SEX DISCRIMINATORY EFFECT OF THE ACANTHOCEPHALAN *ACANTHOCEPHALOIDES PROPINQUUS* ON A GOBIID FISH *GOBIUS BUCCHICHII*

SASAL P.*, FALIEX E.*, DE BURON I.** & MORAND S.*

Summary :

Most studies which aim at detecting effects of parasites on fish show that intermediate stages of parasites affect their host while adult parasites are usually less virulent in the final host. We studied the effect of the acanthocephalan *Acanthocephaloides propinquus* on one of its final hosts, the fish *Gobius bucchichii*. This study showed that the adult parasites affect host fitness. Moreover, our results showed that at the same level of infection in male and female gobiids, the female's reproductive success was negatively correlated to parasite abundance while the male's reproductive success was not. The negative effects on females includes reductions in gonado-somatic index and egg production. We hypothesized that it might be more difficult for females to compensate the cost of parasitism because of the very high cost of egg production. We discussed these results in terms of host population regulation.

KEY WORDS : impact, parasite, acanthocephalan, fish, reproduction, energy allocation.

Résumé : EFFET DIFFÉRENTIEL DE L'ACANTHOCÉPHALE *ACANTHOCEPHALOIDES PROPINQUUS* EN FONCTION DU SEXE DU GOBIE *GOBIUS BUCCHICHII*

La plupart des études qui visent à mettre en évidence un effet des parasites sur les poissons hôtes montrent que les stades intermédiaires du parasite seront plus virulents que les parasites adultes dans l'hôte définitif. Nous avons étudié l'effet de l'acanthocéphale, Acanthocephaloides propinquus *sur l'un de ses hôtes définitifs, le poisson* Gobius bucchichii*. Cette étude révèle que le parasite adulte agit sur la valeur adaptative de son hôte définitif. De plus, nos résultats montrent que malgré des charges parasitaires comparables, le succès reproducteur des femelles était négativement corrélé à la charge parasitaire alors qu'il n'en était rien pour les mâles. Cet effet négatif du parasitisme affecte aussi bien le rapport gonado somatique que la production d'oeufs. Nous émettons l'hypothèse qu'il est plus difficile de compenser un effet du parasitisme pour les femelles que pour les mâles, du fait du coût énergétique élevé de la production des oeufs. Nous discutons les possibles répercussions dans la régulation de la population hôte.*

MOTS CLÉS : *impact, parasite, acanthocéphale, poisson, reproduction, allocation d'énergie.*

INTRODUCTION

Effects of parasites on host fitness have been widely studied over the last twenty years and it now seems undeniable that parasites can affect both the biology and ecology of hosts (e.g. growth, fecundity, condition, survival) (see Esch & Fernandez, 1993; Combes, 1995). From most studies, it appears that the larval stages of macroparasites are potentially more pathogenic than the adult stages (Holmes, 1983). Even if parasites seem to be important in host population regulation (Anderson & May, 1979; May & Anderson, 1979), there is often little evidence of direct mortality induced by parasites (Szalai *et al.*, 1992), presumably because of more efficient predation on sick and weak hosts, which are therefore less frequently sampled (Lester, 1984). Most studies on fish deal with the effects of intermediate stages of parasites on their hosts (Pennycuick, 1971; Kennedy, 1984; Lemly & Esch, 1984; Szalai *et al.*, 1992; Faliex & Morand, 1994; Thomas *et al.*, 1995) or with ectoparasites (Adlard & Lester, 1994). Examples showing a direct or indirect regulating effect of macroparasite on their hosts in the field remain rare (Lemly & Esch, 1984; Adlard & Lester, 1994; Brønseth & Folstad, 1997; Pampoulie *et al.*, 1999). Only some experimental work on a direct life cycle parasite has revealed a possible indirect effect of the parasite on host reproductive success (Kennedy *et al.*, 1987; Heins *et al.*, 2000).

The influence of the acanthocephalan *Acanthocephaloides propinquus* on several biological parameters of fitness (biological condition, fecundity) of one of its definitive hosts, *Gobius bucchichii* (Teleostei, Gobiidae), is investigated in the light of the prediction that adult parasites can also affect their hosts. The objective of this study is to detect if there is a destabilizing effect of the parasite on fish reproductive success.

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* Laboratoire de Biologie Animale, UMR 5555 du CNRS, Université de Perpignan, Avenue de Villeneuve, 66860 Perpignan Cedex, France.
Tel.: (33) (0)4 68 66 20 50 – Fax : (33) (0)4 68 66 22 81.
** Department of Biology, Converse College, Spartanburg SC 29302, USA.
Correspondence: P. Sasal. E-mail : sasal@univ-perp.fr

MATERIALS AND METHODS

Four samples of *G. bucchichii* were obtained between April 1995 and February 1996 in and around the National Park of Port-Cros (Southern France, 42° 27'N; 03° 09'E). A total of 245 fishes were collected at a maximum depth of 5 m, using a hand net. Total body length (TL), standard body length (StdL), total weight (Wt) and somatic weight (all digestive tract and gonads removed) (Ws) were measured to the nearest millimeter and milligram. Gonads and liver were dissected and weighted to the nearest milligram (Wg and Wh, respectively). A condition factor was calculated as $K = (Ws \times 100)/StdL^a$, with Ws in grams and StdL in centimeters (Bolger & Connoly, 1989). Values of the exponent (a) were determined from the simple regression between logarithmic values of standard lengths and somatic weights for each sex. Because the effect on a host population could be more important and more easily detected during reproduction (Møller, 1993) and when food resources are restricted (de Lope *et al.,* 1993), males and females were separated. Sexually mature and immature fish also were separated. Males and females were analyzed separately and size classes corresponding to age classes were determined according to Sasal *et al.* (1996). Percentage of females (population female ratio) was calculated for each sampling date and each size class. Gonadosomatic indices (GSI) were calculated as $GSI = (Wg/Ws) \times 100$ and hepatosomatic indices (HSI) as $HSI = (Wh/Ws) \times 100$ (with Wg, Wh and Ws in grams). The age of first maturity has been determined previously to occur at the end of the first year of life in the Black Sea (Gordina, 1973). However, as body sizes of *G. bucchichii* in the Mediterranean Sea are on average larger than in the Black Sea, the size of first maturity was determined by comparing gonad weights for each sex during and around the reproductive period (from April to September, according to Gordina (1973)). This resulted in the determination of sexual maturity in the Mediterranean at 40 mm (StdL) for males and 55 mm (StdL) for females. Males and females of all size classes before maturity and after maturity were then compared. Female fecundity was calculated by counting the total number of eggs in the ovaries of a significant proportion of the mature females collected at the same period.

Acanthocephalans were removed from the intestine of the fish, placed in distilled water to induce eversion of the proboscis and then preserved in 70 % ethanol. Prevalence (percentage of infected hosts), mean intensity (mean number of parasite per infected host), and mean abundance (total number of parasites divided by the total number of hosts, infected and uninfected) were estimated for each size class and each sex according to Margolis *et al.* (1982) and Bush *et al.* (1997).

All data were log transformed (log+1 for number of parasites because of null values). Regressions were performed on residuals when necessary, i.e. when indirect relationship could occur. Results were considered significant at the 5 % level and values are given as the mean ± SD. Sample size may be different depending on biological indices because of missing data.

RESULTS

HOST POPULATION STRUCTURE

Males were significantly larger than females (StdL (mm) = 62 ± 17; range 34-97; n = 102 and StdL (mm) = 54 ± 15; range 26 - 86; n = 143, respectively; Mann-Whitney, Z = 3.7; $p < 0.001$). The exponent of the weight-length relationship was 2.92 for females and 2.96 for males and allowed the calculation of the condition factor for each fish. The population sex ratio was on the whole not far from being balanced (58 % female). When the size classes were considered, the sex ratio was biased in favour of females for the smaller size classes (fish < 85 mm) and biased in favour of males for the classes of the larger fishes.

The condition factor was significantly higher for females than for males (K mean = 0.0018 ± 0.0003; n = 143 *versus* K mean = 0.0015 ± 0.0002; n = 102, respectively; Mann-Whitney, Z = 9.5; $p < 0.0001$). HSI was also significantly higher for females (HSI mean = 2.63 ± 0.11; n = 142) than for males (HSI mean = 2.21 ± 0.11; n = 101) (Mann-Whitney, Z = 2.2; p = 0.03). GSI was significantly higher for females (GSI mean = 2.90 ± 0.53; n = 91) than for males (GSI mean = 0.68 ± 0.13; n = 94) (Mann-Whitney, Z = 2.86; p = 0.004). These results remained significantly different for the condition factor (K mean for female = $1.5 \times 10^{-3} \pm 0.04 \times 10^{-3}$; n = 39; K mean for male = $1.4 \times 10^{-3} \pm 0.03 \times 10^{-3}$; n = 48; Mann-Whitney, Z = 2.14; p = 0.03) and for for the GSI (GSI mean for female = 5.75 ± 1.08; n = 39; GSI mean for male = 0.96 ± 0.23; n = 48; Mann-Whitney, Z = 2.89; p = 0.004) when only fish providing from the reproductive season were considered in the analysis. The HSI was not different for males and females when fish from the reproductive season were considered (HSI mean for female = 2.90 ± 0.23; n = 39; HSI mean for male = 2.48 ± 0.15; n = 48; Mann-Whitney, Z = 1.11; p = 0.27).

The percentage of infected fish was high for all size classes and for both males and females (Table I). No significant differences in parasite abundance were found between sampling periods, for the whole sample

	Males							Females						
SC (mm)	< 40	[40-55]	[55-70]	[70-85]	[85-100]	≥ 100	Total	< 40	[40-55]	[55-70]	[70-85]	[85-100]	≥ 100	Total
P (%)	–	100	89	88	86	85	91	50	91	90	95	96	100	92
Abund ± SE (range)	–	9.6 ± 1.2 (3-22)	9.4 ± 1.7 (0-23)	10.5 ± 2.9 (0-50)	12.4 ± 2.3 (0-47)	5.4 ± 1.2 (0-14)	10.0 ± 0.9 (0-50)	5.3 ± 3.2 (0-13)	8.6 ± 0.9 (0-26)	11.1 ± 1.8 (0-45)	10.6 ± 1.7 (0-52)	9.6 ± 1.3 (0-23)	4 (4)	9.7 ± 0.7 (0-52)
I ± SE (range)	–	9.6 ± 1.2 (3-22)	10.5 ± 1.6 (1-23)	11.9 ± 3.1 (2-50)	14.4 ± 2.4 (2-47)	6.4 ± 1.2 (1-14)	11.1 ± 1.0 (1-50)	10.5 ± 2.5 (8-13)	9.4 ± 0.9 (1-26)	12.4 ± 1.8 (1-45)	11.2 ± 1.7 (1-52)	10.0 ± 1.3 (1-23)	4 (4)	10.6 ± 0.7 (1-52)
N	–	24	19	17	29	13	102	4	45	30	37	26	1	143

Table I. – Percentage of infected fish (P %), abundance of parasite (Abund) and intensity (I) in males and females *Gobius bucchichii* for each size-class (SC) (based on total length after Sasal *et al.*, 1996). N = fish number in the size-class.

and when mature and immature fish of each sex were considered separately. No significant differences in parasite abundance were found between males and females for the entire sample and when data were controlled for host size (Mann-Whitney, Z = 0.9; p = 0.36). When sexes as well as fish maturity were considered, immature females were significantly more infected (abundance) than mature females (Mann-Whitney, Z = 3.1; p = 0.002).

There was no significant relationship between the number of parasites (log+1 transformed values) and GSI (p = 0.29; n = 231) or HSI (p = 0.85; n = 243) or K (p = 0.62; n = 245). If immature and mature fish were considered separately, the results were identical (Table II). Parasite aggregation, expressed as variance to mean ratio, increased with size class for female *G. bucchichii* of the smaller size classes, then decreased in larger fish (Fig. 1). Similarly, parasite abundance increased significantly between the two first size classes (ANOVA, p < 0.001, df = 63, Games-Howell post-hoc significantly different at level 0.01) and then decreased to a significantly lower value in the last size class (mean abundance for last size class = 3.5; Games-Howell post-hoc significantly different at level 0.01 with mean abundance of the three first size classes).

Parasite Abundance	Non-mature		Mature		
	Females	Males	Females	Males	Total
vs K	p=0.10[a] (n=49)	–	p=0.87 (n=87)	p=0.73 (n=102)	p=0.71 (n=189)
vs HSI	p=0.76[a] (n=49)	–	p=0.21[a] (n=87)	p=0.72[a] (n=101)	p=0.74[a] (n=188)
vs GSI	p=0.41[a] (n=49)	–	**p=0.03** **b=–0.62** **(n= 84)**	p=0.67 (n=94)	p=0.74 (n=178)

[a] Means that data were controled for host size in order to avoid circular relationship.

Table II. – P-values of the simple regressions between parasite abundance and condition factor (K), hepatosomatic index (HSI) and gonadosomatic index (GSI). Bold values are significant.

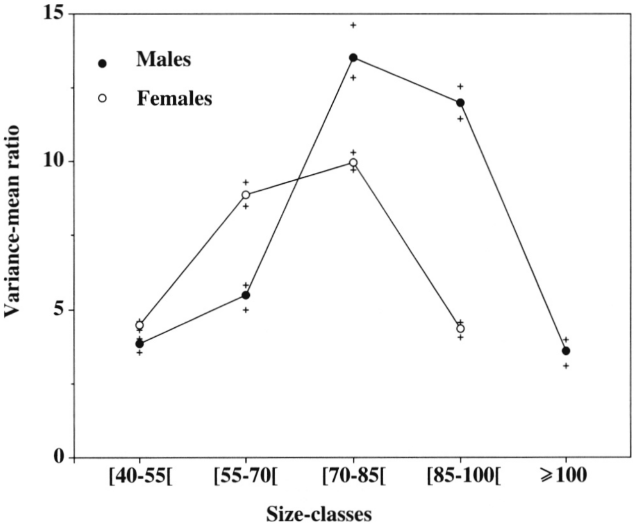

Fig. 1. – Relationship between size-class (mm) of male and female *Gobius bucchichii* and the variance-mean ratio of the parasite *Acanthocephaloides propinquus* + indicate the standard error.

When immature females (< 55 mm) were considered, correlations performed on parasite abundance, GSI, HSI, and K were not significant (all data log transformed and regressions done on standard length residuals when a confounding effect was detected) (Table II).

For mature females (≥ 55 mm), a significant negative relationship between parasite abundance and GSI (b = – 0.62; R^2 = 0.06; n = 84; p = 0.03) was found (Table II. The relationship between acanthocephalan abundance and K or HSI was not significant for this group (Table II). When mature females (≥ 55 mm) providing from the reproductive period were considered alone, the negative relationship between GSI and parasite intensity (both corrected for host size) was significant (Fig. 2: b = – 0.37; R^2 = 0.11; n = 39; p = 0.04). The number of eggs was counted in 29 females providing from one sample period (mean number of eggs = 5097 ± 599; n = 29). We found a significant negative cor-

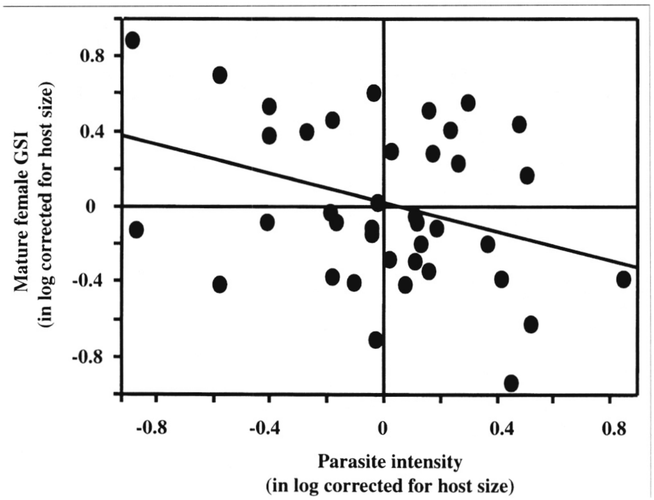

Fig. 2. – Relationship between the parasite intensity and the gonadosomatic index (GSI) of mature female during the same sample period (both in log and corrected for host standard length).

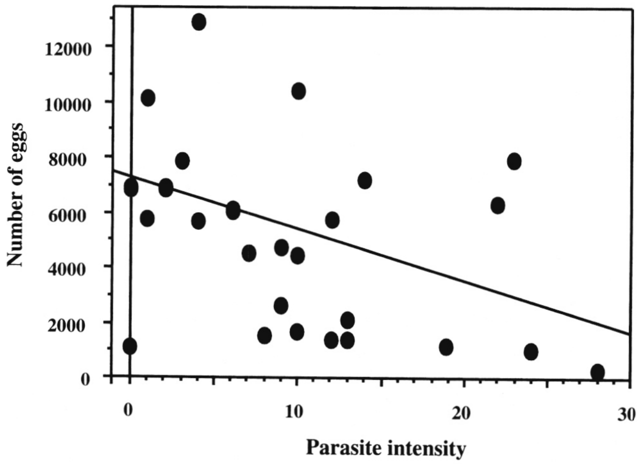

Fig. 3. – Relationship between the parasite intensity and the number of eggs of 29 mature females sampled at the same period.

relation between the number of parasites and egg counts (Fig. 3: $b = -166.7$; $R^2 = 0.16$; $n = 29$; $p = 0.03$). This relationship remained weakly significant when data were controlled for fish size by performing a regression on residual values ($b = -0.19$; $R^2 = 0.14$; $n = 29$; $p = 0.048$). Non parametric Spearman correlation test revealed a significant correlation between the same corrected datas ($n = 29$; $z = -2.18$; $p = 0.029$). The size class-aggregation curve in males was also humped and increased until a maximum value for the size class 70-8 mm (variance-mean abundance ratio = 13.4 ± 0.5) (Fig. 1). Moreover, mean abundance did not change significantly between the size classes (ANOVA, $p = 0.98$, df = 92).

None of the factors tested previously for females were found to be significant for males (Table II).

DISCUSSION

Our results show a selectively different effect of *Acanthocephaloides propinquus* on male and female gobiids with similar levels of infection, in terms of relative gonad production. The results are discussed in terms of energy allocation and behavioural strategy for reproduction.

Life-history theory assumes that there is a trade-off in energy allocation (Sibly & Calow, 1986). That means that the energy allocated to one function (growth or reproduction for example) would be lost to other physiological functions. In our study, male gobiids are significantly larger and have significantly lower biological indices (condition, HIS and GSI) than females. It has been demonstrated that male hatching success (the number of eggs hatching after being cared for by the male) increases with initial brood size, that is with fish size because brood size increases with fish size (Forsgren *et al.,* 1996). The parental investment hypothesis predicts that males should invest and allocate more energy in growth in order to reach sexual maturity during the early years of life (Sargent, 1988; Kraak & van den Berghe, 1992). Furthermore, in parental care species, such as gobiids, larger individuals will defend their young more efficiently (Gross & Sargent, 1985). This investment for males in growth and early sexual maturation will force them to consume more energy and therefore may show lower biological indices than females. The female biased sex ratio found for the smaller size classes would increase competition between males (Kvarnemo & Ahmesjö, 1996; Magnhagen, 1998). Thereafter, it might be more important for a male to have an early sexual maturity for rapid access to females. Females would accumulate energy and reserves (resulting in higher values of GSI, HSI, and K), as investment in egg production is much more costly in term of energy consumption than sperm production (Turner, 1986).

No difference in the level of infection was detected between males and females. The high level of infection and percentage of infected hosts may hide a potential effect on the biological indices studied. A comparison between infected and uninfected fishes of the same size class may have shown evidence of the parasite's effect. However, it might be difficult in field studies to detect pathological impact, as affected individuals should be rapidly eliminated by predation (Holmes, 1983). Moreover, the effect of the parasite (if there is one) may not be obvious on the biological indices studied at the level of the population even if it has been previously demonstrated that host energy metabolism could be affected by acanthocephalans (Connors & Nickol, 1991).

On the one hand, sex hormone secretion for gonad maturation in females after maturity can play an influential role in the regulation of the immune response and therefore favor parasitism (Alexander &

Stimson, 1988; Møller, 1993). On the other hand, because of the immuno handicap effect of testosterone, males are supposed to be more sensitive to parasitism (Folstad & Karter, 1992; Verhulst *et al.*, 1999). Our results seem consistent with the idea that reproductive females represent more sensitive hosts (Munger & Karasov, 1989). This is supported by the size-class-aggregation humped curve (Fig. 2) coupled to an increase of prevalence that is usually the sign of the effect of the parasite on the host population (Anderson & Gordon, 1982; Rousset *et al.*, 1996; Pampoulie *et al.*, 1999). This result may highlight a stronger effect of the parasite on reproductive female survival than on males or non-reproductive females. This hypothesis of an impact on females is reinforced by the negative correlation found between parasite abundance and GSI and fecundity. The presence of a size-class/aggregation humped curve for males without detecting an effect may be because the studied indices were not enougth sensitive (i.e. spermatozoid motility or male hormone dosage may be more sensitive factors).

Finally, if we stayed with the idea of the prudent parasite model, we can imagine that in fact the parasite has no direct effect on the host survival, either on females or males. The cost for males to grow rapidly, in order to increase their reproductive success by increasing both nest size (that means eggs laid) and competition for access to female, seems not to influence them as no differences between young and old fish were detected. Males are responsible for a large part of mating success in gobiids as they guard the nest. During nest guarding, males are starved and this can also lead to a loss of parasites (Crompton, 1985) even if we found no difference in infection within sampling period. The natural physiological constraints on females to produce energetically costly gonads may increase the level of infection of non-mature females. This result could be due to an obligatory important intake of food in order to accumulate energy for egg production.

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REFERENCES

ADLARD R.D. & LESTER R.J.G. Dynamics of the interaction between the parasitic isopod, *Anilocra pomacentri*, and the coral reef fish, *Chromis nitida*. *Parasitology*, 1994, *109*, 311-324.

ALEXANDER J. & STIMSON W.H. Sex hormones and the course of parasitic infection. *Parasitology Today*, 1988, *4*, 189-193.

ANDERSON R.M. & GORDON D.M. Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology*, 1982, *85*, 373-398.

ANDERSON R.M. & MAY R.M. Population biology of infections diseases: Part I. *Nature*, 1979, *280*, 361-367.

BOLGER T. & CONNOLLY P.L. The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology*, 1989, *34*, 171-182.

BUSH A.O., LAFFERTY K.D., LOTZ J.M. & SHOSTAK A.W. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology*, 1997, *83*, 575-583.

BRØNSETH T. & FOLSTAD I. The effect of parasites on courtship dance in threespine sticklebacks: more than meets the eye? *Canadian Journal of Zoology*, 1997, *75*, 589-594.

COMBES C. Interactions durables: Écologie et évolution du parasitisme. Masson, 1995, Paris.

CONNORS V.A. & NICKOL B.B. Effects of *Plagiorhynchus cylindraceus* (Acanthocephala) on the energy metabolism of adult starlings, *Sturnus vulgaris*. *Parasitology*, 1991, *103*, 395-402.

CROMPTON D.W.T. Reproduction. *In:* Biology of the Acanthocephala. Crompton D.W.T. & Nickol B.B. (eds), Cambridge University Press, Cambridge, 1985, 213-272.

DE LOPE F., GONZALEZ G., PÉREZ J.J. & MØLLER A.P. Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental conditions. *Oecologia*, 1993, *95*, 234-240.

ESCH G.W. & FERNANDEZ J.C. A functional biology of parasitism. Ecological and evolutionary implications. Chapman & Hall, London, 1993.

FALIEX E. & MORAND S. Population dynamics of the metacercarial stage of the bucephalid trematode, *Labatrema minimus* (Stossich, 1887) from Salses-Leucate lagoon (France) during the cercarial shedding period. *Journal of Helminthology*, 1994, *68*, 35-40.

FOLSTAD I. & KARTER A.J. Parasites, bright males and the immunocompetence handicap. *American Naturalist*, 1992, *139*, 609-622.

FORSGREN E., KVARNEMO C. & LINDSTRÖM K. Mode of sexual selection determined by resource abundance in two sand goby populations. *Evolution*, 1996, *50*, 646-654.

GORDINA A.D. New data on the biology and development of *Gobius bucchichi* Steindachner (Gobiidae, Pisces) in the Black Sea. *Journal of Ichthyology*, 1973, *13*, 152-155.

GROSS M.R. & SARGENT R.C. The evolution of male and female parental care in fishes. *American Zoologist*, 1985, *25*, 807-822.

HEINS D.C., SINGER S.S. & BAKER J.A. Virulence of the cestode *Schistocephalus solidus* and reproduction in infected threespine stickleback, *Gasterosteus aculeatus*. *Canadian Journal of Zoology*, 2000, *77*, 1967-1974.

HOLMES J.C. Evolutionary relationships between parasitic helminths and their hosts. *In:* Coevolution. Futuyama D.J. & Slatkin M. (eds), Sinauer Associates Inc., Sunderland, 1983, 161-185.

KENNEDY C.R. The use of frequency distributions in an attempt to detect host mortality induced by infections of diplostomatid metacercariae. *Parasitology*, 1984, *89*, 209-220.

KENNEDY C.E.J., ENDLER J.A., POYNTON S.L. & MACMINN H. Parasite load predicts mate choice in guppies. *Behavioural Ecology and Sociobiology*, 1987, *21*, 291-295.

KRAAK S.B.M. & VAN DEN BERGHE E.P. Do female fish assess parental quality by means of test eggs? *Animal Behaviour*, 1992, *44*, 865-867.

KVARNEMO C. & AHNESJÖ I. The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution*, 1996, *11*, 404-408.

LEMLY A.D. & ESCH G.W. Effects of the trematode *Uvulifer ambloplitis* on juvenile bluegill sunfish, *Lepomis macrochirus*: ecological implications. *Journal of Parasitology*, 1984, *70*, 475-492.

LESTER R.J.G. A review of methods for estimating mortality due to parasites in wild fish populations. *Helgolander Meeresunters* 1984, *37*, 53-64.

MAGNHAGEN C. Alternative reproductive tactics and courtship in the common goby. *Journal of Fish Biology*, 1998, *53*, 130-137.

MARGOLIS L., ESCH G.W., HOLMES J.C., KURIS A.M. & SCHAD G.A. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology*, 1982, *68*, 131-133.

MAY R.M. & ANDERSON R.M. Population biology of infections diseases: Part II. *Nature*, 1979, *280*, 455-461.

MØLLER A.P. Ectoparasites increase the cost of reproduction in their hosts. *Journal of Animal Ecology*, 1993, *62*, 309-322.

MUNGER J.C. & KARASOV W.H. Sublethal parasites and host energy budgets: tapeworm infection in white footed mice. *Ecology*, 1989, *70*, 904-921.

PAMPOULIE C., MORAND S., LAMBERT A., ROSECCHI E., BOUCHEREAU J.L. & CRIVELLI A.J. Influence of the trematode *Aphalloides coelomicola* Dollfus, Chabaud & Golvan, 1957 on the fecundity and survival of *Pomatoschistus microps* (Krøyer, 1838) (Teleostei, Gobiidae). *Parasitology*, 1999, *119*, 61-68.

PENNYCUICK L. Quantitative effects of three species of parasites on a population of three-spined sticklebacks, *Gasterosteus aculeatus*. *Journal of Zoology*, 1971, *165*, 143-162.

ROUSSET F., THOMAS F., DE MEEÜS T. & RENAUD F. Inference of parasite induced host mortality from distributions of parasite loads. *Ecology*, 1996, *77*, 2203-2211.

SARGENT R.C. Parental care and egg survival both increase with clutch size in the fathead meanow, *Pimephales promelas*. *Behavioural Ecology and Sociobiology*, 1988, *23*, 33-37.

SASAL P., FALIEX E. & MORAND S. Population structure of *Gobius bucchichii* in a Mediterranean marine reserve and in an unprotected area. *Journal of Fish Biology*, 1996, *49*, 352-356.

SIBLY R.M. & CALOW P. Physiological Ecology of Animals: an evolutionary approach. Blackwell Scientific, Oxford, 1986.

SZALAI A.J., LYSACK W. & DICK T.A. Use of confidence ellipses to detect effects of parasites on the growth of yellow perch, *Perca flavescens*. *Journal of Parasitology*, 1992, *78*, 64-69.

THOMAS F., LAMBERT A., DE MEEÜS T., CÉZILLY F. & RENAUD F. Influence of *Microphallus hoffmanni* (Trematoda, Microphallidae) on the survival, sexual selection, and fecundity of *Gammarus aequicauda* (Amphipoda). *Canadian Journal of Zoology*, 1995, *73*, 1634-1639.

TURNER G. Teleost mating systems and strategies,. *In:* The behaviour of teleost fishes. Pitcher T.J. (ed.), Croomhelm, London, 1986, 253-274.

VERHULST S., DIELEMAN S.J. & PARMENTIER H.K. A tradeoff between immunocompetence and sexual ornamentation in domestic fowl. *Proceedings of the National Academy of Sciences of USA*, 1999, *96*, 4478-4481.

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