

Trade-off between number and intraovarian growth rate of offspring in *Zoarces viviparus*

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Trade-off between number and intraovarian growth rate of offspring was studied using 15 samples of females caught at 7 sites in the Baltic Sea and the Skagerrak. The growth of normal embryos appeared to be synchronous within broods, and there was no correlation between the females' size and relative fecundity. Females with higher relative fecundity had significantly smaller average larval length which may suggest existence of offspring competition for maternal energy supplies. Our results also show that reduced offspring size in females with high relative fecundity did not fully compensate for the increase in offspring number: the ratio of embryo mass to female somatic weight was positively correlated with relative fecundity. The negative relationship between female condition and relative fecundity indicates that increased investment in offspring affects the energetic state of the female. However, the last effect was rather moderate.

Introduction

The reproductive strategy of viviparous animals involves tradeoffs between the number and size of offspring. In mammals, extensive research has been carried out to study the relationship between mean mass of offspring and litter size, the effect of size at birth on survival, and the impact of parental investment on offspring characteristics (e.g. Sikes & Ylönen 1998, Humphries & Boutin 2000, Oksanen *et al.* 2002, 2003). It has been shown that higher fecundity usually reduces birth size of offspring, negatively impacts condition indices of females, and may increase the length of the gestation period (e.g. Yom-Tov 1985, Sikes 1998, Sikes & Ylönen 1998, Millesi *et al.*

1999, Humphries & Boutin 2000, Huber *et al.* 2001). The relationships between the litter size, litter weight, and newborn weight in viviparous reptiles have also been investigated (Pilorge *et al.* 1983). In fish, the evolutionary compromise between few large and many small eggs has been described (Duarte & Alcaraz 1989, Elgar 1990, Jonsson & Jonsson 1999).

The great majority of teleost fish are oviparous. The list of viviparous teleosts is short, and most species release the offspring shortly after their hatching from the egg membranes rather than permit an extended intra-ovarian growth period. Although some sharks and rays are relatively well studied, there are no data available on the possibility of embryonic competition. To

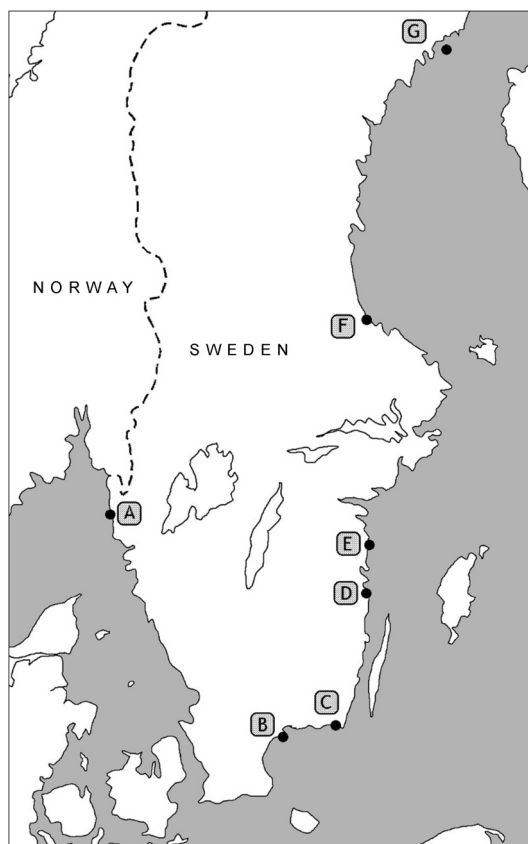


Fig. 1. The sampling sites in the Baltic Sea and the Skagerrak. A = Fjällbacka, B = Kladdenabb, C = Torhamn, D = Marsö, E = Kvädöfjärden, F = Gävlebukten, G = Holmöarna.

the best of our knowledge, there are no studies describing if high relative fecundity of viviparous female fishes results in slower embryo growth, as has been shown in mammalian species (Oksanen *et al.* 2002), nor do we know if an increased reproductive effort negatively impacts the condition of females.

Zoarces viviparus L., the viviparous blenny or eel-pout, offers a possibility to study intra-ovarian embryonic competition. In this species, embryos remain in the ovary 3–4 months after hatching from egg membranes, and depend strongly on the maternal supply of energy (Kristofferson *et al.* 1973, Kristoffersson & Oikari 1975, Korsgaard & Østergaard Andersen 1985, Korsgaard 1986). The female–embryo relationship, such as uptake of different nutrients, has been discussed in several papers (Korsgaard &

Østergaard Andersen 1985, Korsgaard 1986). The absorption of nutrients by embryos occurs mainly through the greatly expanded and richly folded hindgut. Data also suggest that the swallowing movements of embryos enable them to ingest ovarian fluids (Soin 1968, Kristofferson *et al.* 1973). During gestation, the embryo weight increases from 20–30 mg to approximately 250–500 mg, and the average percentage of dry matter increases from 13% to 19% (Kristofferson *et al.* 1973, Vetemaa 1999).

Here we test the hypothesis that the competition for nutrients exists amongst developing embryos of viviparous blenny during the gestation period. To test this we examined fish from the Baltic Sea and the Skagerrak (Fig. 1) and collected data on some of the most important parameters related to maternal investment (fecundity, condition of females and intra-ovarian embryonic growth).

Material and methods

Female viviparous blennies were caught with fyke nets between late October and early December in 1994–1996 (Table 1). Fertilisation usually takes place from late August until September (Kristofferson *et al.* 1973, Götting 1976, Vetemaa 1999), but there are differences between different geographical areas. Given these differences, broods in this study were 50–90 days old at sampling depending on the year and location. Fifteen samples consisting of 27–50 females each, were collected from 7 sites in the Skagerrak, the Baltic Proper and the Gulf of Bothnia (Table 1 and Fig. 1). A total of 662 females were analysed (Table 1). The sampling sites form the network of reference areas in the national environmental monitoring in Sweden. Sampling of viviparous blennies in these areas takes place annually, or when needed as a reference material for case studies in various effluent sites. The material collected in this monitoring framework was used, and no additional fish were sacrificed for this study.

The hydrographic conditions differ considerably between the sampling sites. The surface salinity decreases from 20–25 ppt in the Skagerrak site (A) to 3–4 ppt in the northern Gulf of Bothnia (G). The other sites are rather

similar with salinities between 8 ppt in the southern Baltic Sea and 5 ppt in the southern Gulf of Bothnia. The water temperature might reach 20 °C in all sites and sink to 0 °C. During the gestation period, it is generally colder in the Gulf of Bothnia than in the other areas. Both salinity and temperature are rather unstable in the study areas depending on dominating winds and other climatic conditions.

All studied females were measured to the nearest mm (total length, TL) and weighed (total weight, TW; somatic or eviscerated weight (total weight minus weight of digestive tract, ovary with embryos and liver), SW; and weight of all embryos, EW) to the nearest 0.1 g (scale: Mettler Toledo, sensitivity 0.01 g). At sampling the females were quickly decapitated, and the embryos were immediately removed from the ovary. Before weighing, embryos were blotted on absorbent tissue. The embryo-somatic index was calculated as $ESI = EW/SW \times 100$.

The embryo lengths were measured and divided into 2.5-mm-length groups as follows: 0–2.4 mm = 1; 2.5–4.9 mm = 2; 5.0–7.4 mm = 3; 7.5–9.9 mm = 4; 10.0–12.4 mm = 5; etc. (More precise measurements were not possible due to time restrictions during monitoring works).

We refer to the total number of embryos as total fecundity. Relative fecundity (RF) was calculated as $RF = E/SW$, where *E* denotes the number of embryos. Fulton's condition factor of females was calculated as $CF = 100000W/L^3$, where *W* is somatic weight and *L* total length.

All females were aged, but since the age of female didn't impact the pattern of trade-off between number and intraovarian growth rate of offspring, the age data is not presented.

Results

All samples were pooled by site to reveal if differences exist in the average length of females as a function of varying temperature and salinity regimes across sites. Females from the coldest and lowest saline area, the northern Gulf of Bothnia (G; *n* = 93, TL = 199 ± 35), were significantly smaller than females in other areas. Females from the Skagerrak (A; *n* = 123, TL = 241.6 ± 31) were significantly larger than females in all areas with the exception of the Kladdenabb (Table 2). The females from the southern and central Baltic Proper (B, C, D, E, F), were of intermediate size, and the differences between these areas were mostly not significant (Table 2).

Table 1. The sampling sites (see Fig. 1), dates, the number of females sampled, their average total length (TL ± SD) and the size range (mm).

Site	Date	Sample code	<i>n</i> (females)	Average TL ± SD	TL range
A	24.10.1995	A95a	27	226 ± 23	190–286
A	28.11.1995	A95b	49	237 ± 31	199–334
A	06.11.1996	A96	47	253 ± 30	193–342
B	23.10.1995	B95a	32	241 ± 26	179–304
B	06.12.1995	B95b	44	226 ± 23	170–272
C	30.10.1995	C95a	36	229 ± 27	162–282
C	09.12.1995	C95b	44	211 ± 27	162–269
D	06.11.1995	D95	47	219 ± 30	152–293
D	12.11.1996	D96	49	243 ± 26	188–320
E	04.11.1994	E94	47	227 ± 26	179–322
E	14.11.1995	E95	49	212 ± 24	162–273
E	11.11.1996	E96	48	262 ± 34	159–310
F	16.11.1995	F95	50	223 ± 25	180–308
G	17.11.1995	G95	43	194 ± 37	140–291
G	20.11.1996	G96	50	202 ± 34	147–272

Table 2. Comparisons of the length of females from the study sites (*t*-test). Number indicates difference in the average size in mm (*p* in parentheses). Positive number means that the average female length from the site given in the left column is greater than that from the site given in the row above (e.g. average total length of females in A was 5.0 mm greater than in C, *p* < 0.001).

	B	C	D	E	F	G
A	1.9 (0.057)	5.0 (< 0.001)	2.4 (0.019)	3.6 (< 0.001)	3.6 (< 0.001)	10.3 (< 0.001)
B		2.7 (0.007)	0.3 (0.781)	1.1 (0.259)	1.8 (0.069)	7.4 (< 0.001)
C			–2.6 (0.009)	–2.0 (0.047)	–0.6 (0.557)	4.6 (< 0.001)
D				0.9 (0.374)	1.7 (0.098)	7.5 (< 0.001)
E					1.0 (0.297)	7.4 (< 0.001)
F						4.6 (< 0.001)

The range of total fecundity was between 5 (female from D96; TL = 163 mm, SW = 13.8 g) and 206 (female from A96; TL = 323 mm, SW = 116.7 g). The range of relative fecundity (RF) was between 0.12 (female from G95; 6 embryos; TL = 252 mm, SW = 50.9 g) and 2.23 (female from G95; 99 embryos; TL = 236 mm, SW = 44.3 g). This sample also contained the largest difference between the upper and lower limits of RF (the upper limit was 20.3 times higher than the lower limit). The median difference between the highest and lowest RF was 4.4 times.

The relationship between the female size and RF was examined using Pearson's correlation. A significant relationship was detected in only one of 15 samples ($p = 0.023$), which means that smaller females had lower RF in this sample.

The average RF of females (Table 3) in different areas did not reveal a geographical pattern. The females in areas A, C, D and E had slightly lower RF than females in areas G, B and F. The relationship between RF and the female size (all samples pooled) can be presented as $RF = 0.0295(SW) - 0.0002(SW)^2$, ($r^2 = 0.8$).

The most common embryo length group for a female was used to represent the average length of the brood. This group contained an average of 74% of all larvae, the remaining larvae were

typically equally distributed between the neighbouring larger and smaller groups (bigger and smaller).

Since the average larval lengths were not always normally distributed (Lillefors's test) within a sample, Spearman's correlation was used to test the correlation between the average embryo length and RF. In all 15 samples there was a negative correlation, and in 14 of these cases the relationship was significant ($p < 0.05$; Table 3). That is, females with higher RF had smaller larvae.

Pearson's correlation was used to test the relationship between RF and ESI. In all 15 samples there was a significant ($p < 0.05$) positive correlation, i.e. females with higher RF had also larger total larval mass when compared to the somatic weight of females (Table 3).

The correlation coefficients between CF and RF were negative in 14 of 15 samples, but only in 3 of 15 samples was this correlation statistically significant ($p < 0.05$) (Table 4).

Discussion

During the last two decades the viviparous blenny has been used in biomonitoring of toxic substances in many field studies (e.g. Jacobsson

Table 3. The average RF (based on the somatic weight of females), the correlation between RF and average embryo length (Spearman's correlation coefficient, r_s), and the relationship between RF and ESI (Pearson's correlation coefficient, r_p). The only non-significant correlation ($p > 0.05$) is indicated with an asterisk (*).

Sample	Average RF $\pm$ SD	r_s	r_p
A95a	0.83 $\pm$ 0.27	-0.43	0.63
A95b	0.78 $\pm$ 0.24	-0.57	0.61
A96	0.82 $\pm$ 0.25	-0.34	0.81
B95a	0.95 $\pm$ 0.24	-0.54	0.76
B95b	0.89 $\pm$ 0.27	-0.68	0.34
C95a	0.85 $\pm$ 0.28	-0.41	0.70
C95b	0.82 $\pm$ 0.36	-0.79	0.61
D95	0.79 $\pm$ 0.26	-0.52	0.77
D96	0.80 $\pm$ 0.20	-0.49	0.48
E94	0.69 $\pm$ 0.22	-0.49	0.67
E95	0.83 $\pm$ 0.23	-0.41	0.62
E96	0.74 $\pm$ 0.19	-0.41	0.43
F95	0.89 $\pm$ 0.22	-0.43*	0.65
G95	1.06 $\pm$ 0.41	-0.58	0.58
G96	0.99 $\pm$ 0.30	-0.37	0.63

Table 4. The average condition factor (CF $\pm$ SD), its range and relationship between relative fecundity and condition factor of females (r_p) expressed as Pearson's correlation coefficient (p in parentheses).

Sample	Average CF $\pm$ SD	CF range	r_p
A95a	0.394 $\pm$ 0.044	0.240-0.449	-0.476 (0.012)
A95b	0.374 $\pm$ 0.029	0.300-0.435	-0.367 (0.010)
A96	0.410 $\pm$ 0.034	0.339-0.475	-0.050 (0.736)
B95a	0.287 $\pm$ 0.034	0.156-0.337	-0.275 (0.128)
B95b	0.298 $\pm$ 0.037	0.248-0.454	-0.046 (0.764)
C95a	0.285 $\pm$ 0.032	0.171-0.331	0.014 (0.937)
C95b	0.289 $\pm$ 0.028	0.236-0.353	-0.449 (0.002)
D95	0.328 $\pm$ 0.046	0.251-0.537	-0.211 (0.156)
D96	0.326 $\pm$ 0.025	0.260-0.376	-0.230 (0.115)
E94	0.336 $\pm$ 0.032	0.267-0.410	-0.187 (0.209)
E95	0.333 $\pm$ 0.032	0.263-0.406	-0.009 (0.954)
E96	0.334 $\pm$ 0.040	0.256-0.427	-0.148 (0.317)
F95	0.320 $\pm$ 0.030	0.267-0.385	-0.244 (0.088)
G95	0.298 $\pm$ 0.027	0.251-0.364	-0.169 (0.278)
G96	0.270 $\pm$ 0.022	0.228-0.324	-0.252 (0.077)

& Neuman 1991, Jacobsson *et al.* 1993, Larsson & Førlin 2002). It has been shown that an increased level of pollution may lead to several effects detectable on the population level (for example, low abundance and large mean size; Jacobsson & Neuman 1991), as well as on the individual level (for example, high mortality of embryos; Jacobsson *et al.* 1993). Indeed, pollution may even cause total reproduction failure (Vetemaa *et al.* 1997). The samples used in the present study, however, were gathered from so-called reference areas where there are no pollution sources nearby.

The aim of this paper was not to study how the viviparous blenny responds to varying salinity levels. On the contrary, populations inhabiting different geographic regions were used to guarantee that if intraovarian competition exists, its impact on the female could not be attributed to specific conditions in certain habitats. The fact that the species is abundant in all studied areas indicates that it has adapted well to brackish water. So, even if the areas differ significantly it cannot be said that some areas are more optimal for the species than others.

The study by Pörtner *et al.* (2001) suggests that total fecundity of viviparous blenny is smaller in higher latitudes (for example, the White Sea compared to the Baltic and North Seas). The present study documented minor differences in RF between the sampling sites, but did not reveal any geographical pattern. Jacobsson *et al.* (1993) found that there are no significant differences between main reproduction parameters in the Baltic Sea and Skagerrak. So, the relationship between the number and size of offspring seems to be fairly consistent across areas with different temperature and salinity regimes.

The variation in relative fecundity of females within the samples was high, usually up to 4–5 times. The reason for this is unclear, but some very low values are probably caused by low fertilisation rate or early death of some embryos. Although different rules apply to oviparous fishes, even here some oviparous species show high variation. For example, the relative fecundity in a sample of round goby (*Neogobius melanostomus* Pallas) varied more than 6 times (Wandzel 2000), and in the case of common

dentex (*Dentex dentex* L.), more than 10 times (Loir *et al.* 2001).

Within local viviparous blenny populations, the synchronicity of gonad development is high (Götting 1976). In addition, both the times of fertilisation and the start of the embryonic development is rather simultaneous. According to the study made in the Kattegat, the fertilisation of all females in the Batfjorden Bay took place within 2–3 days (Vetemaa 1999). The existing data show that the hatching of a brood takes place at the same time, and the average size of normally developing embryos does not differ much within broods (Soin 1968, Jacobsson *et al.* 1993, Vetemaa 1999).

There was a negative correlation between embryo length and relative fecundity in all samples, and in 14 of 15 samples this was significant (Table 4). This indicates that there may exist competition between the embryos of viviparous blenny for maternal energy supply. Our results show that reduced size of offspring in females with higher relative fecundity did not fully compensate for the increase in offspring number, because the embryo-somatic index was positively correlated with the relative fecundity of females (Table 3). The same has been shown, for example, in mammals where increasing litter size of rodents increases total mass of litter, but decreases the mass of individual offspring (Humphries & Boutin 2000, Kunkele 2000).

Even if the present study revealed that higher relative fecundity resulted in a lower growth rate of the embryos (measured at the mid of gestation), it remains to be a topic of further studies if this also leads to a smaller parturition size as in mammals (e.g. Kunkele 2000). The data available indicate that this is not the case, however. The length of the gestation in mammals is highly fixed, usually differing less than 10% among females (e.g. rodents, Sumner *et al.* 2003; horse, Perez *et al.* 2003). In the viviparous blenny, the gestation length varies between 4–6 months, showing high variation within and across populations (Vetemaa 1999). Thus, it is possible that the gestation period is prolonged in females with high relative fecundity and low embryo growth rate.

Increased litter size does not usually result in decreased condition in mammals. For example,

gestating rodents compensate for the energy cost of offspring production by increasing remarkably their daily food intake (guinea pig, Kunkele 2000; voles, Liu *et al.* 2003). Female blennies, alternatively, feed very little during the second half of gestation (Vetemaa 1999). The negative correlation between the condition factor and relative fecundity demonstrated here indicates that increased investment in offspring affects the energetic state of the female. This effect seems moderate, however, given the rather weak correlations.

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