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# Recent data of the biology of the twaite shad, *Alosa fallax* returning for spawning to the Szczecin Lagoon (southern Baltic Sea)

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**Abstract:** In 2022–2023 specimens of *A. fallax* are recorded for the first time in approximately 17 years in Szczecin Lagoon. We collected 11 specimens of juveniles, 9 premature and mature females, and 9 premature and mature males (20.3–40.7 cm of total length, aged from 1+ to 4+). The 2+ aged fish was slightly dominated (34.5% of the whole sample). Females in the Szczecin Lagoon were ready to spawn in the age of 3+ and 4+ years, while males partly in 2+, and in the age of 3+ and 4+. Fulton's condition factor of this fish was 0.93±0.14 and Clark's 0.78±0.14. Analysis of correlations between the total length and individual weight of fish revealed that the growth of *A. fallax* was allometric ($b$ < 3.0). The range of gonadosomatic index (*GSI*) was 0.12–26.59%, while the mean of the absolute and relative fecundity was 58,756 eggs per female and 139,650 eggs per kilogram of body weight.

The obtained results indicate the occurrence of an anadromous population of *Alosa fallax* in the studied water areas. However, there is still a need to obtain detailed information on the population status and the biology of *A. fallax* in these areas in order to designate special conservation areas (SACs) for their protection, especially taking into account spawning habitats.

**Keywords:** age of spawning, *Alosa fallax*, Bornholm Basin, fish condition, gonadosomatic index (*GSI*), Pomeranian Bay, protected species

## INTRODUCTION

The twaite shad, *Alosa fallax* (Lacépède, 1803), an anadromous species, is distributed in the northeast Atlantic along coasts and in the seas surrounding Europe, including the North Sea, the Mediterranean Sea, and the Black Sea (Froese and Pauly, 2023). It also occurs sporadically in the Baltic Sea (Rokicki, Rolbiecki and Skóra, 2009).

*Alosa fallax* spends much of its life pelagically in the open waters of coastal seas and migrates into large rivers or lagoons to spawn. Adult fish enter estuaries annually, and then from April to June they migrate upstream. Spawning occurs repeatedly during several nights from May to June (Quignard and Douchement, 1991; Bruslé and Quignard, 2001). The adults usually survive spawning and return to the sea in the fall. Similarly, juveniles (around 7–8 cm total length – *TL*) start their downstream migration into the sea in fall. The maximum recorded size are 60 cm (commonly 40 cm), and weight are 1.5 kg (Quignard and Douchement, 1991; Freyhof and Kottelat, 2008).

According to Quignard and Douchement (1991) *A. fallax* was very common in a number of Baltic and other European waters a century ago, but it became very rare or completely extinct in many waters of its former distribution area during the 1980s. Currently, just a few rivers have higher population sizes including those in the Garonne–Dordogne River system in France or the Elbe River in Germany (Quignard and Douchement, 1991).

Probably, increased pollution from nutrients, heavy metals, and other pollutants in the lagoons of the southern Baltic, blocking of migration routes with dam constructions for hydropower, destroying spawning habitats, and warmer winter periods in these areas over the last 15 years may have affected *A. fallax* population decreases (Thiel *et al.*, 2007; Thiel *et al.*, 2008; HELCOM, 2013). There is no clear evidence regarding which factors have contributed to the disappearance of *A. fallax*.

In the Southern Baltic Sea *A. fallax* catch data were characterised by a 20-year-cyclicity in subdivisions (SD) 24–26 from 1887 to 1959. Based on the available data cannot be possible to confirm that the cyclicity of yields is also true for the population dynamics of *A. fallax* in this area. Nonetheless, there are some indices that in last decade the number of records of *A. fallax* increased (Thiel *et al.*, 2008).

In SD 24–26, a maximum annual yield was noted in 1940, while the minimum – in 1958. Until 1960 catches originated mainly from the Pomeranian Bay and adjacent waters (SD 24), the Gulf of Gdańsk, and the Curonian Lagoon (SD 26) (Thiel *et al.*, 2007). According to Pęczalska (1973), in the years 1953 and 1955 numerous migrations of *A. fallax* to the Szczecin Lagoon were observed, followed by successful spawning. However, from 1960 to 1989, only four records of *A. fallax* were registered in the Southern Baltic Sea, originated from German coastal waters. After a long absence lasting until the mid-1990s, the *A. fallax* population has been increasing in Polish (Szulc and Domagała, 1999; Skóra, 2001; Szulc *et al.*, 2001; Domagała and Szulc, 2007; Draganik, Wyszyński and Kapusta, 2007; Skóra *et al.*, 2012), in Lithuanian (Svagzdys, 1999; Repečka, 2003; Maksimov, 2004; Bacevičius, 2007), and in German (Winkler *et al.*, 2000; Thiel *et al.*, 2007; Thiel *et al.*, 2008) Baltic waters. A total of over 100 records was noted in SD 20–27 from 1990 to 2005 (Thiel *et al.*, 2007). It has to be stressed that the data available from the Baltic Sea included only the period up to 2005 (e.g., Gulf of Gdańsk – Rokicki, Rolbiecki and Skóra (2009), Więcaszek and Skóra (1999); Pomeranian Bay and Szczecin Lagoon – Domagała and Szulc (2007); southern Baltic – Thiel *et al.* (2007), Thiel *et al.* (2008); Curonian Lagoon – Repečka (2003)). Kukuev and Orlov (2018) described the population of *A. fallax* from the Curonian Lagoon using samples collected in 2008–2009; but since then, there have been no reports of its occurrence in the Baltic Sea.

Globally, *A. fallax* is categorised as LC (least concern), since its status was good, and populations of it had been increasing in the North and Baltic seas (Freyhof and Kottelat, 2008).

However, because of decreases in number and distribution, *A. fallax* has been included in Appendix III of the Bern Convention and Annexes II and V of the EC Habitats Directive (Convention, 1982; Council Directive, 1992; Froese and Pauly, 2023). The inclusion of *A. fallax* in the Habitats Directive obliges European Union member states to assess the numbers and exploitation of populations and to designate special areas for conservation (SACs) to safeguard them.

*Alosa fallax* has also been strictly protected under Polish law since 1995 (Skóra, 2001), however from 2016 it has become only a partial protected species (Rozporządzenie, 2016).

Aprahamian *et al.* (2003) concluded that there was a great need for detailed information on the status of *A. fallax* in most parts of its distribution area, especially in the western and southern Baltic Sea, where biological data on this species are very scant. Also Thiel *et al.* (2008) pointed out that it seems to be crucial to start an international study about distribution, habitat use, genetics, morphology and conservation status of *A. fallax* from different regions of the Baltic Sea, North Sea and their transitional water.

The aims of this study were to analyse the present occurrence of *A. fallax* in the Szczecin Lagoon (southwestern Baltic Sea Basin), to assess fish condition (including the gonadosomatic index – *GSI* and the relationship between total length and weight), fecundity, as well to compare these data with historical data from the period before 2002.

## MATERIALS AND METHODS

### STUDY AREA

The Szczecin Lagoon is situated in the Oder River estuarine system (ORES), which consists of three major components: the northern most part is the Pomeranian Bay (ICES III Subdivision SD 24), a brackish (salinity about 6–7 PSU) Baltic embayment, which receives inflows of usually oligohaline (salinity about 1 PSU) to fresh water from the Szczecin Lagoon. The middle ORES component intercepts River Oder waters and is periodically affected by incursions of seawater from the Pomeranian Bay (Radziejewska and Schernewski, 2008). The southern most part of ORES is formed by the downstream reaches of the Oder and the adjacent Lake Dąbie, where salinity seldom exceeds 0.4 PSU (Jasińska, 1993).

### MATERIAL

Samples of the twaite shad for this study were caught as bycatch during monthly research samplings of vimba bream (*Vimba vimba*), and whitefish (*Coregonus lavaretus*), in the Szczecin Lagoon, from May to July in 2022 and 2023. One *A. fallax* specimen caught in September 2018 in Lake Dąbie by a commercial fisher was also included. Detailed characteristics of the samples examined are presented in Table 1.

The historical *A. fallax* material (a total of nine specimens) was used to compare the biological parameters of fish condition with the present data. Six specimens were collected from the bycatch of commercial fisheries in the Pomeranian Bay, and three adult females were caught in the Szczecin Lagoon, respectively during the periods of May 1997–July 1998, and May 2000–July 2002. Figure 1 presents both current and historical sites of sampling.

### METHODS

The fish were measured (total length – *TL*) to the nearest millimeter, weighed (total weight – *W* and gonad weight – *WG*) to the nearest gram, and age was determined using scales

**Table 1.** Detailed characteristics of the sample examined of *A. fallax* from the Szczecin Lagoon ($n$ = 29) and from the Lake Dąbie ($n$ = 1) in the chronological order

| Date of sampling | Location of sampling | *n* | Total length (cm) | Standard length (cm) | Body weight (g) |
|---|---|---|---|---|---|
| 15 Sep 2018 | Lake Dąbie: 53°26'56"N, 14°39'34"E | 1 | 37.4 | 32.0 | 463.0 |
| 26 May and 4 June 2022 | Szczecin Lagoon: 53°45'20"N, 14°31'00"E | 5 | 40.5–40.7 | 34.0–34.3 | 558.6–632.2 |
| 27 May 2022 | Szczecin Lagoon: 53°47'00"N, 14°19'89"E | 6 | 28.1–30.9 | 24.1–25.1 | 193.3–234.4 |
| 5 Jun 2022 | Szczecin Lagoon: 53°46'04"–53°46'37"N 14°17'19"–14°17'92"E | 5 | 27.5–28.5 | 23.1–24.0 | 168.1–190.0 |
| 30 Jun and 5 July 2022 | Szczecin Lagoon: 53°47'00"N, 14°19'89"E | 5 | 29.0–31.6 | 24.2–28.7 | 154.1–320.3 |
| 7 Jul 2022 | Szczecin Lagoon: 53°47'00"N, 14°19'89"E | 2 | 18.3–20.3 | 15.3–18.3 | 70.7–97.1 |
| 29 Jun 2023 | Szczecin Lagoon: 53°46'04"–53°46'37"N 14°17'19"–14°17'92"E | 6 | 18.8–28.4 | 16.4–23.4 | 62.4–183.0 |

Explanations: $n$ = number of individuals.
Source: own elaboration.

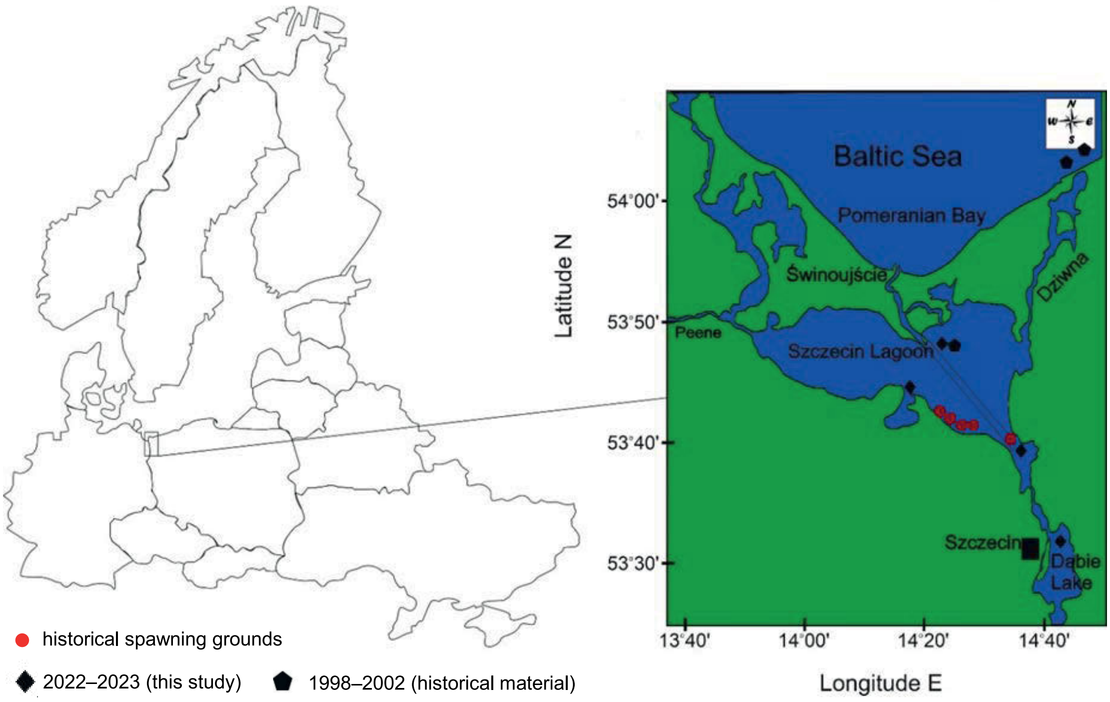


**Fig. 1.** Locations of sampling of *Alosa fallax* with historical spawning grounds (Pęczalska, 1973; Domagała and Szulc, 2007); source: own elaboration and literature

(Jackson, 2007). The present sample was divided into four groups according to estimated age. The first group included fish aged 1+ (*TL*: 18.3–20.3 cm), the second – fish aged 2+ (*TL*: 21.5–29.0 cm), the third – fish aged 3+ (*TL*: 28.5–33.6 cm), and the fourth –fish aged 4+ (*TL*: 37.0–40.7 cm).

Fish condition was estimated with Fulton's fish condition factor $K$ and the Clark index. The condition factor was calculated with the Fulton formula:

$$K = \left(\frac{W}{TL^3}\right)100 \quad (1)$$

where: $W$ = total fish weight (g), $TL$ = total fish length (cm) (Rokicki, Rolbiecki and Skóra, 2009).

The Clark index was calculated with the same formula, but gutted fish weight was used instead of total fish weight (Ritterbusch-Nauwerck, 1995). Student's $t$-test was used to verify the hypothesis that there is a lack of differences in condition coefficients between males and females (in the program Statistica 13.0).

The relationship between length and weight was calculated using the following classical equation (Froese, 2006):

$$W = a \cdot TL^b \tag{2}$$

where: $a$, $b$ = the equation parameters calculated applying a linear regression model using the logarithmic form of equation (Froese, Tsikliras and Stergiou, 2011):

$$\log W = \log a + b \log L \tag{3}$$

Parameter $b$ indicates isometric growth in body proportions if $b = 3$, or allometric growth if $b \neq 3$ (Froese, 2006). Length–weight relationships are of great importance in fishery assessment studies since they provide information about the growth of the fish, its general fitness.

The sex and maturity stage of gonads were determined macroscopically based on their appearance, e.g., coloration, size, shape and on relative size of the gonads. Maturity stages were determined according to the *scale* defined by *Maier* (Kosior and Kuczyński, 1997). Moreover, the gonadosomatic index (*GSI*) was calculated to assess changes in fish maturity and spawning stage (Nachón *et al*., 2015) according to formula:

$$GSI = \frac{Wg}{W} 100 \tag{4}$$

where: $Wg$ = gonad weight (g).

The ovaries and testes from each female and male were removed and weighed to the nearest 0.01 g. In mature females, sub-samples of approximately 1 g were taken from the anterior, central, and posterior regions of each ovary and preserved in 4% formalin. The number of oocytes in each sub-sample was counted ($S$), and fecundity was computed from means. Individual absolute fecundity ($F$) was computed, by using following formula of:

$$F = \frac{Wg \cdot S}{ws} \tag{5}$$

where: $S$ = number of eggs in the subsample, $ws$ = weight of sub-sample (g).

The relative fecundity ($FR$) was the number of eggs per kilogram of body weight (Kjesbo *et al*., 1991).

## RESULTS

The former records of the species in this area (historical material) we noted in 1997–2002 (nine specimens) in the area of the Pomeranian Bay and Szczecin Lagoon. Next in May–July 2022 and 2023, 29 specimens were caught in the Szczecin Lagoon, during monthly research samplings of *Vimba vimba* and *Coregonus lavaretus*, caught as bycatch.

In this study (29 fish collected in 2022 and 2023), we recorded juveniles (11 specimens), nine females (four premature and five matures), and nine males (five premature and four mature ones), aged from 1+ to 4+ – Photo 1. The fish 2+ aged slightly dominated in captures (34.5% of the whole sample).

**Photo 1.** Scale of mature female of *Alosa fallax* aged 4+ from Szczecin Lagoon (May, 1998) (phot.: *B. Więcaszek*)

Juveniles (1+) constituted to 31.5%, fish aged 3+ – to 29.1% and fish aged 4+ – to 4.9%.

The mean values of Fulton's condition factor for all of the fish were 0.93 ±0.14, while the mean values for Clark's factor were 0.78 ±0.14. Juvenile fishes (1+) had the highest Fulton's (1.08) and Clark's (0.96) indices of condition. The older fish (from 2+ to 4+) had lower condition indices and Clark's of this group was 0.85 ±0.09, and 0.69 ±0.06, respectively (Tab. 2). Females and males had similar body condition for both Fulton's ($t$ = 0.486, $p$ > 0.05) and Clark's ($t$ = 0.357, $p$ > 0.05) indices. Historical data on *A. fallax* from the Szczecin Lagoon and the Pomeranian Bay collected in 1997–1998 and 2000–2002, respectively indicated that the ranges of the values of Fulton's for adult fish were 0.76–1.0, and for Clark's condition factors were 0.62–0.89.

The analysis of the correlations between total lengths and individual weights of all the fish ($W = 0.04TL^{2.5442}$) revealed that *A. fallax* growth was allometric ($b$ < 3.0), statistically significant ($p$ < 0.05), and had a high correlation coefficient ($R$ > 0.96).

The mean *GSI* value was the smallest for the juveniles (0.27%). The *GSI* increased markedly in fish aged 2+ (to 3.17% in females and 2.30% in males), although it was still low for some immature males aged 2+ (0.63%). For males aged 3+ and 4+, the ranges of *GSI* were 6.01–15.9% and 4.7–10.5%, respectively. The range of *GSI* values for adult females aged 3+ was 5.34–6.72% (*TL*: 31.9–33.6 cm), while for females aged 4+ it was 14.32–26.59% (*TL*: 40.5–40.7 cm) – Table 2. According to historical data on *A. fallax* (nine individuals) collected from the Szczecin Lagoon and the Pomeranian Bay the ranges of *GSI* values for adult females ranged from 5.69 to 17.75, while for males – from 5.16 to 5.30. The highest value of *GSI* was recorded in female (*TL*: 36.0 cm) caught in the Szczecin Lagoon, the historical spawning ground for *A. fallax* (Tab. 3).

The individual absolute fecundity ($F$), estimated for five mature females, with the highest *GSI*, ranged from 29,111 to 86,352 eggs, while relative fecundity ($FR$) values ranged from 128,222 to 158,875.The mean value of $F$ was 58,756 eggs, whereas the $FR$ amounted to 139,650 eggs (Tab. 4).

**Table 2.** The Fulton's, Clark's, and gonadosomatic index (*GSI*) values in age groups of *Alosa fallax* from the Szczecin Lagoon and Dąbie Lake

| Class | Sex | Number of specimens | Total length ±*SD* (cm) | Standard length ±*SD* (cm) | Fulton index mean ±*SD* | Clark index mean ±*SD* | *GSI* (%)<br>range<br>mean ± *SD* |
|---|---|---|---|---|---|---|---|
| 1+ | juv. | 10 | 19.5 ±0.60 | 16.5 ±0.80 | 1.08 ±0.08 | 0.93 ±0.09 | 0.12–0.47<br>0.27 ±0.10 |
| 2+ | F | 4 | 29.3 ±2.40 | 24.5 ±2.20 | 0.82 ±0.57 | 0.68 ±0.05 | 0.85–6.72<br>3.17 ±2.47 |
| | M | 4 | 28.4 ±1.60 | 23.5 ±0.70 | 0.82 ±0.09 | 0.66 ±0.09 | 0.13–5.32<br>2.30 ±2.27 |
| | juv. | 1 | 24.5 | 20.6 | 0.85 | 0.72 | 0.63<br>0.63 |
| | all | 9 | 28.2 ±2.70 | 23.5 ±2.10 | 0.82 ±0.07 | 0.68 ±0.07 | 0.13–6.72<br>2.54 ±2.37 |
| 3+ | F | 4 | 31.0 ±0.90 | 27.3 ±0.00 | 0.86 ±0.08 | 0.71 ±0.06 | 5.01–6.95<br>5.89 ±0.55 |
| | M | 4 | 28.5 ±0.00 | 23.7 ±0.20 | 0.81 ±0.01 | 0.68 ±0.00 | 5.01–6.95<br>5.98 ±0.97 |
| | all | 8 | 29.7 ±1.40 | 25.5 ±1.80 | 0.84 ±0.06 | 0.70 ±0.05 | 5.01–6.95<br>5.93 ±0.79 |
| 4+ | F | 1 | 40.6 | 34.1 | 0.89 | 0.67 | 14.23–26.59<br>20.41 |
| | M | 1 | 37.0 | 32.0 | 0.91 | 0.64 | 7.30<br>7.30 |
| | all | 2 | 39.4 ±1.70 | 33.4 ±1.00 | 0.90 ±0.05 | 0.66 ±0.03 | 7.3–26.59<br>16.04 ±7.98 |
| All | F | 9 | 29.7 ±6.80 | 25.2 ±5.80 | 0.89 ±0.13 | 0.73 ±0.12 | 0.21–26.59<br>6.27 ±7.56 |
| | M | 9 | 27.6 ±4.60 | 23.0 ±4.00 | 0.87 ±0.11 | 0.71 ±0.11 | 0.12–7.30<br>3.13 ±2.85 |
| | juv. | 11 | 21.1 ±2.68 | 18.0 ±2.20 | 1.03 ±0.12 | 0.88 ±0.11 | 0.12–0.64<br>0.35 ±0.16 |
| | all | 29 | 26.8 ±6.25 | 22.6 ±5.20 | 0.91 ±0.14 | 0.75 ±0.13 | 0.12–26.59<br>3.78 ±5.62 |

Explanations: F = female, M = male, juv. = juvenile, *SD* = standard deviation.
Source: own study.

**Table 3.** Data on *Alosa fallax* from Szczecin Lagoon and Pomeranian Bay collected in 1997–1998 and 2000–2002

| Total lengths (cm) | *N* | Date and location of sampling | Range of total weight (g) | Fulton's index | Clark's index | Gonadosomatic index (%) |
|---|---|---|---|---|---|---|
| 19.0 (juvenile) | 1 | 22 May 1997, Szczecin Lagoon | 62.0 | 0.90 | 0.76 | – |
| 32.4–36.2 (F) | 3 | 22 May 1997, Szczecin Lagoon | 260.1–423.0 | 0.76– 0.89 | 0.62–0.68 | 6.75–17.75 |
| 43.5–45.4 (F) | 2 | 1 June 1998, Pomeranian Bay | 890.0 | 0.95 | 0.78 | 5.69 |
| 45.0 (M) | 2 | 30 May 2000, Pomeranian Bay | 900.0–910.0 | 0.99–1.00 | 0.88–0.89 | 5.16–5.30 |
| 35.1 (M) | 1 | 28 May 2002, Pomeranian Bay | 371.0 | 0.86 | 0.75 | 6.77 |

Explanations: F = female, M = male, *N* = number of specimens.
Source: own elaboration based on historical data (own data from 1997–2002).

**Table 4.** Absolute (*F*) and relative fecundity (*FR*) of mature females of *Alosa fallax* from the Szczecin Lagoon

| Individual fecundity | *TL*: 40.7 4+<br>*W*: 558 | *TL*: 40.5 4+<br>*W*: 632 | *TL*: 33.6 3+<br>*W*: 320 | *TL*: 31.9 3+<br>*W*: 257 | *TL*: 30.1 3+<br>*W*: 211.1 | Range | Mean |
|---|---|---|---|---|---|---|---|
| Absolute (*F*) | 71,625 | 86,352 | 42,356 | 34,685 | 29,111 | 29,111–86,352 | 58,756 |
| Relative (*FR*) | 128,222 | 136,590 | 158,875 | 134,856 | 138,623 | 128,222–158,875 | 139,650 |

Explanations: *TL* = total length (cm), *W* = total weight (g), 3+, 4+ = age in years.
Source: own study.

## DISCUSSION

In Europe, relatively little is known concerning the biology of *A. fallax*; especially the juvenile life stages are very poorly understood (Aprahamian *et al*., 2003; Thiel *et al*., 2008). In the Baltic Sea, *A. fallax* is also a poorly known species (Aprahamian *et al*., 2003; Kukuev and Orlov, 2018).

In this study, we found specimens of *A. fallax* occurred after 17 years of absence in the area of its historical spawning places in the Szczecin Lagoon. Some specimens were recorded in 1997–1998 and 2000–2002 in the Pomeranian Bay and Szczecin Lagoon. The last records of this species in these areas were noted in 2005 by Domagała and Szulc (2007). Since then, no records were noted. Dudko *et al.* (2015), who conducted fish composition in the Pomeranian Bay in 2006–2015, did not find any records of *A. fallax* in the area. Similarly, the research carried out by Więcaszek *et al.* (2023) in 2010–2019 in the Pomeranian Bay, did not reveal the presence of *A. fallax*.

The freshwater phase of *A. fallax* spawning migrations begins in early May at the northern limits of its range of occurrence, usually extending for 2–3 months for northern stocks, and is associated with temperatures of 10–12°C (Sabatié, 1993; Magath and Thiel, 2013). Anadromous populations mature at ages ranging from two to nine years old with a majority of females maturing at 4–5 years, and males maturing one year earlier (Bruslé and Quignard, 2001; Bensettiti *et al.* (coord.), 2002; Aprahamian *et al*., 2003). First-year adults undertake the spawning migration as practice, while second year or older specimens spawn above sandy and muddy substrates. Nearly all populations of *A. fallax* have a high proportion of repeat spawners, and most populations have high proportions of fish that spawn two or three times (Sabatié, 1993; Aprahamian *et al.* 2003).

According to Muus and Nielsen (1999), the length at maturity of this species is between *TL* of 30.0–40.0 cm. Maitland and Lyle (2005) indicate that females are ready to spawn at *TL* of 36.0 cm, while males – at *TL* of 34.0 cm. Similarly, in this study females in the Szczecin Lagoon were ready to spawn at *TL* of 30.1–40.7 cm, while males – at *TL* of 30.6–37.0 cm.

We recorded juveniles (1+) and individuals from 2+, 3+ and 4+ age groups. The immature females were aged 2+, with low *GSI* (0.85–1.79%), while mature females were aged 3+ and 4+ (*GSI* ranges 5.55–6.71% and 14.23–26.59%, respectively). In the 2+ aged group of males, almost half (43%) of individuals were mature, with the mean value of *GSI* = 5.36%. Males aged 3+ and 4+ were mature with the means of *GSI* were 5.98 and 7.30%, respectively (Tab. 2). Analysis of *GSI* of adult *A. fallax* specimens, of total length above 32.0 cm, from the Pomeranian Bay and Szczecin Lagoon caught in 1997–1998 and 2000–2002 showed similar range of values when compared to the current sample under study. In turn, in the Ulla River (NW Iberian Peninsula), mature female age ranged from four to seven years (Nachón *et al*., 2015). The *GSI* values ranged from 6.6 to 21.4%, with the mean 12.5% (Nachón *et al*., 2015). They were very close to our results, whereas *A. fallax* collected along the Atlantic coasts had slightly higher *GSI* values range, from 13.8 to 27.8% (Sabatié, 1993; Aprahamian *et al*., 2003).

Absolute fecundity of this species has been reported to range from 25,940 to 675,000 eggs, and relative fecundity from 42,540 to 403,562 eggs (Sabatié, 1993). For a given size, female in better condition exhibit higher fecundity (*Kjesbo et al*., *1991*), what was confirmed by results of our study (Tab. 4). Mean value of *F* in the Ulla River was 96,471 oocytes, while those for relative fecundity *FR* was 87,142 oocytes (Nachón *et al*., 2015), and in Sebou (Morocco) was about 50,000 oocytes (*F*) and 103,270 oocytes (*FR*), respectively (Sabatié, 1993). In Gironde estuary, *F* of *A. fallax* was 97,926 eggs and *FR* – 147,378 eggs per 1,000 g (Taverny, 1991). In this study the mean value of *F* and *FR* was lower (58,756 and 139,650 oocytes, respectively). The low value of *F* of fish from Szczecin Lagoon than in study by Nachón *et al.* (2015) and Taverny (1991) was due to the shorter length of our fish. Our study provides for the first time data on the fecundity of *A. fallax* in Polish waters.

The condition of the *A. fallax* from the Oder estuary examined for this study did not differ substantially from that noted in other European populations. The specimens examined for the current study had an average Fulton's coefficient of 0.93, while that reported for fish from the Gulf of Gdańsk (Poland) was 0.91–0.96 (Rokicki, Rolbiecki and Skóra, 2009), and that of the population from the Danube River (Bulgaria) was 0.90 (Nachev *et al*., 2022). In the Ulla River the mean Fulton's condition factor was 0.91 (range 0.67–1.09) (Nachón *et al*., 2015). The current study did not reveal large differences in condition among specimens of different length or sex classes, but a wide range of values for Fulton's and Clark's conditions factors were noted at 0.63–1.24 and 0.55–1.08, respectively, which could have resulted from the fish being caught at different times of the year. For example, the highest condition measured by the Fulton coefficient was observed in fish caught in May (0.98–1.24) and September (0.88), while the lowest in June (0.63–0.86) and July (0.64–0.81). This is due to the fact that the fish from June and July have already spawned (Sabatié, 1993; Magath and Thiel, 2013). The ranges of Fulton's and Clark's conditions factors were very similar when data from this study was compared to the historical material from the Pomeranian Bay from the 1998–2002 period (Tab. 3). As Višnjic-Jeftic *et al.* (2013) reported, the period in which fish are caught, the length of their spawning migrations, and the prevalence of parasitic infection can all substantially influence fish condition (Rokicki, Rolbiecki and Skóra, 2009; Gérard *et al*., 2016). The lowest values of Fulton's coefficient and *GSI* were reported for fishes immediately following spawning (Stankus, 2009). Additionally, as Višnjic-Jeftic *et al.* (2013) reported, fish condition decreases as distances covered to spawning grounds increase. During anadromous migration, fish utilise the lipids and protein stored in their bodies as sources of energy (Leonard and McCormick, 1999). For example, the Fulton's condition coefficient of *Alosa immaculata* from the Black Sea was 1.21 for females and 1.02 for males (Samsun, 1995), but during their spawning migration in the River Danube it fell to 0.76 (after migrating 743 km of the river – Kolarov, 1985), and it was even as low as 0.65 (after migrating 861 km of the river – Višnjic-Jeftic *et al*., 2013).

This study confirmed that *A. fallax* occurrence shows the multiannual fluctuations in the area of the Pomeranian Bay and the spawning sites in the Szczecin Lagoon. The last known historical spawning grounds of this species in the Szczecin Lagoon in the Polish part, were noted in the vicinity of the Chełminek Isle (Pęczalska, 1973), and according to Domagała and Szulc (2007) the spawning grounds were found also off 300 m from the coast at the level of Brzózki and Warnołęki villages in the Szczecin Lagoon (Fig. 1).

Still, according to Thiel *et al.* (2008), it is essential to monitor *A. fallax* in order to establish the status of the species against a predetermined set of conservation objectives. Data should be collected from various countries in a consistent and systematic manner.

## CONCLUSIONS

This study confirmed that *Alosa fallax* occurrence shows the multiannual fluctuations in the area of the Pomeranian Bay and the spawning sites in the Szczecin Lagoon.

Females in the Szczecin Lagoon were ready to spawn in the age of 3+ and 4+ years (*TL*: 30.1–40.7 cm), while males were mature partly in 2+ (*TL* about 28.0 cm), and mature in the age of 3+ and 4+ (*TL*: 30.6–37.0 cm).

Because there is few data on the reproduction of the *A. fallax* in Pomeranian Bay and in adjacent waters, there is still need for detailed information on the status of this species in these areas, to designate special areas for conservation (SACs) to safeguard them, especially including the spawning habitats.

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## CONFLICT OF INTERESTS

All authors declare that they have no conflict of interests.

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