ABSTRACT. A comparison was made of the incubation period and the dynamics of the hatching of the offspring of three groups of fish (brown trout, sea trout that had smoltified, sea trout that had not smoltified) that were reared under the same conditions and spawned on the same day. The length of the incubation period differed ranging from 304 to 376°D among the offspring of individual fish as well as among the fish groups. The eggs of brown trout developed the most slowly (average 347°D), while those of the smoltified sea trout developed the quickest (average 336°D). No dependence was determined between incubation period and egg size. The longer the incubation period was, the shorter the entire hatching period was, but its peak was more extended lasting from 5 to 34°D. The duration of the hatching peak decreased as the average egg size increased.

Key words: SEA TROUT (SALMO TRUTTA L), INCUBATION, HATCHING, HATCHERY

INTRODUCTION

For salmonid fish such as sea trout, Salmo trutta L., or salmon, Salmo salar L., the first days following hatching are a critical period. The larvae are subjected to very high mortality dependent on density that results from strong competition for position (Elliott 1994). The fish that have the advantage in this competition are those that leave the nest in a more advanced developmental stage (Garcia de Leaniz et al. 2000) and are larger (Chapman 1962). Most importantly, however, the fish with the most advantageous situation are those that hatch earlier (Mason and Chapman 1965, Elliott 1986, Chandler and Bjornn 1988). Over time, these differences become more pronounced (Garcia de Leaniz et al. 2000), and the fish differ in size (Thorpe 1977), which has a fundamental impact on their futures (Thorpe 1989, Metcalfe and Thorpe 1992, Dębowski 2002). A difference of a few days in the hatch period can result in a year’s difference in the time of migration (Metcalfe and Thorpe 1992). Meanwhile, spawning within a single salmon
population can extend to a period as long as ten weeks (Heggberget 1988, Fleming 1996). The length of the egg incubation period also varies. In addition to the obvious dependence on environmental conditions (Humpesch 1985, Elliott and Hurley 1998), it can vary among different populations (Donaghy and Verspoor 1997, Berg and Moen 1999), among the offspring of individual fish (Berg and Moen 1999, Vollestad and Lillehammer 2000), and even within a batch of eggs from a single female (Kaj and Lewicka 1962, Bonis³awska et al. 2000, Garcia de Leaniz et al. 2000).

The aim of the work was to examine the impact the origin of sea trout and brown trout and their life histories had on the length of the egg incubation period and the dynamics and length of the hatching period as well as any dependencies between them.

MATERIALS AND METHODS

The milt and eggs used in the experiment were obtained from sea trout that were the offspring of fish caught in the lower Vistula River. These fish were reared at the Department of Salmonid Research in Rutki of the Inland Fisheries Institute in Olsztyn (northern Poland). The first group (TN) was comprised of three females and three males that had not smoltified and had matured at ages of 1+ (males) and 3+ (females) and had been selected from among fish aged 6+ with a known life history (Dębowski 2002). The second group (TS) was comprised of fish that had smoltified at the age of 1+ and had matured at the aged of 2+ (males) or 3+ (females). The third group (TT) was comprised of brown trout that originated from the stock also held at the Rutki facility. The characteristics of the spawners are presented in Table 1.

<table>
<thead>
<tr>
<th>Group</th>
<th>Sex</th>
<th>Total length (range: mm)</th>
<th>Body weight (range: g)</th>
<th>Range of volume of 30 eggs (cm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TN</td>
<td>Female</td>
<td>465 - 467</td>
<td>1184 - 1254</td>
<td>2.5 - 3.6</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>509 - 554</td>
<td>1504 - 1820</td>
<td>-</td>
</tr>
<tr>
<td>TS</td>
<td>Female</td>
<td>477 - 502</td>
<td>1276 - 1466</td>
<td>2.6 - 3.0</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>488 - 544</td>
<td>1350 - 1616</td>
<td>-</td>
</tr>
<tr>
<td>TT</td>
<td>Female</td>
<td>470 - 510</td>
<td>1422 - 1726</td>
<td>2.8 - 3.1</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>480 - 490</td>
<td>1344 - 1742</td>
<td>-</td>
</tr>
</tbody>
</table>

A comparison was made of three groups of fish that were reared under the same conditions: two groups of sea trout of the same origin but with different life histories
and a group of brown trout of a different origin but with a similar life history to the TN sea trout group.

Artificial spawning was performed on November 14, 2001 by cross fertilizing all of the males and females in each group. Thus, nine portions of fertilized eggs were obtained from each group for a total of 27. These were placed in separate inserts in longitudinal flow troughs. The water temperature throughout the incubation period ranged from 0.1 to 6.0°C at an average of 2.65°C. None of the analyzed traits depended on the position of the insert in the trough (Kruskal-Wallis test). The size of the eggs was measured in a cylinder filled with water as the volume of 30 eggs expressed as cm³. It ranged from 2.5 to 3.6 cm³ (Table 1) and did not differ among the groups of fish (Kruskal-Wallis test). After the eggs had reached the eyed stage on February 15, 2002, 300 eggs were left in each insert. Once hatching had begun, initially the number of hatched larvae and then later that of unhatched eggs was counted daily between 10:00 and 12:00.

The dates when the first larvae appeared, 50% of the larvae had hatched, and the last larvae hatched were analyzed. These were expressed as the number of days from the beginning of incubation (spawning date). The hatching period was described according to the times in which the following percentages of larvae hatched: the first 5%; the subsequent 45% (from 5 to 50%); the subsequent 45% (from 50 to 95%); the final 5%. The length of the entire hatching period and that of the middle 90% of larvae (disregarding the first and last 5%) were also analyzed. The lengths of the periods were expressed in the number of degree-days (°D) or as full days.

The dependence between the previously mentioned variables that determined the course of hatching – egg size, egg group, and origin, were analyzed both in the context of the group and the individual males and females within groups. Non-parametric tests were applied – the Kruskal-Wallis test for comparing variation in various groups and the Spearman correlation to test the dependence of two variables. Statistical analysis was conducted with the STATISTICA program (StatSoft Inc. 2003).

**RESULTS**

**HATCHING PERIOD**

The first larvae appeared on 23 March, which was after 129 days of incubation or the equivalent of 304°D. The variation (range) of the period during which all por-
tions of eggs began hatching was 9 days or 35°D (Fig. 1). No dependence was confirmed between the beginning of hatching and egg size. It was confirmed, however, that it was not the same for all of the offspring of all the females (P < 0.029) or males (P < 0.038). It also varied among the different groups of fish (P < 0.004), and the trout (group TT) began hatching significantly later than did the fish from group TS. The period when hatching began in the eggs of the sea trout was compared using the Mann-Whitney U test, which also indicated differences between them. The larvae from the TS eggs hatched earlier than did those from the TN eggs (P < 0.025). While no differences were detected among the offspring of the sea trout females and males, such differences were noted among the males in the trout group (P < 0.049).

The differences in the hatching period of 50% of the larvae was up to 6 days and ranged from 136 to 142 days of incubation or from 328 to 361°D (Fig. 1). This period also did not depend on egg size (Fig. 2), but it did differ among the offspring of individual females (P < 0.007) and males (P < 0.017). Significant differences (P < 0.001) were determined among eggs of different origin, with hatching occurring later in group TT than in group TS. Only in one group, TT, was there also a significant difference confirmed between females (P < 0.047). The hatching period of half of the larvae was correlated (r = 0.537, P < 0.01) with the date on which hatching began.

![Fig. 1. Variations (range) in the period when hatching started (D₀), 50% of the larvae hatched (D₅₀), the conclusion of hatching (D₁₀₀), and temperature (T).](image-url)
The difference in the maximum length of incubation was 7 days (from 138 to 145 days) and 37°D (from 339 to 376; Fig. 1). The period in which hatching finished varied among the individual females (P < 0.019) and males (P < 0.022). It was significantly later in the brown trout (TT) than it was in both of the remaining groups (P < 0.002). In the brown trout group, these differences were also confirmed for individual females (P < 0.045) and for males (P < 0.048) from the TN group. The end of hatching was correlated with the beginning (r = 0.525, P < 0.01) and the middle (r = 0.773, P < 0.01).

**COURSE OF HATCHING**

The hatching of the first 5% of the larvae took from 0 to 8 days or 0 to 33°D. Although the length of this period did not depend on the size of the eggs, it was not the same with all of the females (P < 0.050). No differences were confirmed, however, among the groups of fish. This was inversely correlated with the date hatching started (r = -0.752, P < 0.01).

The hatching period of the next 45% of the larvae was far less variable at 0 to 3 days or 0 to 17°D. This did not depend on either when hatching started or the length of the materials.
hatching period of the first 5% of the larvae. No differences were detected among the various fish or their groups.

The subsequent 45% (from 50 to 95%) of the larvae hatched within a period of 1 to 4 days or from 5 to 22°D. The length of this period did not depend on egg size, but it varied among eggs of different origin (P < 0.013). The hatching period of the trout larvae (group TT) was the longest. No differences were noted among the individual males or females. A correlation was confirmed with the hatching date of half of the larvae (r = 0.495, P < 0.01).

The hatching of the last 5% of the larvae lasted from 0 to 3 days or from 0 to 17°D. This was independent of both the size and origin of the eggs. It was also not correlated with the date of the beginning or middle hatching periods, the length of the hatching period of the first 5%, or the preceding 45% (from 50 to 95%). It was, however, inversely dependent on the length of the hatching period of the first 45% of the larvae (5 to 50%) (r = -0.467, P < 0.02).

LENGTH OF HATCHING PERIOD

The entire hatching period was from 3 to 11 days or from 17 to 49°D. It did not depend on the date that hatching began, but it was positively correlated with the hatching period of the first 5% of the larvae (r = 0.698, P < 0.01). It also did not depend on the dates analyzed above, the length of the hatching periods, or on the size or origin of the eggs.

The analysis of the hatching period of 1 to 6 days or 5 to 33°D of 90% of the larvae (omitting the first and last 5%) indicated that this period was inversely dependent on egg size (r = -0.454, P < 0.02; Fig. 3) and did not depend on the date that hatching began. It was, however, correlated with the 5 to 50% (r = 0.664, P < 0.01) and the 50 to 95% (r = 0.648, P < 0.01) larval hatching periods as well as with the hatching period of 50% of the larvae (r = 0.545, P < 0.01; Fig. 4) and the conclusion of the hatching period (r = 0.418, P < 0.02). There was also a correlation with the length of the entire hatching period (r = 0.411, P < 0.03).

DISCUSSION

This experiment demonstrated that variation in the lengths of the egg incubation and the hatching periods is fairly large. Bonisławska et al. (2000) proposed the general thesis that the length of the incubation period increases along with egg size, which was confirmed by studies of the eggs of different fish species, different females, and the eggs
Fig. 3. Dependence between the hatching time of the middle 90% of the larvae and egg size.

Fig. 4. Dependence between the hatching times of the middle 90 and 50% of the larvae.
of a single sea trout female. Kaj and Lewicka (1962) obtained the opposite result in a similar experiment. This dependency was not confirmed in the current experiment, as was the case in the research on Arctic char, *Salvelinus alpinus* (L.) by Vollestad and Lillehammer (2000) and Wallace and Aasjord (1984).

The length of the incubation period differs among the offspring of individual fish and among both females and males. This phenomenon was described earlier for both sea trout (Vollestad and Lillehammer 2000) and salmon (Berg and Moen 1999). The current authors also confirmed this between populations, and in the case of the current study, between brown trout and sea trout, with the incubation period of the former being longer. Consequently, the origin of the fish also had an impact on the length of the incubation period. This was confirmed by the results obtained by Donaghy and Verspoor (1997) in their investigations of two salmon populations. Berg and Moen (1999) also reported similar variability in incubation periods between and within populations and concluded that this is an adaptive trait specific to populations. This is not, however, a widespread opinion. Wallace and Heggberget (1988) did not detect any differences between Norwegian populations of salmon in their investigations of the dependence of between incubation period and water temperature. The question remains whether the differences noted in the current study were only the result of differences between populations, or if they were due to the fact that one of the populations was anadromous. Halačka (1995) expressed the opinion that the development of brown trout eggs is slower than that of sea trout eggs. This was not confirmed in the investigation by Killeen et al. (1999) in which the eggs of anadromous and non-migratory fish from the same spawning grounds were compared. Additionally, these authors observed that the differences confirmed by Halačka (1995) could have been due simply to differences between populations. The comparison of the sea trout pond stock to that from the Vistula River in the current experiment is similarly problematic. However, there is no comparison of the eggs of sea trout with different life histories that originate from one anadromous population. The differences between their incubation times were neither large nor statistically significant, but they were symptomatic. The eggs of the fish with a non-anadromous life history developed more slowly. Although it is difficult to explain this variation, it does appear that it confirms the conviction that there is a genetic background to the differing life histories of anadromous fish (Thorpe and Morgan 1978, Bailey et al. 1980, Jonsson 1982, Thorpe et al. 1983).
Throughout hatching, the most varied and usually the longest phase was the initial one, in which single larvae hatched. This is an expression of the differentiation of the eggs in each portion, and, while this is partially hereditary, it is most certainly largely random in character. This is why the length of the hatching period is better described by that of the middle 90% of the larvae, and this was longer the later hatching occurred. In other words, the difference in the hatching period that resulted from slower embryonic development increased during hatching itself and was not equalized, as could be expected in light of how important it is for the fate of the hatched larvae. The length of the hatching period decreased as the size of the eggs increased, which concurs with the observations of Kaj and Lewicka (1962), but not with those of Wallace and Aasjord (1984).

Even when spawning occurs simultaneously, the larvae hatch over a period of time. There are differences among the offspring of individual fish as well as among populations and, possibly, among segments of them. This results from differences in the incubation tempo as well as in the course of hatching itself.

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STRESZCZENIE

WPŁYW POCHODZENIA I WIELKOŚCI IKRY NA TERMIN I PRZEBIEG KLUCIA TROCI (SALMO TRUTTA L.)

Porównano długość inkubacji i dynamikę wylęgania się potomstwa trzech grup ryb wytartych w tym samym dniu: pstrągów potokowych ze stada tarlaków z ośrodka zarybieniowego i dwóch grup troci wyhodowanych z ikry uzyskanej od ryb złowionych w dolnej Wiśle; ryby, które zrównoważyły i ryby, które nie zrównoważyły (tab. 1). Pierwsze larwy pojawiały się między 129 i 138 dniem, a ostatnie między 138 i 145 dniem inkubacji (rys. 1). Długość inkubacji różniła się między potomstwem poszczególnych ryb i grup ryb. Ikra pstrągów rozwijała się najwolniej, a troci uprzednio zrównoważonej – najszybciej. Nie stwierdzono zależności między długością inkubacji a wielkością ikry (rys. 2). Długość okresu wylęgania wahała się od 3 do 11 dni i nie zależała od pochodzenia ikry. Najbardziej zmieniona była faza pojawiania się pojedynczych sztuk wylęgu (do 5% wylęgu) – od 0 do 8 dni. Była tym dłuższa, im wcześniej rozpoczęło się wyklucie. Podobną zależność stwierdzono też dla długości całego okresu wylęgania, a przeciwnej dla okresu wylęgania się środkowych 90% larw: trwał on od 1 do 6 dni i rozciągła się w miarę przedłużania inkubacji (rys. 4). Długość trwania szczytu wylęgania malała ze wzrostem średniej wielkości ikry (rys. 3).