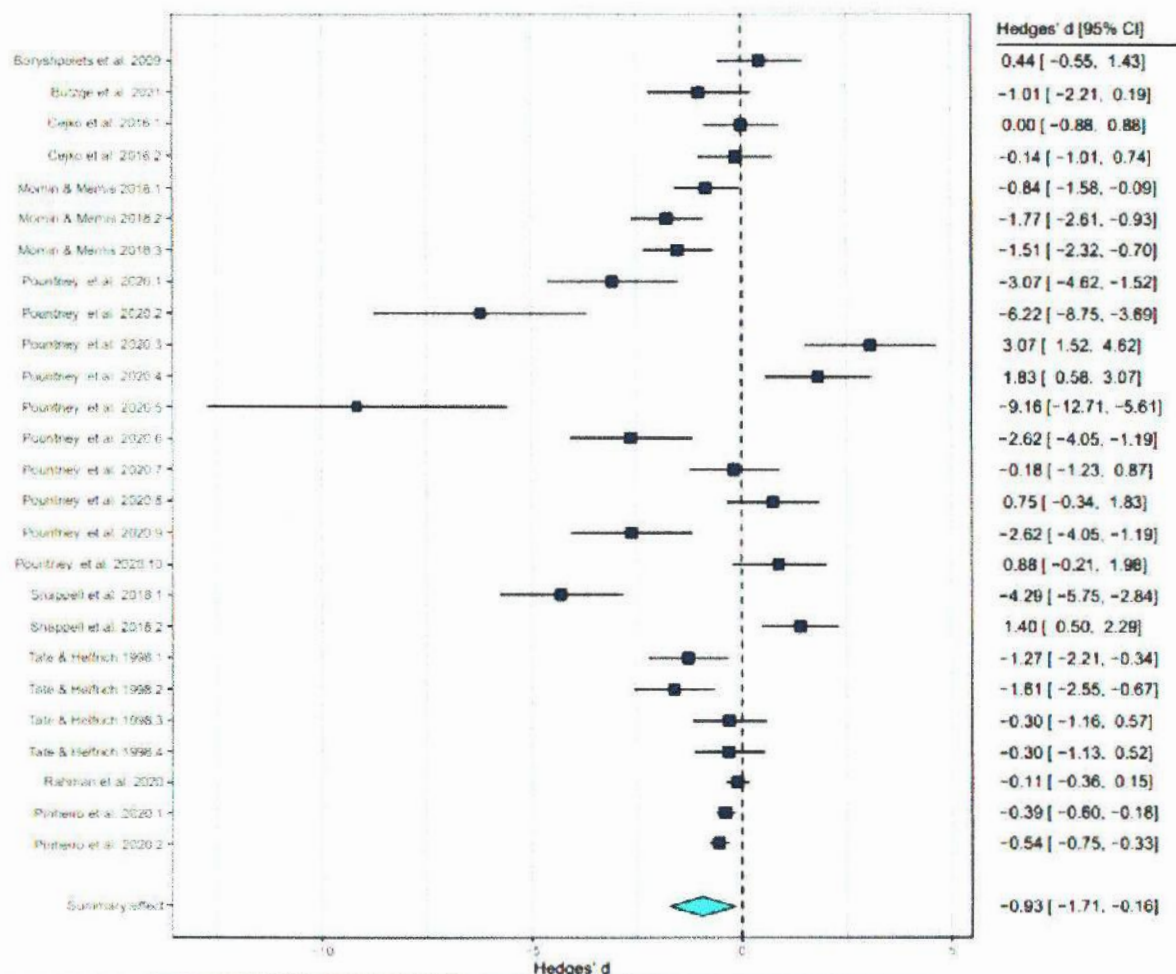


Figure 6. Forest plot reporting the effect size (Hedges' d) for sperm density in different studies. Mean and 95% confidence interval (CI) effect sizes are reported. The estimated summary effect size is indicated at the bottom of the figure. When a study includes multiple treatment levels, it is presented with a '.numeric number' after the publication year.

The random-effect model with independent observations showed a significant residual heterogeneity ($df = 25$, $QE = 197.88$, $p < 0.001$) and a larger estimated amount of total heterogeneity ($\tau^2: 3.67$). The mean sperm density displayed a significant negative overall effect size (estimate [CI_{lower} , CI_{upper}] = $-0.93 [-1.71, -0.16]$, $p < 0.05$) and the forest plot shows potential outliers (Fig. 7). Therefore, the sensitivity analysis was done by removing the outliers which showed almost same significant negative overall effect size (estimate [CI_{lower} , CI_{upper}] = $-0.73 [-1.40, -0.06]$, $p < 0.05$). Test for funnel plot asymmetry provided $z = -3.58$ and $p > 0.001$.

The p -value less than 0.05 of this funnel plot asymmetry test implicated publication bias (Fig. 7). In addition, rank correlation test between the effect sizes and their precision for funnel plot asymmetry computed Kendall's tau = -0.22 and $p = 0.14$. So, the null-hypothesis of no small-study effects is not rejected also suggesting publication bias.

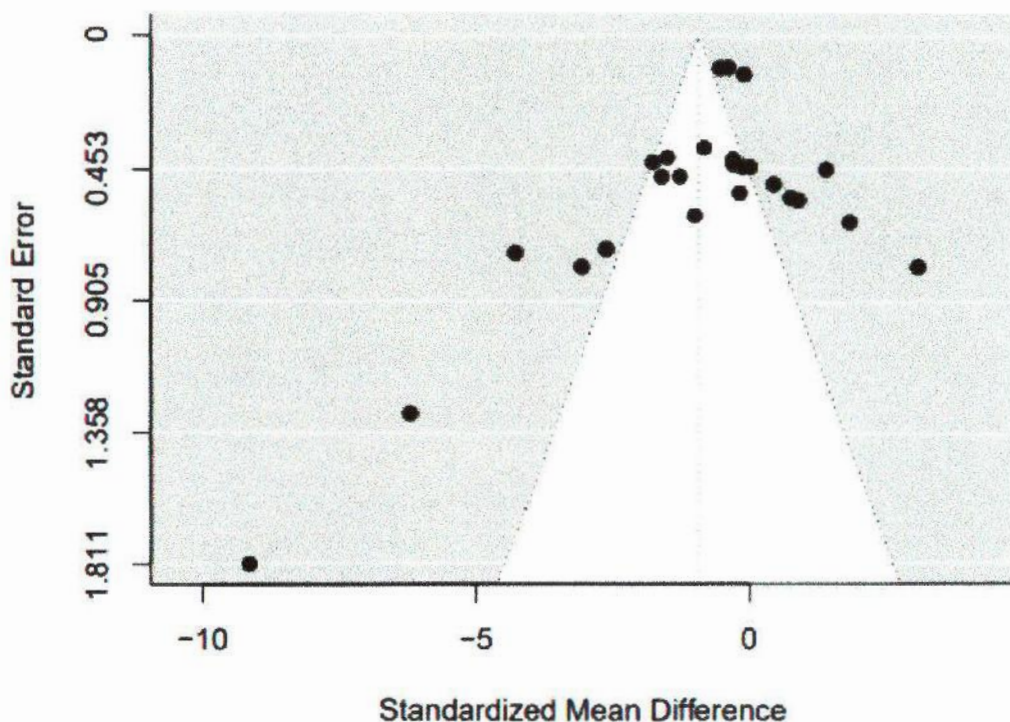


Figure 7. Funnel plot depicting the effect size of each study (x-axis) in relation to the precision of that study (SE; y-axis). Here points are not scattered symmetrically within the funnel suggesting a publication bias

The baujat plot showed the studies of Pountney et al. 2020 5, 2, 3 & Shappell et al. 2018 1 have higher values on both the x- and y-axis that may be considered to be influential cases on over all results (Fig 8).

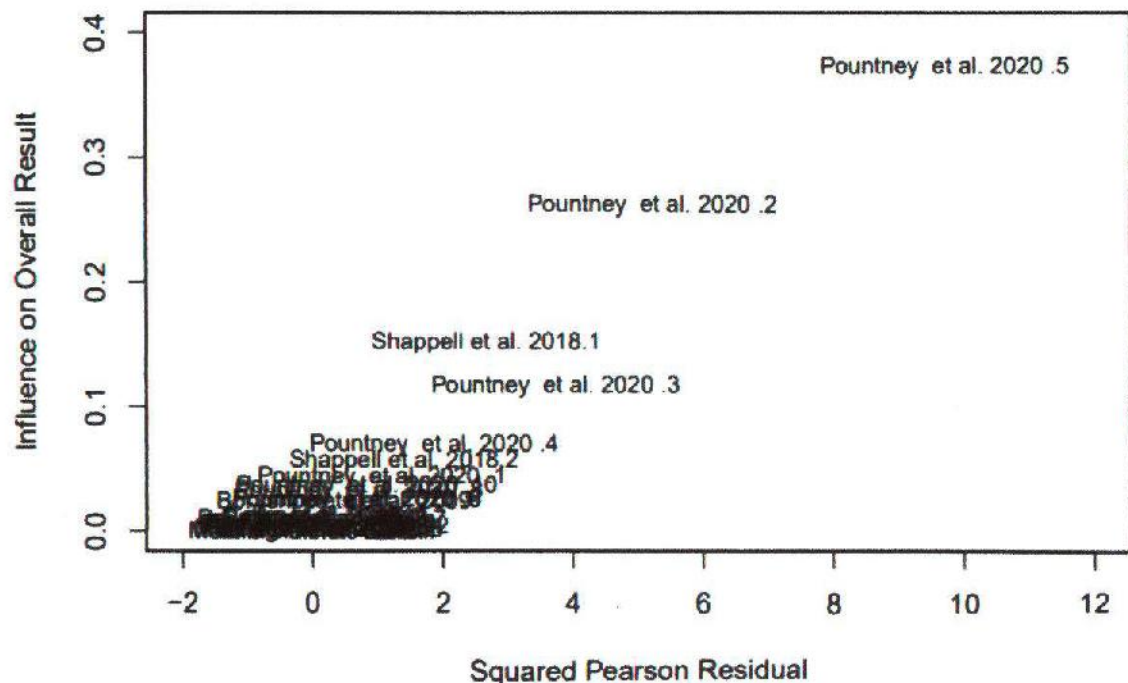


Figure 8. Baujat plot showing the heterogeneity in sperm density meta-analytic data. The plot shows the overall heterogeneity contribution of each effect size in x-axis, while the y-axis shows the influence of each effect size on the pooled result.

The aggregated analysis of these multiple treatments showed a total of 9 studies were included in the analysis. The observed aggregated outcomes ranged from -1.73 to 0.44 , with the majority of estimates being positive (89%). The estimated pooled effects size of the model was $d = -0.58$ (95% CI: -0.99 to -0.179). Therefore, the average outcome differed significantly from zero ($z = -2.79$, $p < 0.01$). A forest plot showing the observed outcomes and the estimate based on the random-effects model is shown in Fig. 9.

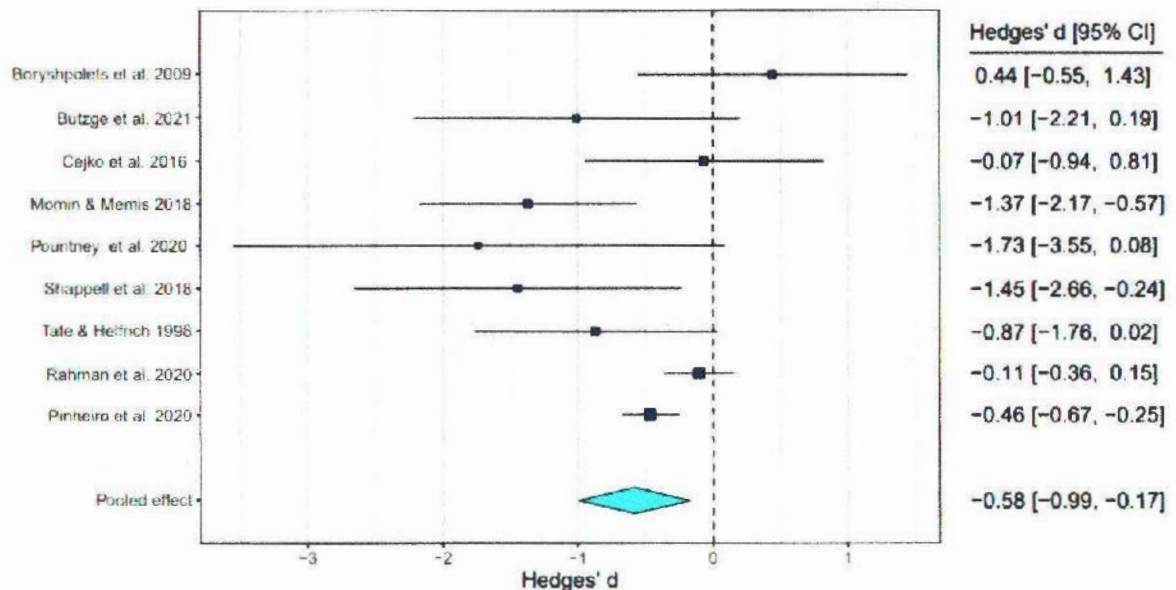


Figure 9. Forest plot reporting the effect size (Hedges' d) for aggregated sperm density in different studies having multiple treatments. Hedges' d and 95% confidence interval (CI) effect sizes are reported. The estimated pooled effect size is indicated at the bottom of the figure (cyan diamond shape).

3.3 Effects on sperm morphology

A total of 3 studies having 11 multilevel experiments tested the effects of elevated temperature on sperm morphology (Table 1). The random-effect model with independent observations showed a non-significant residual heterogeneity ($df = 10$, $QE = 16.74$, $p = 0.08$) and a lower estimated amount of total heterogeneity ($\tau^2: 0.03$). The mean sperm morphology displayed a non-significant negative overall effect size (estimate [CI_{lower} , CI_{upper}] = -0.13 [-0.35 , -0.08], $p = 0.23$).

Table 1. Effects of elevated temperature on different fish sperm morphology

Sperm traits	Multi level effect size	Pooled effect size	Study location	Study species	Study environment	Treatment temp. (°C)	Control temp. (°C)	References
Morphology (%)	1.34	1.34	Brazil	<i>Oncorhynchus mykiss</i>	Freshwater in lab	19	15	Butzge et al. 2021
	-0.29 – 0.05	-0.12	Brazil	<i>Astyanax altiparanae</i>	Freshwater in lab	30	25	Pinheiro et al. 2020
	-1.22 – 0.17	-0.27	Brazil	<i>Steindachneridion parahybae</i>	Freshwater in pond	35	24	Sanches et al. 2015

3.4 Effects on sperm motility

A total of 25 studies with 219 multilevel experiments tested the effects of elevated temperature on sperm motility (Table 2). The random-effect model with independent observations showed a significant residual heterogeneity ($df = 218$, $QE = 1704.93$, $p < 0.001$) and a larger estimated amount of total heterogeneity ($\tau^2: 3.47$). The mean sperm motility displayed a non-significant positive overall effect size (estimate [CI_{lower} , CI_{upper}] = 0.04 [-0.22, 0.31], $p = 0.74$).

Table 2. Effects of elevated temperature on different fish sperm motility

Sperm traits	Multilevel effect size	Pooled effect size	Study location	Study species	Study environment	Treatment temp (°C)	Control temp (°C)	References
Motility (%)	-4. 20 – -0.17	-1.37	Italy	<i>Paracentrotus lividus</i>	Marinewater in lab	13, 18 and 23	6	Albrizio et al. 2019
	-2.23 – -0. 88	-1.34	South Bohemia	<i>Sander lucioperca</i>	Freshwater in lab	3	2	Blecha et al. 2015
	-0. 70 – -0. 58	-0.64	Canada	<i>Poecilia reticulata</i>	Freshwater in lab	28 and 30	25	Breckels & Neff 2013
	-0. 59	-0.59	Brazil	<i>Oncorhynchus mykiss</i>	Freshwater in lab	19	15	Butzge et al. 2021
	-4. 51 – -0. 12	-1.39	Poland	<i>Lampetra fluviatilis</i>	Marinewater in hatchery	10 and 14	7	Cejko et al. 2016
	-45. 28 – -0. 56	-22.92	South Bohemia	<i>Cyprinus carpio</i>	Freshwater in farm	14 and 24	4	Dadras et al. 2016
	-0.66 – -0.46	-0.56	South Bohemia	<i>C. carpio</i>	Freshwater in tank	14 and 24	4	Dadras et al. 2017
	-5. 26 – -1. 75	-4.14	South Bohemia	<i>Acipenser ruthenus</i>	Marinewater in lab	14 and 24	4	Dadras et al. 2019
	-4. 52 – 4.26	-0.84	South Bohemia	<i>Lota lota</i>	Freshwater in lab	10, 20 and 30	4	Dadras et al. 2021

Motility (%)	Multilevel effect size	Pooled effect size	Study location	Study species	Study environment	Treatment temp (°C)	Control temp (°C)	References
	2.56 – 6.14	4.35	Chile	<i>Genypterus blacodes</i>	Marinewater in lab	8 and 16	4	Dumorne et al. 2018
	-1.94 – 43.02	4.76	France	<i>Oreochromis niloticus</i>	Freshwater in tank	20, 25, 30, 35, 40 and 45	10 and 15	Dzyuba et al. 2019
	1.48	1.48	South Bohemia	<i>A. ruthenus</i>	Marinewater in pond	14	2	Dzyuba et al. 2021
	-1.65 – -1.43	-1.54	China	<i>Nibeal biflora</i>	Marinewater in tank	25	4	He et al. 2012
	-1.52 – -0.59	-1.06	Austria	<i>Salmo trutta</i>	Marinewater in farm	9	5	Lahnsteiner & Leitner 2013
	-2.59 – 2.16	-0.28	Austria	<i>S. trutta</i>	Marinewater in lab	4, 6, 8, 10, 12, 14 and 16	2 and 4	Lahnsteiner & Mansour 2012
	-2.85 – 2.00	-0.41	Austria	<i>S. trutta</i>	Marinewater in lab	9, 11 and 13	3, 5 and 7	Lahnsteiner 2012
	-80.16 – -0.60	-35.77	Korea	<i>Larimichthys polyactis</i>	Marinewater in tank	20, 30 and 40	10	Le et al. 2011
	-0.94 – -0.42	-0.68	Netherlands	<i>Gasterosteus aculeatus</i>	Marinewater in lab	15 and 25	5	Mehlis & Bakker 2014

Sperm traits	Multilevel effect size	Pooled effect size	Study location	Study species	Study environment	Treatment temp (°C)	Control temp (°C)	References
Motility (%)	-0.68 – 1.86	0.93	Turkey	<i>O. mykiss</i>	Freshwater in pond	14	9	Momin & Memis 2018
	-3.02	-3.02	Brazil	<i>Astyanax altiparanae</i>	Freshwater in lab	40	22	Nascimento et al. 2020
	-0.47 – 3.53	1.43	Hungary	<i>Sander lucioperca</i>	Freshwater in lab	15	11	Ozgur et al. 2021
	-0.12 – 0.66	-0.03	Brazil	<i>A. altiparanae</i>	Freshwater in lab	30	25	Pinheiro et al. 2020
	-0.89 – -0.20	-0.57	South Bohemia	<i>L. lota</i>	Freshwater in lab	15	4	Rahi et al. 2021
	-30.39 – 8.67	-1.38	Brazil	<i>Steindachneridion paraguayae</i>	Freshwater in pond	35	24	Sanches et al. 2015
	-1.51 – -0.42	-0.97	USA	Sunshine bass (<i>Morone chrysops</i> × <i>M. saxatilis</i>)	Freshwater in lab	21 and 24	19	Tate & Helfrich 1998

3.5 Effects on sperm survival rate

A total of 4 studies having 33 multilevel experiments tested the effects of elevated temperature on sperm survival rate (Fig. 10). Mean effect sizes (Hedge's d) and 95% confidence interval (CI) for each study are depicted in Fig. 11.

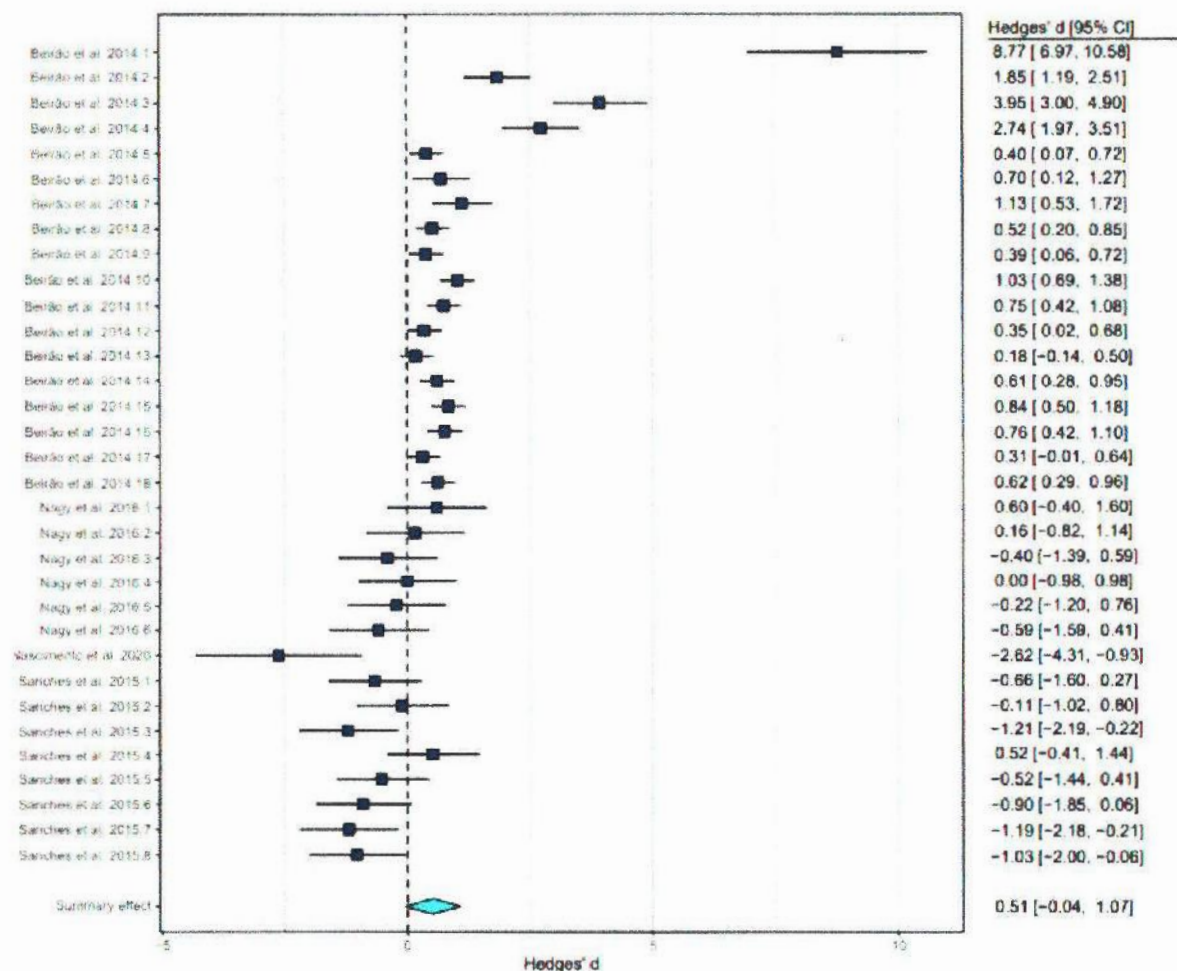


Figure 10. Forest plot reporting the effect size (Hedges' d) for sperm survival rate in different studies. Mean and 95% confidence interval (CI) effect sizes are reported. The estimated summary effect size is indicated at the bottom of the figure. When a study includes multiple treatment levels, it is presented with a '.numeric number' after the publication year.

The random-effect model with independent observations showed a significant residual heterogeneity ($df = 32$, $QE = 325.49$, $p < 0.001$) and estimated amount of total heterogeneity (τ^2 : 1.94). The mean sperm survival rate displayed a significant positive overall effect size (estimate $[CI_{lower}, CI_{upper}] = 0.51 [-0.04, 1.07]$, $p < 0.05$) and the forest plot shows potential outliers (Fig 10). Therefore, the sensitivity analysis was done by removing the outliers which showed more significant positive overall effect size (estimate $[CI_{lower}, CI_{upper}] = 0.61 [0.18, 1.03]$, $p < 0.01$). Test for funnel plot asymmetry provided $z = 0.84$ and $p = 0.40$. The p -value higher than 0.05 implicated no publication bias (Fig. 11). In addition, rank correlation test between the effect sizes and their precision for funnel plot asymmetry computed Kendall's tau = -0.10 and $p = 0.34$. So, the null-hypothesis of no small-study effects is rejected suggesting no publication bias.

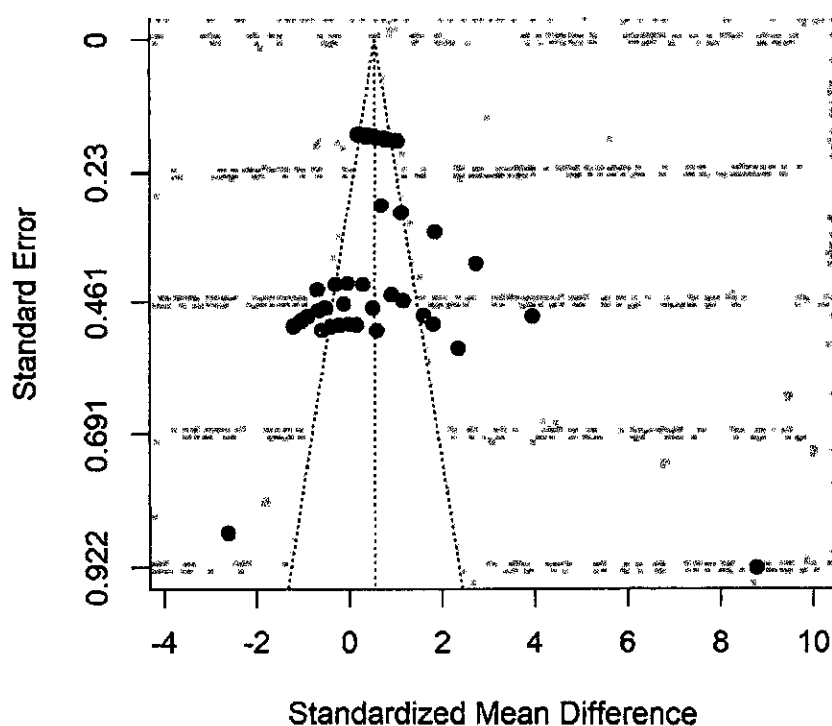


Figure 11. Funnel plot depicting the effect size of each study (x-axis) in relation to the precision of that study (SE; y-axis). Points are scattered symmetrically within the funnel suggesting no publication bias.

The baujat plot showed the studies of Nascimento et al. 2020 and Beirao et al. 2014g have higher values on both the x- and y-axis that may be considered to be influential cases on overall results (Fig. 12).

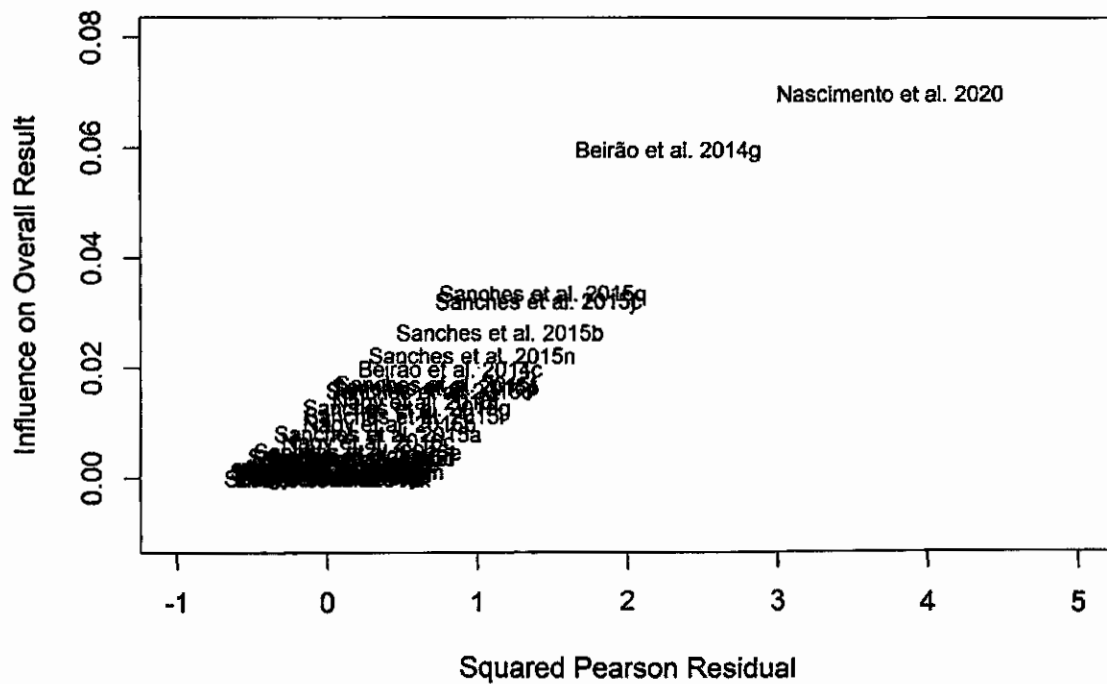


Figure 12. Baujat plot showing the heterogeneity in sperm survival rate meta-analytic data. The plot shows the contribution of each study to the overall Q-test statistic for heterogeneity on the horizontal axis versus the influence of each study.

The aggregated analysis of these multiple treatments showed a total of 4 studies were included in the analysis. The observed aggregated outcomes ranged from -2.62 to 0.95 , with the majority of estimates being positive (75%). The estimated pooled effects size of the model was $d = -0.45$ (95% CI: -1.81 to 0.92). Therefore, the average outcome did not differ significantly from zero ($z = -0.64$, $p = 0.52$). A forest plot showing the observed outcomes and the estimate based on the random-effects model is shown in Fig. 13.

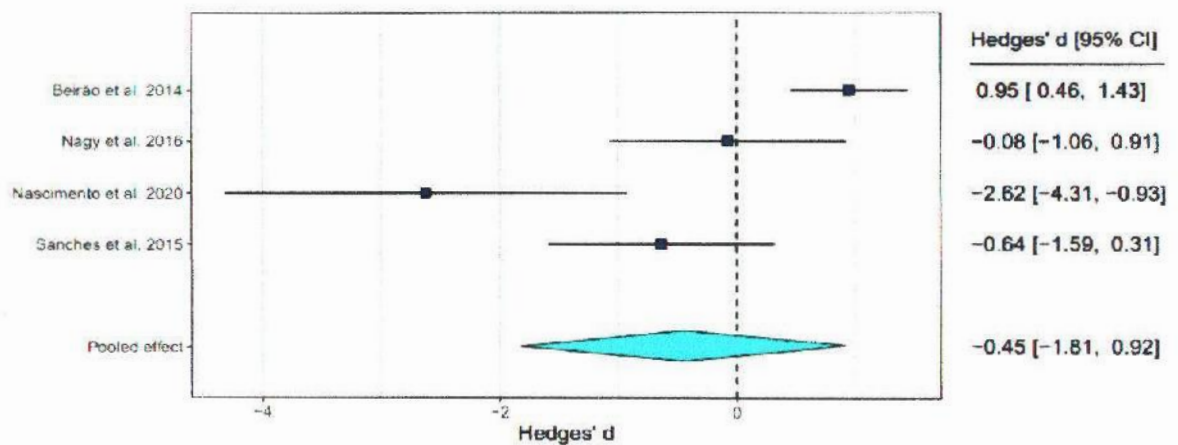


Figure 13. Forest plot reporting the effect size (Hedges' d) for aggregated sperm survival rate in different studies having multiple treatments. Hedges' d and 95% confidence interval (CI) effect sizes are reported. The estimated pooled effect size is indicated at the bottom of the figure (cyan diamond shape).

3.6 Effects on sperm velocity

A total of 20 studies having 152 multilevel treatments tested the effects of elevated temperature on sperm velocity (Fig. 14). Mean effect sizes (Hedges' d) and 95% confidence interval (CI) for each study are depicted in Fig. 14.

Figure 14. Forest plot reporting the effect size (Hedges' d) for sperm velocity in different studies. Mean and 95% confidence interval (CI) effect sizes are reported. The estimated summary effect size is indicated at the bottom of the figure. When a study includes multiple treatment levels, it is presented with a 'numeric number' after the publication year.

The random-effect model with independent observations showed a significant residual heterogeneity ($df = 151$, $QE = 1412.77$, $p < 0.001$) and estimated amount of total heterogeneity ($\tau^2: 8.47$). The mean sperm velocity displayed a significantly positive overall effect size (estimate [CI_{lower} , CI_{upper}] = 0.60 [0.11, 1.09], $p < 0.05$) and the forest plot shows potential outliers (Fig. 14). Therefore, the sensitivity analysis was done by removing the outliers which showed the same effect size (estimate [CI_{lower} , CI_{upper}] = 0.63 [0.14, 1.11], $p < 0.05$).

Test for funnel plot asymmetry provided $z = 8.81$ and $p < .0001$. The p -value less than 0.05 implicated a publication bias (Fig. 15). In addition, rank correlation test between the effect sizes and their precision for funnel plot asymmetry computed Kendall's tau = 0.31 and $p < .0001$. So, the null-hypothesis of no small-study effects is not rejected also suggesting a publication bias.

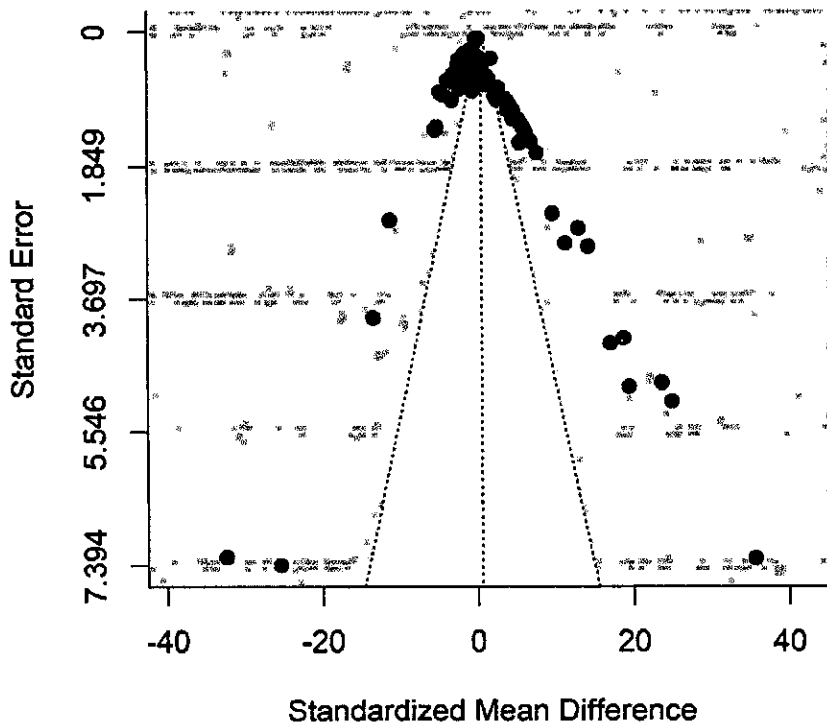


Figure 15. Funnel plot depicting the effect size of each study (x-axis) in relation to the precision of that study (SE; y-axis). Points are not scattered symmetrically within the funnel suggesting a publication bias.

The baujat plot showed some the studies of Dadras et al. 2016, 2019, 2021; Dzyuba et al. 2019 and Le et al. 2011 have higher values on both the x- and y-axis that may be considered to be influential cases on overall results (Fig. 16).

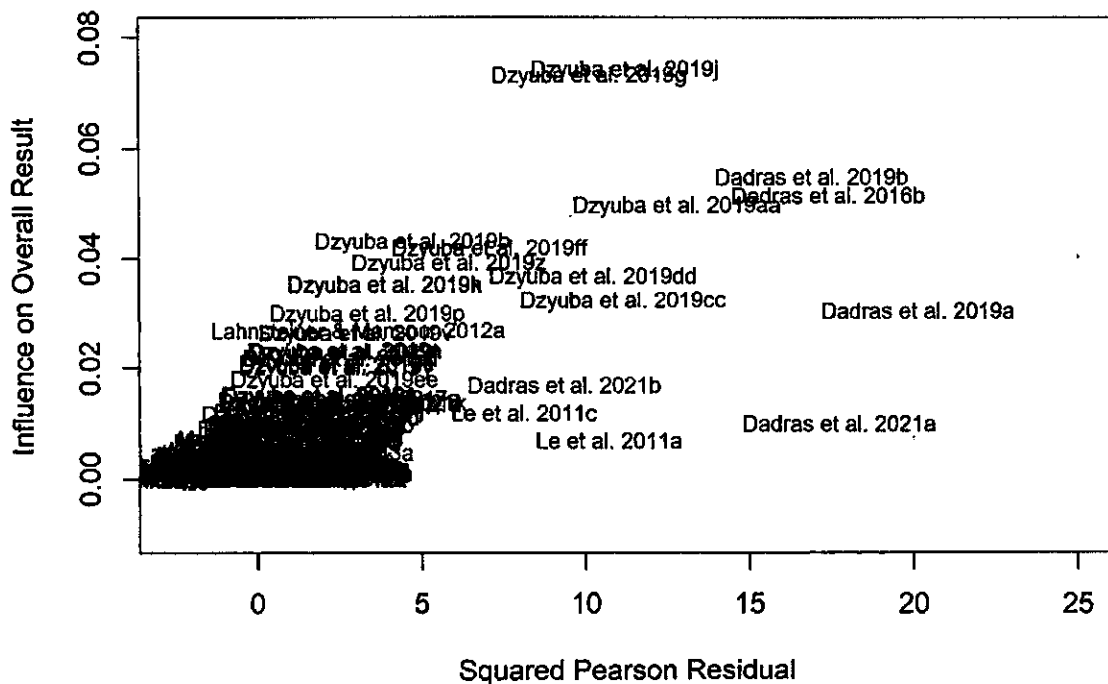


Figure 16. Baujat plot showing the heterogeneity in sperm survival rate meta-analytic data. The plot shows the contribution of each study to the overall Q-test statistic for heterogeneity on the horizontal axis versus the influence of each study.

The aggregated analysis of these multiple treatments showed a total of 20 studies were included in the analysis. The observed aggregated outcomes ranged from -13.16 to 29.64 , with the majority of estimates being positive (65%). The estimated pooled effects size of the model was $d = -0.01$ (95% CI: -0.97 to 0.95). Therefore, the average outcome did not differ significantly from zero ($z = -0.03$, $p = 0.97$). A forest plot showing the observed outcomes and the estimate based on the random-effects model is shown in Fig. 17.

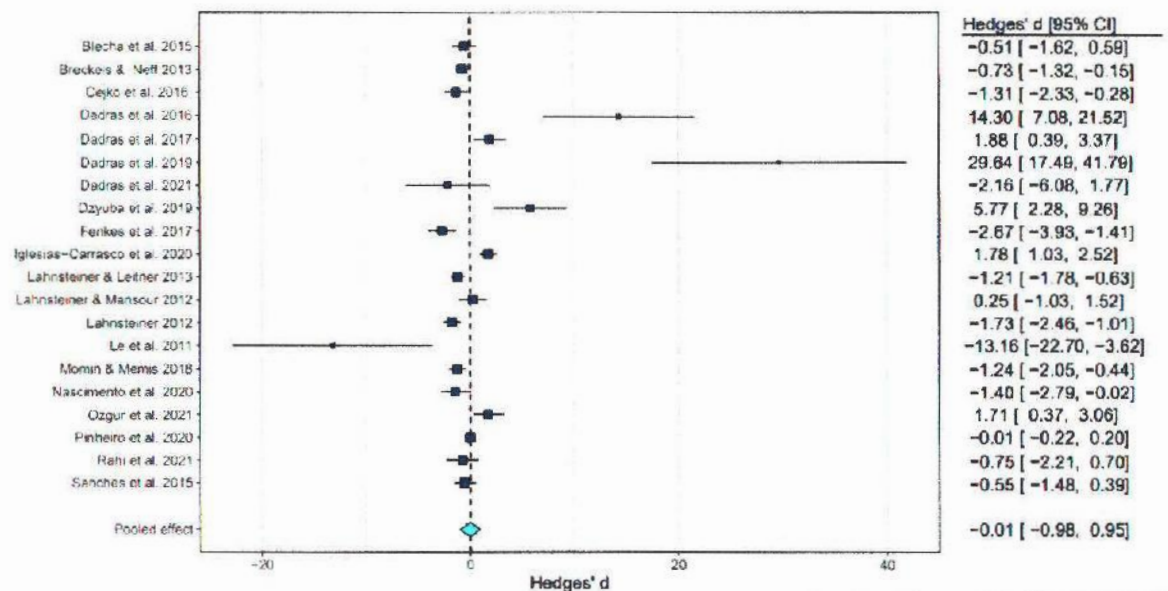


Figure 17. Forest plot reporting the effect size (Hedges' d) for aggregated sperm velocity in different studies having multiple treatments. Hedges' d and 95% confidence interval (CI) effect sizes are reported. The estimated pooled effect size is indicated at the bottom of the figure (cyan diamond shape).

3.7 Effects on sperm volume

A total of 6 studies with 13 multilevel treatments tested the effects of elevated temperature on sperm volume (Table 3). The random-effect model with independent observations showed a significant residual heterogeneity ($df = 12$, $QE = 80.54$, $p < 0.001$) and a larger estimated amount of total heterogeneity ($\tau^2: 2.06$). The mean sperm volume displayed a non-significant negative overall effect size (estimate [CI_{lower} , CI_{upper}] = $-0.19 [-1.02, 0.64]$, $p = 0.65$).

Table 3. Effects of elevated temperature on different fish sperm volume

Sperm traits	Multilevel effect size	Pooled effect size	Study location	Study species	Study environment	Treatment temp (°C)	Control temp (°C)	References
Volume (ml)	0.96 – 4.68	2.82	South Bohemia	<i>Sander lucioperca</i>	Freshwater in lab	3	2	Blecha et al. 2015
	-1.70	-1.70	Brazil	<i>Oncorhynchus mykiss</i>	Freshwater in lab	19	15	Butzge et al. 2021
	-0.47 – 0.30	-0.08	Poland	<i>Lampetra fluviatilis</i>	Marinewater in hatchery	10 and 14	7	Cejko et al. 2016
	-1.40 – -0.51	-0.95	Austria	<i>Salmo trutta</i>	Marinewater in farm	9	5	Lahnsteiner & Leitner 2013
	-0.81 – 1.45	0.02	Turkey	<i>O. mykiss</i>	Freshwater in pond	14	9	Momin & Memis 2018
	-1.13	-1.13	Hungary	<i>S. lucioperca</i>	Freshwater in lab	15	11	Ozgur et al. 2021

Chapter-4

4. Discussion

The reality of worldwide warming is presently irrefutable (Collins et al. 2019; Frolicher et al. 2018). Temperature is one of the foremost critical physicochemical factors that decide the overall functioning of aquatic communities (Miranda et al. 2013). The reproduction in fish, compared with other physiological forms, usually happens in a bounded temperature extend (Portner and Farrell 2008) and thus, little changes in water temperature might essentially influence this process. In this context, abnormal water temperature seems create a mismatch between propagation and ideal environmental conditions for offspring advancement (Durant et al. 2007). The rise in the number of publications in recent years (Fig. 2) revealed the attention of researchers about the effects of global warming on different fish sperm traits. Based on the analysis, European countries take the lead in research on this particular topic (Figs. 3ab) which is not surprising because these European countries have modern research facilities as well as they invest a lot of money for this kind of research. Unfortunately, no African country was found to conduct any research on this topic that has been eligible for this meta-analysis. Therefore, poor countries having valuable fisheries resources should collaborate with the interested rich countries to explore the effects of global warming on the reproductive traits of different fish species. Although 22 species were investigated during these studies (Fig. 4), more species should be included in the future research particularly many important and endangered species are required to expose whether they are sensitive to the elevated temperature and how to protect them and their offspring for the sustainable production and conservation. The analysis revealed that the majority of these studies were carried out under the laboratory conditions (Fig. 5a), however, further research should be conducted in the natural environment where the fish live to know how the wild species are practically affected under the global warming conditions. Since most of the studies converged freshwater and marine water species, some future studies should be conducted with the brackish water species as they are vulnerable with the global warming (Mitra 2013).

In the present study, a significant negative effect of elevated temperature on sperm density has been revealed. Most of the reviewed studies showed that sperm density in different fish species was significantly lower with the elevation of temperature. For examples, Cejko et al. (2016) found that sperm density in *Lampetra fluviatilis* was significantly lower at higher temperature (14°C)

than that of lower temperature (10°C), and Momin and Memis (2018) also showed with *Oncorhynchus mykiss* that sperm density was significantly lower at higher temperature (14°C) than that of lower temperature (9°C). One of the major reasons for this critical decrease of sperm density can be due to the slower formation of spermatozoa during spermiation process within the higher temperature compared to the lower temperature (Momin and Memis 2018). In *Cyclopterus lumpus*, elevated temperatures during gametogenesis was shown to reduce spermatocrit and that's why sperm density was reduced (Tveiten and Johnsen 1999; Pountney et al. 2020). Pountney et al. (2020) and Shappell et al. (2018) also showed consistent results with different species and experimental designs that elevated temperature significantly reduced sperm density. They found the overall negative effect of elevated temperature on sperm density, however, some of their multiple experiments showed positive effects. In the study, there were two different experimental conditions for each temperature in where two types of feeds were incorporated and when feeds were given at 3% body weight of fish then one experiment showed positive effect resulting in increasing sperm density (Shappell et al. 2018). Sperm density was lower in control temperature in where feeds were given at 0.75% body weight of fish (Shappell et al. 2018). Pountney et al. (2020) conducted a study with *C. lumpus* and observed the sperm density was higher at the elevated temperature (14°C) than that of control one (6°C). As the plasma levels of testosterone and 11-ketotestosterone are higher in fish held at high in comparison to low temperature, cAMP levels slowly increased at higher temperature than the lower temperature which also could be a reason for lower sperm density at elevated temperature (Cosson et al. 1995). Studies show that the low sperm density could affect the results of the fertilization rate (Momin and Memis 2018) and hatching success (Myers et al. 2020) in many fish species.

The meta-analysis revealed a significant positive effect of elevated temperature on sperm survival rate in different fish species. For example, Beirao et al. (2014) found that sperm survival rate was significantly higher in *Gadus morhua* at elevated temperature (12°C) than that of cold temperature (3°C). Increasing water temperature could be attributed to both a decrease in water viscosity and an increase in sperm metabolism that may increase the percentage of spermatozoa or higher survival of spermatozoa (Beirao et al. 2014). Similarly Nagy et al. (2016) with *Carassius auratus gibelio*, and Sanches et al. (2015) with *Steindachneridion parahybae* found overall positive effects of elevated temperature on sperm survival. But, among multiple experimental levels, some of the experiments showed the negative effect size. In the study of Sanches et al.



(2015), sperm survival was reduced at elevated temperature (35°C) but they found a good survival rate soon after collection of the sperm at the same temperature (35°C). With the passage of time they found reduced sperm survival rate at the same temperature (35°C) that resulting in negative effect of sperm survival rate among multiple treatment levels. In their experiment, they considered storage time with temperature and sperm quality of fish.

In the present review work, most of the studies showed that sperm velocity was significantly higher with the elevation of temperature. In a study, Dzyuba et al. (2019) found that sperm velocity was significantly higher in *Oreochromis niloticus* at elevated temperature (50°C) than that of cold temperature (10°C). Similar kind of findings were shown by Dadras et al. (2016; 2017) in *Cyprinus carpio*, Dadras et al. (2019) in *Acipenser ruthenus* and *O. mykiss*, Dadras et al. (2021) in *Lota lota*, Dzyuba et al. (2019) in *O. niloticus*, and Ozgur et al. (2021) in *Sander lucioperca*. Usually, an increase in temperature leads to an increase in sperm speed, which is caused by expanded flagellar beating and higher ATP utilization (Alavi and Cosson 2005; Beirao et al. 2014). Cosson et al. (1985), and Billard and Cosson (1992) found that flagellar beating recurrence and values were higher (from 32Hz to 55 Hz) in *O. mykiss* at raised temperature 21°C to 26°C than that of cold temperature (5°C), and after that the sperm speed was increased than that of cold water. Billard and Cosson (1986) observed that a marked increase of the flagellar beat frequency of demembrated or reactivated sperm flagella (from 23 to 82 Hz) when there was an increment within the temperature from 5 to 25 °C. This flagellar beat recurrence would be related with an expanding ATP utilization rate with expanding temperatures (Billard and Cosson 1986). The resulting increase of sperm speed is because of the temperature impact, basically on the axoneme of the sperm tail (Billard and Cosson 1986). Sperm cells may have a slower metabolism at low temperatures than at higher temperatures (Billard and Cosson 1992). Fish species which are specified above for examining sperm speed are basically warm water reproducer and this may be another reason of expanding sperm speed with rise of temperature. But some other studies like Breckels and Neff (2013) in *Poecilia reticulata*, Cejko et al. (2016) in *L. fluviatilis*, Fenkes et al. (2017) in *Salmo trutta*, Lahnsteiner 2012 in *S. trutta*, Lahnsteiner & Mansour (2012) in *S. trutta*, *L. lota*, Le et al. (2011) in *Larimichthys polyactis*, and Momin & Memis (2018) in *O. mykiss* found negative effects of elevated temperature on sperm velocity in multiple experimental levels. Numerous factors (e.g., broodstock origin, nutrition, hormonal treatment and manipulation) are associated with the development, maturation and fertilization of male fish (Mylonas et al. 2010).

Fish that reproduce cold water have a lower temperature range tolerance than that reproduce elevated temperature (Lahnsteiner and Mansour 2012). In the study of Cejko et al. (2016) showed decreased sperm velocity in *L. fluviatilis* at higher temperature (14°C) than that of the lower temperature (7°C) because this species reproduces at lower temperature. *S. trutta* and *L. lota*, also reproduce in cold water (Lahnsteiner and Mansour 2012). *L. polyactis* spawn in the winter (Le et al. 2011). Protein denaturation brought forth by high temperatures resulted in diseases in the sperm tail (Pinheiro et al. 2020) that might be another reason for a reduction of sperm velocity at elevated temperature.

Although no significant effect of elevated temperature on sperm morphology has been revealed in this study, an overall negative effect of higher temperature on sperm morphology has been found. For example, Pinheiro et al. (2020) with *Astyanax altiparanae*, and Sanches et al. (2015) with *S. parahybae* found that the higher number of abnormal sperm was present at elevated temperature (35°C) than that of lower temperature (5°C). *S. parahybae* mainly reproduces at cold temperature and therefore, it may be a reason of the presence of higher number of abnormal sperm with the elevation of temperature. Temperature may influence the occurrence of anomalies in sperm (Pinheiro et al. 2020). In *A. altiparanae*, percentage of morphologically normal sperm was decreased at elevated temperature (30°C) compared to those exposed at lower temperature (20°C and 25°C) (Pinheiro et al. 2020). High temperature affects morphologically normal spermatozoa and the percentage of live spermatozoa (Dadras et al. 2017). At high temperatures, fish sperm's DNA integrity deteriorates (Lahnsteiner and Leitner 2013). Higher temperature alters the spermatozoon chromatin stability, acrosome integrity, and mitochondrial integrity (Dadras et al. 2017). Protein denaturation brought forth by high temperatures resulted in diseases in the sperm tail (Pinheiro et al. 2020). When exposed to extreme temperatures, increasing metabolic rates may be linked to the degradation of sperm morphology (Billard 1995). Aspartate aminotransferase, respiration, and malate dehydrogenase all exhibit enzymatic activity that is directly correlated with sperm quality, according to Lahnsteiner et al. (1998). These elements may have contributed to the normal sperm's quick decline at higher temperatures because the enzymatic activity is directly connected to temperature (Sanches et al. 2015).

An overall negative effect of higher temperature on sperm volume has been revealed in this meta-analysis. For instance, Momin and Memis (2018) working with *O. mykiss* found that sperm volume was lower at 14°C than at 9°C, and Lahnsteiner and Leitner (2013) found lower

sperm volume in *S. trutta* at elevated temperature (9°C) than that of lower temperature (5°C). Cejko et al. (2016) in *L. fluviatilis*, Lahnsteiner and Leitner (2013) in *S. trutta*, and Ozgur et al. (2021) in *S. lucioperca* found similar findings where sperm volume showed a negative relation with the elevated temperature. Low level of plasma sex steroid is found at higher temperature compared to lower temperature and it may be a major cause of decreased sperm volume of fish at elevated temperature (Dorts et al. 2012).

Although no significant effect of elevated temperature on sperm motility has been revealed in this study, an overall positive effect was shown by different studies. The observations of Boryshpolets et al. (2011) in *C. carpio*, Dzyuba et al. (2019) in *O. niloticus*, Dumorne et al. (2018) in *Genypterus blacodes*, Dzyuba et al. (2021) in *A. ruthenus*, Momin and Memis (2018) in *O. mykiss*, Ozgur et al. (2021) in *S. lucioperca*, and Sanches et al. (2015) in *S. parahybae* were similar to this finding, i.e., sperm are more motile at higher temperature. They found that the sperm of the cold-water group required a significantly longer period to achieve the maximum percentage of motility. At the elevated temperature, the seminal plasma peroxidase and seminal lysozyme activity is decreased, which are important oxidative defensive enzyme in brown trout seminal plasma (Lahnsteiner and Mansour 2012). This enzyme is positively correlated with sperm motility in brown trout (Lahnsteiner and Leitner 2013). There are some studies which focused on the specific ions that trigger sperm motility such as K^+ , Ca^{2+} and Mg^{2+} that are present in seawater and their influence on sperm motility and activation are evident (Dumorne et al. 2018; Cosson 2004). In cyprinids, K^+ particle can increase sperm velocity and motility (Morisawa et al. 1983; Krasznai et al. 2000). Sperm motility can be started by modification of the concentration of Ca^{2+} particles in numerous species such as in cyprinids, extracellular Ca^{2+} may be a prerequisite for the start of live sperm motility (Krasznai et al. 2000). A study reported that an increase in temperature, flagellar beating frequency is higher that might increase the sperm motility (Billard and Cosson 1988). An increase in velocity caused by a temperature rise within the swimming solution leads to a shorter length of motility, and then again, bringing down the swimming temperature comes about in a prolonged length of motility and diminished cell speed (Schlenk and Kahmann 1938; Ginzburg 1968; Stoss 1983). On the other hand, Albrizio et al. (2019) in *Paracentrotus lividus*, Blecha et al. (2015) in *S. lucioperca*, Breckels and Neff (2013) in *P. reticulata*, Butzge et al. (2021) in *O. mykiss*, Cejko et al. (2016) in *L. fluviatilis*, Dadras et al. (2016, 2017) in *C. carpio*, Dadras et al. (2021) in *L. lota*, Lahnsteiner and Leitner (2013) in *S. trutta*, Lahnsteiner and Mansour (2012) in *S. trutta*

and *L. lota*, and Le et al. (2011) in *L. polyactis* found negative effects of elevated temperature on sperm motility in multiple experimental levels. At higher temperatures velocity increases and that is why energy resources is limited in fish spermatozoa and metabolic processes leads to lower motility rate and duration (Purchase et al. 2010; Dadras et al. 2016). Lahnsteiner and Mansour (2012) investigated the impact of temperature on the duration of sperm motility in three other cold-water fish species (*S. trutta*, *L. lota*, and *Thymallus thymallus*), and came to the conclusion that a higher temperature is detrimental for extending sperm motility after sperm activation.

By compiling the findings of many studies in the field of elevated temperature and sperm quality, it is evident through this meat-analysis that some sperm traits such as sperm velocity, motility, and survival rate are increased with the elevation of temperature. On the other hand, sperm morphology, density, and volume are decreased with the elevation of temperature.

Chapter-5

5. Conclusion

Global warming is an alarming issue now and temperature is rising day by day. As a result, all individual have to experience many difficulties in their life time. After compilation of many studies through a meta-analysis, the present study clearly indicates the influence of elevated temperature on some sperm traits in different fish species throughout the world. The response of fish spermatozoa to elevated temperature is an increase of velocity, motility and survival rate. In contrast, temperature elevation may decrease the sperm concentration, volume and morphology. Thus, the elevated temperature can severely influence the sperm performance by affecting the fertilization rate, hatching success and offspring fitness in many fish. Therefore, further more research should be carried out to explore the underneath mechanisms about the positive or negative effects of elevated temperature and other climate change variables on different sperm traits and their functions.

Chapter-6

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