

Parasitism, space constraints, and gonad asymmetry in the pollan (*Coregonus autumnalis*)

Chris Harrod and David Griffiths

Abstract: Both sexes of Lough Neagh pollan (*Coregonus autumnalis*) show directional asymmetry in gonad mass, the left being larger than the right in 70% of individuals. The frequency and degree of asymmetry are size independent in males but become progressively more marked in females of >120 g somatic mass. There is little evidence to support the hypothesis that the size of the body cavity constrains gonad size. Pollan are heavily and size-dependently infected by metacercariae of the trematode *Ichthyocotylurus erraticus*. Total gonad mass in both sexes of pollan is negatively correlated with infection intensity of this parasite. In females, mean egg size shows no trend but fecundity declines and the degree of asymmetry in ovary mass increases with infection intensity up to a threshold, beyond which it remains constant. While directional asymmetry in gonad size is strongly developmentally controlled in many fish species, variation in the degree of gonad asymmetry in pollan provides a potentially sensitive indicator of stress.

Résumé : Les deux sexes du pollan (*Coregonus autumnalis*) au Lough Neagh présentent une asymétrie directionnelle de la masse de leurs gonades, la gauche étant plus grande que la droite chez 70 % des individus. La fréquence et l'importance de l'asymétrie sont indépendantes de la taille chez les mâles, mais elles deviennent progressivement plus marquées chez les femelles de masse somatique >120 g. Il y a peu d'indications pour appuyer l'hypothèse selon laquelle la dimension de la cavité corporelle restreint la taille des gonades. Les pollans sont fortement infectés par les métacercaires du trématode *Ichthyocotylurus erraticus* et l'infection varie en fonction de la taille. Il y a une corrélation négative entre la masse totale des gonades chez les pollans et l'intensité de l'infection par ce parasite. Chez les femelles, la taille moyenne des œufs ne suit aucune tendance particulière; en revanche, la fécondité décline et l'importance de l'asymétrie de la masse ovarienne augmente en fonction de la gravité de l'infection jusqu'à une limite supérieure au-delà de laquelle elles demeurent constantes. Bien que l'asymétrie directionnelle de la taille des gonades soit fortement contrôlée par le développement chez plusieurs espèces de poissons, la variation de l'importance de l'asymétrie des gonades chez les pollans fournit un indicateur potentiellement sensible du stress.

[Traduit par la Rédaction]

Introduction

Asymmetries in paired structures are subject to both genetic and environmental influences. In some species, the asymmetry is largely under developmental or genetic control and extreme. For example, there is no left testis in most *Oryzias* species (Hamaguchi 1996), the left ovary has more or less disappeared in mbuna, the rock-frequenting group of cichlid species in Lake Malawi (Fryer and Iles 1972), and only the right ovary is functional in six genera of cartilaginous fishes and only the left in two genera (Dodd 1983). Other asymmetries are less extreme and have attracted much attention recently because they have been shown to be influenced by environmental factors (Clarke 1995; Møller 1997). Fluctuating asymmetry has most frequently been examined

as a measure of environmental stress, but variation in the degree of directional asymmetry has also been linked to stress (Sasal and Pampoulie 2000). However, directional asymmetry in internal structures such as gonads, in a body cavity of finite size, could also be a consequence of space constraints (Brown and Kamp 1942; MacGregor 1968). The distended abdomens characteristic of gravid female fish close to spawning time suggest that abdominal space might limit ovary size and affect symmetry.

Directional gonad asymmetry has been observed in whitefish (*Coregonus lavaretus*) (Heese 1990), salmonids (*Oncorhynchus* spp.) (Rounsefell 1957; A. Hendry, Department of Biology, McGill University, Montréal, QC H3A 2K6, Canada, unpublished data), Atlantic salmon (*Salmo salar*) (C. Harrod, personal observation), brown trout (*Salmo trutta*) (Brown and Kamp 1942), and other fishes, e.g., anguillid eels (Tesch 2003), anchovies (*Anchoa naso*, *Engraulis mordax*, and *Engraulis encrasicolus*) (MacGregor 1968; Vallisneri and Scapolatempo 2000), capelin (*Mallotus villosus*) (Winters 1971), and albacore (*Thunnus alalunga*) (Ramon and Bailey 1996). In most species, the left gonad is larger than the right.

Asymmetry in paired fins has been correlated with reproductive effects (Hechter et al. 2000; Wedekind and Müller 2004) and with parasitism (Reimchen 1997; Sasal and Pampoulie 2000). Parasitism can affect fish physiology and

Received 6 October 2004. Accepted 19 May 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 2 November 2005.
J18341

C. Harrod¹ and D. Griffiths.² School of Environmental Sciences, University of Ulster, Coleraine, BT52 1SA, UK.

¹Present address: Department of Physiological Ecology, Max Planck Institute for Limnology, Postfach 165, 24300 Plön, Germany.

²Corresponding author (e-mail: d.griffiths@ulster.ac.uk).

reproductive potential (e.g., Arme and Owen 1968; Pampoulie et al. 1999; Tolonen et al. 2002), but parasitism has not been associated with gonad asymmetry.

Pollan (Arctic cisco in North America) (*Coregonus autumnalis*) occur as glacial relicts in Ireland, far outside their main high arctic range, and are subject to a variety of environmental stressors, both external and internal (Harrod et al. 2001, 2002; Harrod and Griffiths 2005). Almost all adult fish in Lough Neagh (99.9% of fish older than 1+, $n = 2126$) are infected with metacercariae of a trematode, *Ichthyocotylurus erraticus*, at densities (median infection intensity, i.e., the number of parasites per fish, 536 in fish 2+ and older) considerably greater than those shown to cause death or reduced condition in other fish species (Harrod and Griffiths 2005). The pericardial aggregations of the parasite probably affect heart function, and this, coupled with low oxygen concentrations in hypertrophic Lough Neagh, could reduce fitness by affecting survival, condition, or reproduction. Females are more heavily infected than males. *Ichthyocotylurus erraticus* affects somatic condition and liver size in pollan (Harrod and Griffiths 2005) and condition, liver, and reproductive indices and heart mass in *C. lavaretus* in Loch Lomond (Dolezel and Crompton 2000).

Harrod and Griffiths (2004) described the reproductive biology of pollan in Lough Neagh, the only stock to have been examined in detail. This paper describes patterns of gonad asymmetry in pollan and investigates to what extent space constraints and parasitism are correlated with these patterns. We find no support for the space constraints hypothesis but demonstrate differences in the pattern of asymmetry between male and female fish and show that asymmetry in females is linked to infection intensity.

Materials and methods

Pollan were sampled from Lough Neagh (6°25'W, 54°35'N) using surface- and bottom-set multipanel gill nets on five occasions from September to early December 1999, when fish normally spawn. Fish were aged from scales following the procedure of Wilson and Pitcher (1984). The contents of the body cavity were divided into gonads, liver, and alimentary canal and each weighed separately to the nearest 0.01 g. Sex was assessed through visual inspection of the gonads. Left and right gonads of 136 female and 94 male fish were weighed individually. Ripe ovaries (maturation stage 5; Lagler 1978) were stored individually in Bouin's fixative prior to measurement of egg size and fecundity. Pollan hearts and any encysted *Ichthyocotylurus* metacercariae found in the pericardial cavity were stored in 80% alcohol. To measure infection intensity, cysts were teased from the heart and host reactive tissue using mounted needles and this material squeezed between microscope slides before counting cysts under a low-power microscope.

Asymmetry was measured as the signed difference between left and right gonad mass, the signed difference expressed as a percentage of the left gonad mass or the ratio of left to right gonad mass. Most analyses were restricted to fish with ripe gonads (stage 5). When investigating the effect of parasitism, the analysis was restricted to fish collected shortly before spawning (November) for which all three

measures of reproductive potential (i.e., ovary size, egg size, and fecundity) were available.

Asymmetry might vary with fish size (Somarakis et al. 1997). Two measures of fish size were used to detect effects on gonads and on the body cavity contents. When examining relationships between body cavity components, gutted mass (i.e., total body mass minus body cavity content mass) was used as the independent variable, while in investigations of possible parasite effects on gonads, somatic mass (i.e., total body mass minus gonad mass) was used. Regressions of right versus left gonad mass were carried out: this tests for a fish size effect, since gonad size is correlated with fish size (see below). Slopes of log-transformed gonad mass regressions significantly different from 1 indicate that there is a body size effect, while intercepts significantly different from 1 indicate asymmetry. To show nonlinear trends, locally weighted scatterplot smoothing (LOWESS) was used. To test the possibility, suggested by the data, that the degree of asymmetry (Y) changes above a threshold body size or infection intensity (X), linear and piecewise (Toms and Lesperance 2003) models

$$Y = a + bX$$

$$Y = a + b_1X + b_2(X - T) \quad (X > T)$$

were fitted to the data using nonlinear least squares regression. The terms in parentheses in the piecewise model control where the change in slope (T) occurs. The small-sample Akaike's Information Criterion (AIC_c) was calculated for each model because the ratio of number of observations to number of estimated parameters was appreciably below 40 for most data sets. Model fits were then compared with AIC_c , Akaike weights, and evidence (Akaike weight) ratios (Burnham and Anderson 1998). Since gonad size, infection intensity, and degree of asymmetry varied with body size and age, the effects of the latter were controlled for by partial correlation. All errors are standard errors.

Results

Paired t tests showed left gonad masses to be significantly larger than right in both sexes (Table 1): the percent difference was much greater in females. Note, however, that the right gonads were larger than the left in about one third of the fish (Fig. 1). In the absence of estimates of measurement error, we assumed that gonads were asymmetric if they differed in mass by more than 10%: about 70% of fish showed differences of this magnitude or greater. The distribution of differences between left and right gonad masses in female or male fish in gonad state 5 showed no significant skewness or kurtosis.

The pattern of asymmetry differs between the sexes (Table 2): the degree of gonad asymmetry was size dependent in females but not in males. Note that this conclusion does not depend on whether ordinary least squares or reduced major axis regression is used. The frequency of ovarian asymmetry was also size dependent. Only half of the 20 smallest fish examined (maximum somatic mass 129 g) had larger left ovaries, but this had risen to 85% for the 20 largest fish (minimum somatic mass 177 g) and one fish had symmetrical ovaries.

Table 1. Comparison of left and right gonads of pollan (*Coregonus autumnalis*) in maturity stage 5.

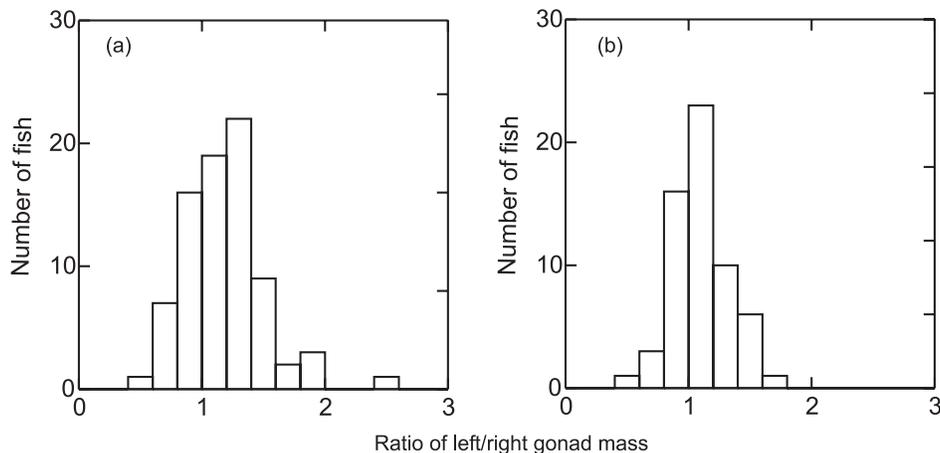
Sex	Mean left gonad mass (g)	Mean right gonad mass (g)	% difference	n	t	P	% fish with left > right
Female	12.85	11.43	11.1	76	4.10	<0.001	68
Male	1.08	1.01	6.5	60	2.51	0.02	68

Note: The paired *t* tests were performed on log-transformed data but the reported masses are the back-transformed values.

Table 2. Summary of regression statistics of log right pollan gonad mass against log left gonad mass.

Sex	<i>a</i> ± SE	<i>t</i> (<i>a</i> = 0)	<i>P</i>	OLS <i>b</i> ± SE	<i>t</i> (<i>b</i> = 1)	<i>P</i>	RMA <i>b</i>	<i>n</i>
Female	0.184±0.057	3.23	<0.01	0.788±0.051	4.10	<0.001	0.901	76
Male	-0.025±0.012	2.12	<0.05	0.871±0.079	1.64	>0.10	1.058	60

Note: OLS, ordinary least squares; RMA, reduced major axis.

Fig. 1. Histograms of left to right gonad mass ratios for (a) male and (b) female pollan (*Coregonus autumnalis*).

Size-linked asymmetry was much more marked in ripe fish but was still significant in fish with late-developing ovaries (Fig. 2). However, the degree of asymmetry, when expressed as a percentage of left gonad mass, did not differ between fish of a given somatic mass in the two gonad states (analysis of covariance: slopes, $F_{[1,190]} = 0.44$; intercepts, $F_{[1,191]} = 2.52$). For fish with ripe ovaries, piecewise regression gave a better fit than the linear model ($AIC_c = 3.90$). The Akaike weights (0.87 and 0.12) show that the piecewise model is seven times more likely to be the better model. Ovarian asymmetry did not appear until fish reached a somatic mass of 120 ± 12 g, equivalent to a fork length of 235 mm (age 2+ fish).

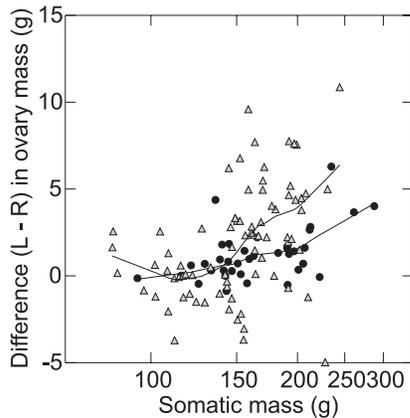
The ratio of left to right gonad size varied with somatic mass, but the slope and intercept of this relationship did not depend on sampling date (slopes, $F_{[4,100]} = 1.23$; intercepts, $F_{[4,104]} = 0.43$). Hence, the degree of asymmetry in gonad size did not vary over the sampling period (1 September to 21 November 1999) despite total gonad mass, adjusted for fish size, increasing by a factor of 3.5 over this period.

Body cavity components varied strongly with body size, as did the number of *Ichthyocotylurus* (Table 3). Ovary, gut, and liver increased in size with gutted mass at the same rate (analysis of covariance: slopes, $F_{[2,92]} = 1.20$, $P > 0.05$). Ovary and combined gut and liver masses were positively correlated ($r = 0.60$, $P < 0.01$, $n = 22$), but this relationship disappeared after controlling for gutted mass (partial $r = -0.23$).

Similarly, there were no significant partial correlations between right or left ovary masses or the size difference in ovary mass and combined gut and liver mass when gutted mass was controlled (i.e., there was no evidence of a body cavity size constraint).

Ichthyocotylurus numbers increased with gonad size in both sexes: the slopes and intercepts did not differ between the sexes. Partial correlations were calculated to control for the effect of somatic mass. Gonad mass declined with increasing *Ichthyocotylurus* numbers in both sexes (male partial $r = -0.38$, 26 df, $P < 0.05$; female partial $r = -0.72$, 17 df, $P < 0.001$) (Fig. 3). *Ichthyocotylurus* numbers were not correlated with gonad asymmetry in males, but females were affected: the difference between right and left gonad masses expressed in absolute (or percentage) terms increased with the number of *Ichthyocotylurus* to a plateau (Fig. 4). Piecewise regression gave a better fit to these data than the linear model ($AIC_c = 4.76$): the Akaike weights (0.92 and 0.08) show that the piecewise model is 11 times more likely to be the better model. The degree of asymmetry in gonad size was significantly correlated with the number of parasites below the breakpoint of 855 (± 213) parasites per fish ($r = 0.58$, $P < 0.01$, $n = 25$) and the intercept was not significantly different from 0 ($a = 0.90 \pm 0.88$) (i.e., uninfected fish had symmetrical ovaries). Increasing ovarian asymmetry with infection intensity in fish with less than 855 *Ichthyocotylurus* was not related to fish size or age. There was no

Fig. 2. The degree of gonad size asymmetry varies with fish size in female pollan (*Coregonus autumnalis*) with late-maturing ovaries (circles) and ripe ovaries (triangles).



change in the degree of asymmetry for fish with larger infection intensities (mean difference in ovary mass = $18.7\% \pm 3.8\%$).

Mean egg size (diameter) did not differ between left and right ovaries (paired t test: $t = 0.52$, 61 df). Egg size increased with fish mass and infection intensity ($r = 0.58$, 35 df, $P < 0.001$, and $r = 0.43$, 35 df, $P < 0.01$, respectively), but after controlling for mass, there was no parasite effect (partial $r = 0.17$). Egg size was independent of fish size for any age of fish (i.e., egg size was not related to growth rate). There was no correlation between skewness in egg size of left and right ovaries ($r = 0.16$, $P > 0.05$, $n = 116$). Skewness increased as ovaries developed ($r = 0.48$, $P < 0.001$, $n = 116$): skewness was correlated with gonad mass when somatic mass was controlled for (partial $r = 0.52$, 88 df, $P < 0.001$). However, skewness was not related to infection intensity after controlling for somatic mass (partial $r = -0.06$, 66 df).

Fecundity declined slowly and egg size increased rapidly as spawning date approached (log fecundity = $2.50 - 0.0011 \pm 0.0004 \times \text{day} + 0.79 \pm 0.10 \times \log \text{ somatic mass}$ ($R^2 = 0.43$, $n = 84$), log egg diameter = $-1.18 - 0.0030 \pm 0.0002 \times \text{day} + 0.24 \pm 0.05 \times \log \text{ somatic mass}$ ($R^2 = 0.77$, $n = 84$), where day is the number of days since 1 January 1999). There was a significant negative correlation between egg size and fecundity after controlling for body size and day (partial $r = -0.38$, 80 df, $P < 0.001$). Fecundity declined with increasing infection intensity (Fig. 5) when the effect of somatic mass was controlled (partial $r = -0.59$, 34 df, $P < 0.001$).

Discussion

The literature contains a number of vague references to the effect that gonad asymmetry is not uncommon in fishes (e.g., MacGregor 1968; Sanwal and Khanna 1972; Ramon and Bailey 1996), but there is insufficient information to determine its frequency. In species in which both gonads develop, the ovary size ratio ranges from 8.8 in capelin (Winters 1971) to around 1.3 in trout, anchovies, and pollan (Brown and Kamp 1942; MacGregor 1968; Vallisneri and Scapolatempo 2000). The left gonad is usually the larger (11/14 species), suggesting some general constraint (whether physical or phylogenetic; Harvey and Pagel 1993). However,

Table 3. Regression slopes of pollan body cavity components as a function of gutted mass and infection intensity as a function of somatic mass (all variables log transformed; all fish in gonad state 5 collected on 10–11 November 1999).

	b	r^2	n	P
Ovary mass	1.375 ± 0.229	0.64	22	<0.001
Testis mass	0.969 ± 0.178	0.73	13	<0.001
Gut mass	1.400 ± 0.186	0.62	37	<0.001
Liver mass	1.915 ± 0.180	0.76	37	<0.001
Infection intensity	2.592 ± 0.429	0.52	36	<0.001

geographic variation in the degree (capelin, Winters 1971; albacore, Ramon and Bailey 1996) and even direction (sock-eye salmon (*Oncorhynchus nerka*), Rounsefell 1957) of asymmetry has been reported, consistent with an environmental influence.

Pollan provide only very limited support for the space constraint hypothesis. The testes were more symmetrical than the much larger ovaries as predicted by this hypothesis, but the ovaries did not become more asymmetrical as they developed and spawning date approached (although absolute size differences did increase). In November, the ovaries constituted a median of 69.5% ($n = 50$) of the mass of the body cavity contents. MacGregor (1968) argued that since gonads are the last organs to develop in the body cavity, they will occupy whatever space is available. Brown and Kamp (1942) noted that gonad asymmetry in female *S. trutta* was associated with the anatomical configuration of the intestine, which, in its posterior region, bends to one side (usually the right). Pollan might be similarly affected, but we have no information on the orientation of the anterior portion of the intestine. While the left gonad was larger in most pollan, consistent with this explanation, the converse was true in about 30% of fish. There is probably little selective pressure on internal (gonad) asymmetry but strong pressure on external morphology, since this is likely to affect swimming ability. If this is correct, internal asymmetry in one organ would be expected to necessitate a compensatory asymmetry in other internal structures. However, there was no evidence of such compensation in pollan. If the other body cavity structures differ in their compressibility, one might expect the degree of asymmetry to change as ovaries develop, but we found no support for a temporal change in relative asymmetry. Furthermore, if, as our results suggest, egg number is largely determined early in the reproductive cycle and well before egg size (Kinnison et al. 2001), space constraints are unlikely to be important. The negative correlation between fecundity and egg size after controlling for body size is consistent with a space constraint. However, this seems unlikely to be the cause, since the correlation occurred both early (September) and late (November) in the reproductive cycle despite a threefold increase in gonad mass over this period: the correlation seems more likely to reflect an energetic trade-off.

This study shows that variation in the degree of directional asymmetry is associated with parasite infection intensity in females but not in males. While asymmetry was independent of fish size and not affected by infection intensity in male pollan, total testis mass declined with increasing levels of parasitism. Total ovary mass was also correlated

Fig. 3. (a) Pollan (*Coregonus autumnalis*) testis and (b) ovary masses decline with increasing numbers of *Ichthyocotylurus* after controlling for the effects of body size (log somatic mass).

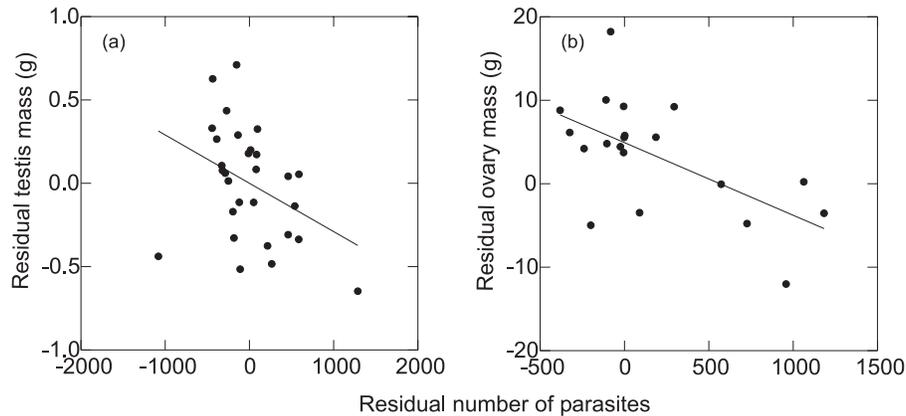
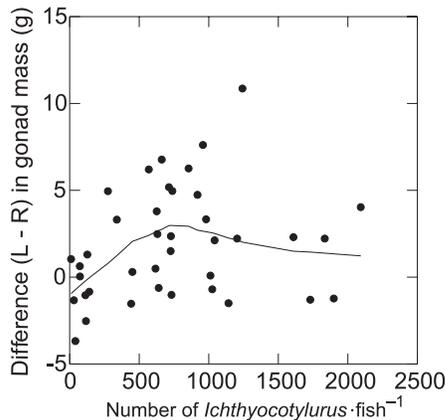


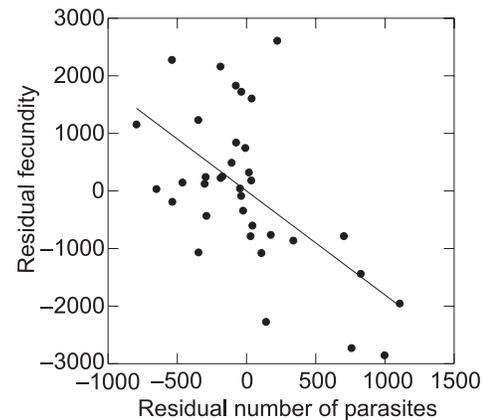
Fig. 4. Change in absolute asymmetry in pollan (*Coregonus autumnalis*) ovary mass as a function of infection intensity.



with parasitism, and asymmetry increased above a fish size threshold because infection intensity was itself fish size dependent. Fecundity declined strongly with increasing parasite numbers, but there was no asymmetry in egg size or evidence that infection intensity affected egg size. The extremely high infection intensities observed (median intensity 536 and range 5–3941 in fish 2 or more years old and with 10% of fish more than twice the median) suggest that *Ichthyocotylurus* has a minor effect on survival, although there are clear energetic effects, with both somatic and liver condition being reduced (Harrod and Griffiths 2005). However, the mechanism by which parasitism generates the gonad asymmetry is unknown. While it is tempting to conclude that parasitism by *Ichthyocotylurus* reduces fitness by affecting gonad size, we have insufficient information to estimate lifetime reproductive success and the correlations do not exclude the possibility that fish that are stressed for other reasons are also more susceptible to parasitism.

Pollan were also attacked, less frequently, by the small intestinal cestode *Proteocephalus exiguus* (45% of fish) and the ectoparasitic copepod *Argulus foliaceus* (0.3%). Infection intensity by *Proteocephalus* was far less than by *Ichthyocotylurus*, with no sign of gut distortion, and consequently, we have assumed that the latter had the major impacts. Lough Neagh supports large numbers of waterbirds, which are the final host of *Ichthyocotylurus*, and one would

Fig. 5. Pollan (*Coregonus autumnalis*) fecundity declines with increasing numbers of *Ichthyocotylurus* after controlling for the effects of body size (log somatic mass).



expect greater gonad symmetry in populations with lower infection intensities. Unfortunately, there is no information on relative gonad sizes in the other three, endangered, Irish populations or on the species in its normal, high arctic range.

One might expect reproductive traits to be more sensitive indicators of biotic stress than meristic traits. The latter are subject to effects throughout the life of the fish and these traits might well be determined in the early stages of development. However, gonad development only occurs in larger individuals and is probably determined on an annual, rather than a whole life, basis. The asymmetry in pollan gonads is consistent with this possibility: the majority of small fish showed relatively low levels of infection by *Ichthyocotylurus* (Harrod and Griffiths 2005) and symmetric gonads, but the intensity of infection increased dramatically for fish larger than 200 mm fork length. However, as the earlier discussion makes clear, gonad asymmetry is not always an indicator of stress.

We have demonstrated that variation in the degree of gonad asymmetry and in fecundity is associated with levels of biotic stress (parasite infection intensity) in one species. We suggest that such measures have the potential to act as sensitive indicators of stress. The study highlights the need for more systematic reporting of inter- and intra-specific varia-

tion in relative gonad sizes and examination of the factors that influence that asymmetry.

Acknowledgements

Many thanks go to Andrew Hendry, Colin Adams, Chris Goldspink, Sam Irwin, and two anonymous referees for helpful comments on the manuscript and to the staff and students of the former Limnology Laboratory for practical help. Lough Neagh Fishermen's Co-operative and the Department of Agriculture, Northern Ireland (DANI) gave permission to fish. C.H. was funded through a Department of Education, Northern Ireland (DENI) postgraduate research studentship.

References

- Arme, C., and Owen, R.W. 1968. Occurrence and pathology of *Ligula intestinalis* infections in British fishes. *J. Parasitol.* **54**: 272–280.
- Brown, C.J.D., and Kamp, G.C. 1942. Gonad measurements and egg counts of brown trout (*Salmo trutta*) from the Madison River, Montana. *Trans. Am. Fish. Soc.* **71**: 195–200.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Clarke, G.M. 1995. Relationships between developmental stability and fitness: application for conservation biology. *Conserv. Biol.* **9**: 18–24.
- Dodd, J. M. 1983. Reproduction in cartilaginous fishes (Chondrichthyes). In *Fish physiology*. Vol. 9A. Edited by W.S. Hoar, D.J. Randall, and E.M. Donaldson. Academic Press, New York. pp. 31–95.
- Dolezel, M.C., and Crompton, D.W.T. 2000. Platyhelminth infections in powan, *Coregonus lavaretus* (L.), from Loch Eck and Loch Lomond, Scotland. *Helminthologia*, **37**: 147–152.
- Fryer, G., and Iles, T.D. 1972. The cichlid fishes of the Great Lakes of Africa. Oliver and Boyd, Edinburgh.
- Hamaguchi, S. 1996. Bilaterally asymmetrical testes in fishes of the genus *Oryzias*. *Zool. Sci. (Tokyo)*, **13**: 757–763.
- Harrod, C., and Griffiths, D. 2004. Reproduction and fecundity of the Irish pollan (*Coregonus autumnalis* Pallas, 1776), a threatened lake coregonid. *Ann. Zool. Fenn.* **41**: 117–124.
- Harrod, C., and Griffiths, D. 2005. *Ichthyocotylurus erraticus* (Digenea: Strigeidae): factors affecting infection intensity and the effects of infection on pollan (*Coregonus autumnalis*), a glacial relict fish. *Parasitology*, **131**: 511–519.
- Harrod, C., Griffiths, D., McCarthy, T.K., and Rosell, R. 2001. The Irish pollan, *Coregonus autumnalis*: options for its conservation. *J. Fish Biol.* **59**(Suppl. A): 339–355.
- Harrod, C., Griffiths, D., Rosell, R., and McCarthy, T.K. 2002. Current status of the pollan (*Coregonus autumnalis* Pallas 1776) in Ireland. *Arch. Hydrobiol. Spec. Issue Adv. Limnol.* **57**: 627–638.
- Harvey, P.H., and Pagel, M.D. 1993. The comparative method in evolutionary biology. Oxford University Press, Oxford.
- Hechter, R.P., Moodie, P.F., and Moodie, G.E.E. 2000. Pectoral fin asymmetry, dimorphism and fecundity in the brook stickleback, *Culaea inconstans*. *Behaviour*, **137**: 999–1009.
- Heese, T. 1990. Gonad development and fecundity of whitefish *Coregonus lavaretus* (L. 1758) from the Pomeranian Bay. *Acta Ichthyol. Pisc.* **20**: 3–12.
- Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number allocation in new and indigenous salmon populations. *Evolution*, **55**: 1656–1667.
- Lagler, K.F. 1978. Capture, sampling and examination of fishes. In *Methods for assessment of fish production in fresh waters*. Edited by T. Bagenal. Blackwell Scientific Publications, Oxford. pp. 7–47.
- MacGregor, J.S. 1968. Fecundity of the northern anchovy, *Engraulis mordax* Girard. *Calif. Fish Game*, **54**: 281–288.
- Møller, A.P. 1997. Developmental stability and fitness. *Am. Nat.* **149**: 916–932.
- Pampoulie, C., Morand, S., Lambert, A., Rosecchi, E., Bouchereau, J.L., and Crivelli, A.J. 1999. Influence of the trematode *Aphalloides coelomicola* Dollfus, Chabaud and Golvan, 1957 on the fecundity and survival of *Pomatoschistus microps* (Krøyer, 1838) (Teleostei: Gobiidae). *Parasitology*, **119**: 61–67.
- Ramon, D., and Bailey, K. 1996. Spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific Ocean. *Fish. Bull.* **94**: 724–733.
- Reimchen, T.E. 1997. Parasitism of asymmetrical pelvic phenotypes in stickleback. *Can. J. Zool.* **75**: 2084–2094.
- Rounsefell, G.A. 1957. Fecundity of North American Salmonidae. *Fish. Bull. U.S. Fish Wildl. Serv.* **122**: 451–468.
- Sanwal, R., and Khanna, S.S. 1972. Seasonal changes in the testes of a freshwater fish *Channa gachua*. *Acta Anat.* **83**: 139–148.
- Sasal, P., and Pampoulie, C. 2000. Asymmetry, reproductive success and parasitism of *Pomatoschistus microps* in a French lagoon. *J. Fish Biol.* **57**: 382–390.
- Somarakis, S., Kostikas, I., and Tsimenides, N. 1997. Fluctuating asymmetry in the otoliths of larval fish as an indicator of condition: conceptual and methodological aspects. *J. Fish Biol.* **51**(Suppl. A): 30–38.
- Tesch, F.-W. 2003. The eel. 5th ed. Blackwell Science, Oxford.
- Tolonen, A., Palavuo, M., Muje, P., and Rita, H. 2002. Energy density and fecundity in subarctic European whitefish (*Coregonus lavaretus* (L.)) infected by *Diphyllbothrium ditremum* plerocercoids. *Arch. Hydrobiol. Spec. Issue Adv. Limnol.* **57**: 527–535.
- Toms, J.D., and Lesperance, M.L. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology*, **84**: 2034–2041.
- Vallisneri, M., and Scapolatempo, M. 2000. The population patterns and reproductive biology of *Engraulis encrasicolus* L. (Engraulidae, Teleostei) in the northern and middle Adriatic Sea. *Boll. Soc. Adriat. Sci. Trieste*, **80**: 81–86.
- Wedekind, C., and Müller, R. 2004. Parental characteristics versus egg survival: towards an improved genetic management in the supportive breeding of lake whitefish. *Ann. Zool. Fenn.* **41**: 105–115.
- Wilson, J.P.F., and Pitcher, T.J. 1984. Age determination and growth of the pollan, *Coregonus autumnalis pollan* Thompson, of Lough Neagh, Northern Ireland. *J. Fish Biol.* **24**: 151–163.
- Winters, G.H. 1971. Fecundity of the left and right ovaries of Grand Bank capelin (*Mallotus villosus*). *J. Fish. Res. Board Can.* **28**: 1029–1033.