Ann. Zool. Fennici 33: 643–651 ISSN 0003-455X
Helsinki 28 November 1996

Relationships between stocking density, growth, cannibalism and survival rate in intensively cultured larvae and juveniles of perch (*Perca fluviatilis*)

Charles Mélard, Etienne Baras, Laurent Mary & Patrick Kestemont

Mélard, C., Baras, E. & Mary, L., University of Liège, Laboratory of Fish Demography and Aquaculture, 10, Chemin de la Justice, B-4500 Tihange, Belgium
Kestemont, P., Facultés Notre-Dame de la Paix de Namur, Unité d'Ecologie des Eaux Douces (UNECED), Rue de Bruxelles, 61, B-5000 Namur, Belgium

Received 21 August 1995, accepted 12 March 1996

The influence of stocking density on the dynamics of growth, cannibalism and survival (GCS) was investigated in cultured larvae (0–44 day old fish, 500–4 000 fish m^{-2}, 20–23°C) and juveniles (60–143 day old fish, 95–2 380 fish m^{-2}, 23°C) of perch *Perca fluviatilis*. High stocking density granted significantly ($P < 0.01$) more homogeneous growth patterns within the cultured stocks that decreased the overall mortality rate and emergence of cannibals. The impact of cannibalism was proportionally decreased when fish grew more slowly. Weaned juvenile perch showed higher growth at high stocking density ($P < 0.05$). Cannibalism was suppressed by size-sorting after 24 days of rearing and was most intense at intermediate densities till this moment ($P < 0.01$).

1. Introduction

Initially regarded as relatively rare (e.g. Lorenz 1966), cannibalism now emerges as a common phenomenon affecting population dynamics. In recent literature reviews dedicated to cannibalism in fish, Smith and Reay (1991) and Hecht and Pienaar (1993) reported the existence of cannibalism in 36 of 410 fish families. Dominey and Blumer (1984) even assumed that the absence of cannibalism would be exceptional in predatory fish species. Cannibalism in fish was found to take place at various size or ages and to extend within and between cohort or age classes, depending on species and environmental conditions (review in Smith & Reay 1991, Hecht & Pienaar 1993). With respect to intensive controlled aquaculture environments, intracohort cannibalism plausibly is the most relevant phenomenon to be investigated. Because young fish exhibit allometric growth patterns (e.g. Appelbaum 1986) and show higher growth potentials than older individuals, the intensity of cannibalism would plausibly reach a maximum in the early weeks or months of the life history when the variability of individual growth would be maximum (De Angelis *et al.* 1979, Shirahata 1984, Hecht & Appelbaum 1988, Van Damme *et al.* 1989, reviews in Smith & Reay 1991, Hecht & Pienaar 1993).

If most authors agree on the impact of size heterogeneity on the intensity of cannibalism, the functional mechanisms that generate or favour this heterogeneity are still debated. Valerio and Barlow (1986) invoked the influence of genetic differences whilst others (Brown 1957, Hecht & Appelbaum

1988, Pienaar 1990 in Hecht & Pienaar 1993) suggested that the preponderant influence of behavioural factors generating a dominance hierarchy reaching its climax in cannibalistic behaviour. In addition to endogenous variables, the intensity of cannibalism will be modulated by environmental variables; turbidity, light intensity, shelter availability (Pienaar 1990 in Hecht & Pienaar 1993), food availability (Hokanson & Lien 1986), adequacy of diet to nutritional requirements (Lewis & Heidinger 1986, in Hecht & Pienaar 1993) and population density (Van Damme *et al.* 1989). In an aquaculture environment, the two latter variables can be easily tuned, emphasising the need to quantify their influence on the intensity of cannibalism. Such studies are most relevant for species commercialised at a relatively low weight, where the production of weaned juveniles represents the major contribution to the product final cost, such as the European perch *Perca fluviatilis*.

During the last 10 to 15 years, there has been a growing interest in intensive perch culture (Mélard & Philippart 1984, Fontaine *et al.* 1993, Mélard *et al.* 1994, Tamazouzt *et al.* 1994) to answer the demand of an European market of about 5 to 10 thousand tons, mainly consisting in 120–140 g fish (Fontaine *et al.* 1993, Mélard *et al.* 1996). Still Percid fish are known to show cannibalistic tendencies, especially during early-life history stages (Thorpe 1977, Craig 1987, McIntyre *et al.* 1987) which have to be mastered or at least minimised before reaching an actual intensive production stage.

The objective of this study was to quantify the influence of fish density on growth patterns, survival rates and intensity of cannibalism among larval and juvenile perch in commercial-like intensive rearing systems. With respect to the hazards of frequently handling larvae at a most sensible stage, the initial growth-cannibalism-survival (GCS) dynamics was examined as a 44-day experiment corresponding to the weaning period. The influence of density on GCS dynamics at older stages was assessed on a two week basis.

2. Material and methods

2.1. Larval stages

In spring 1993 and 1994, captive breeders (≥ 250 g) showed unforced spawning on branches laid in 4 m^2 tanks. The egg ribbons were incubated over 6 to 7 days at 15°C till the eye-pigmentation stage of embryonic development. The eggs were then transferred into the larval rearing facilities at 20°C to 23°C after a two-hours period of thermal acclimation. Stocking densities were determined from weights over samples of 500 eggs.

Larval rearing facilities consisted in 10 m^2 (4.5 m^3) outdoor concrete tanks flowed with mixed water from the River Meuse and effluents from the Tihange nuclear power plants to maintain a constant temperature during the 44-day experiments (20.0 ± 0.3°C in 1993 and 23.0 ± 0.2°C in 1994). An air diffuser was placed in each tank to maintain the oxygen level around 8 ppm. The tanks were fertilised with an initial single input of 1.5 kg of manure that allowed the development of phytoplankton then zooplankton (rotifers). The eggs were stocked in the tanks on the eve of the forecast hatching day, at a time when the availability of zooplankton was at its maximum (i.e. 7 days after fertilisation). From hatching onwards the tanks were partly (80%) shaded to prevent any further development of filamentous algae that may trap newly hatched larvae. During the first days, the water renewal rate was null to prevent the flushing of rotifers: constant temperatures thus had to be maintained by heat exchangers (U-shaped tubes, 32 mm in diameter, overall exchange surface: 6 m^2) laid on the bottom of the tank. Tanks were then progressively tuned to flow through systems with water renewal rates from 1.0 to 1.8 m^3 h^{-1}, depending on stocking density. Temperature and oxygen levels were monitored twice a day with a WTW Oxy-91 portable oxymeter and nitrate, nitrite and ammonium concentrations twice a week with a Hach Dr-2000 spectrophotometer. Concentrations of rotifers were determined from daily counts on a 2-l sample during the week before stocking perch and on each day during the experiment.

Five stocking densities ranging from 500 to 4 000 fish m^{-2} were tested (with replication for all tests at 23°C). The fish were fed close to the maximum food ration determined from the equation proposed by Mélard and Kestemont (1994):

$$R_{\max} \text{ (\% body weight)} = 45.902\, W^{-0.265},\ W = \text{body weight (mg)}$$

Since young perch are unlikely to survive repeated handling at the larval stage, no intermediate assessment of survival and biomass was made during the 44-day experiments. Rations were adjusted to body weight from weekly samples collected by a 0.25 m^2 square fishing net. Food rations were further empirically adjusted by the observer based on apparent food consumption at the population level (that would possibly reflect differences in survival and growth patterns) and to avoid any pollution of the environment resulting from overfeeding. During the first six feeding days, the diet consisted in live nauplii of *Artemia salina* (≤ 400 µm, 45.2% of protein content) only. The weaning period extended from the 7th to the 40th day of feeding. Larger *Artemia* nauplii (around 500 µm) were distributed in decreasing proportions of the total food ratio: i.e. 70, 60, 50, 35 then 15% for weaning weeks 1 to 5. The formulated dry diet used at the start of the weaning period had a 54% protein content (Nippaï Food). From day 33 onwards, it was replaced with a standard 50% protein diet (Biomar) with a higher lipid content (18% vs. 4% initially). Food distribution was exclusively diurnal using automatic

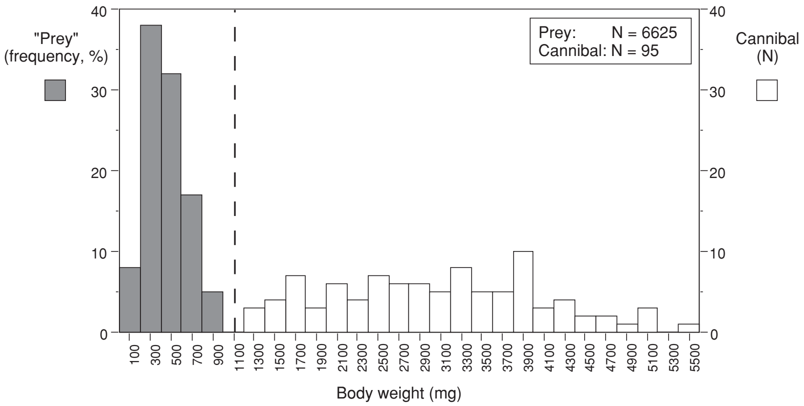

Fig. 1. Illustration of typical bimodal weight distribution at the end of a larval rearing period (44 day old fish, initial stocking density = 2 000 fish m^{-2}, 5 × 2 m^2 tank, 23°C). The discrimination between cannibals and preys is based on a biometric relationship, implying that a fish needs to outweigh others by a 7.5 to 1 ratio to be ranked as a cannibal.

feeders for formulated diets and manual distribution (six then four times a day) for *Artemia* nauplii. All distributions took place in the non shaded area of the tank, with the central air diffuser limiting the dispersion of food in the non shaded parts.

At the end of the 44-day rearing period, fish were counted and sorted in two categories, based on an obviously bimodal size and weight distribution (Fig. 1). Fish from the upper part of the distribution were weighed individually (nearest 0.01 g) whilst the weight distribution in the lower part of the population was determined from a 100 fish sample. Fast growing fish were ranked as potential cannibals based on a biometric relationship determined from observed situations when cannibalism of obviously too large prey resulted in the death of the cannibal ($R^2 = 0.943$, $df = 14$): Lt prey (mm) = 0.14 + 0.55Lt cannibal (mm). From weight-length relationships, large fish were thus empirically assumed to have cannibalistic tendencies — or potentialities — if the ratio between their weight and the weight of smallest preys (P_5 of the distribution) exceeded 7.5.

With respect to the black-box connotation of the rearing system, the relationships between stocking density and fish survival, growth and density of cannibals at the end of the 44-day experimental period were determined from multivariate (stepwise multiple-regression) analyses, using the relative availability of rotifers as an additional environmental variable.

2.2. Juvenile stages

Sixty day old weaned fish originating from the experiments described above were reared at 23°C in 2.2 m^2 (0.5 m^3) flow-through square PVC tanks at initial stocking densities ranging from 95 to 2 380 fish m^{-2}. The initial size distributions were assumed not to permit initial cannibalism (see above). Fish were given formulated diets (50% protein, 18% lipid, Biomar) distributed by automatic feeders during daytime. The tanks were checked daily for fish mortality originating from other causes than cannibalism. Since juvenile perch were far less sensitive to handling than larvae, fish growth, survival rate and emergence of cannibals could be assessed on an approximate two-week basis. At each control, fish assumed to have cannibalistic tendencies or potentialities with respect to the distribution of body weights were removed from the population. The impact of cannibalism during a rearing period was measured by comparing the difference between the stocks at two consecutive controls and the running sum of dead fish from daily counts.

3. Results

3.1. Larval stages

At the end of the 44-day rearing period at 23°C, non cannibal perch larvae had reached a mean weight ranging from 368 to 868 mg (Fig. 2), the extreme values corresponding to stocking densities of 500 and 4 000 fish m^{-2}, respectively. The coefficient of variation of mean body weight was negatively correlated with stocking density (Log-Log relationship, $R^2 = 0.940$). The low growth and huge size variability observed at low densities may reflect a poor efficiency of weaning. Growth rates at 20°C showed less variability between densities (Fig. 2) but were always far below the values observed at 23°C, with the maximum difference observed at 4 000 fish m^{-2} (396 vs. 868 mg). The mean specific growth rate (SGR, % day^{-1}) was modelled as ($R^2 = 0.848$, $df = 12, P < 0.01$):

$$SGR = -2.938 + 0.766\mathrm{T} - 0.535\mathrm{Log}\,(ICR),$$

where T = water temperature (°C) and ICR = initial concentration of rotifers (rotifers fish^{-1}). Still the lower growth observed at the highest stocking density (4 000 fish m^{-2}) at 20°C was associated with a

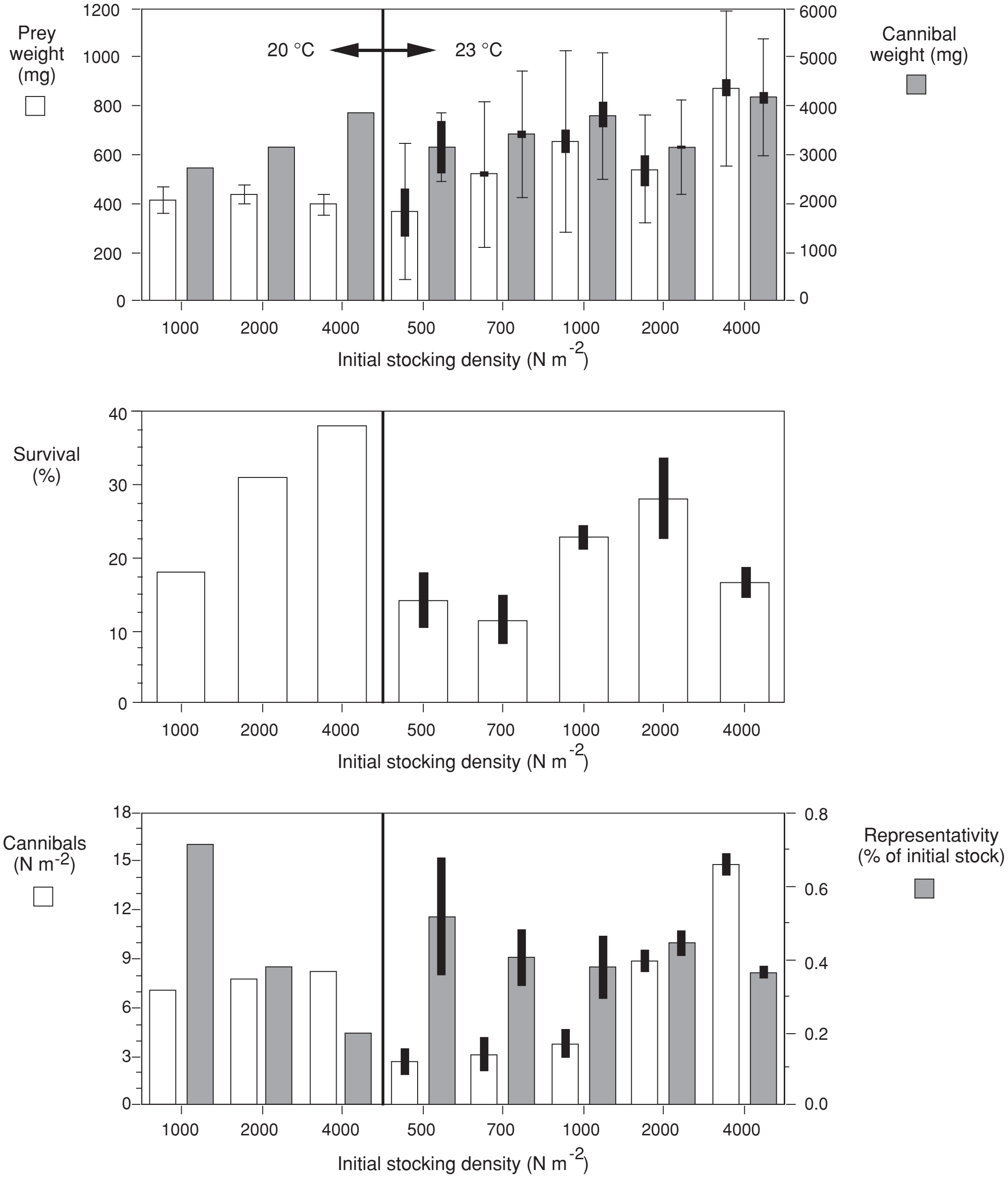

Fig. 2. Growth, survival and emergence of cannibalism in 44-day old perch larvae reared in flow through 5 × 2 m^2 tanks at initial stocking densities from 500 to 4 000 fish m^{-2}. Error bars on weight graphs are standard deviations of mean body weight. Thick dark bars correspond to discrepancies between replicates at 23°C (not significant, except mean weight of prey at 500 fish m^{-2}, $P < 0.05$).

much higher survival rate than at 23°C (39% vs. 20%, respectively): the final biomass at the two thermal regimes only differed by 5%. The comparison between the results at different thermal regimes thus suggests that all data sets (regardless of temperature) may be pooled for the comprehensive analysis of the evolution of the growth-survival-cannibalism dynamics.

The stepwise multiple-regression analysis over the final density of cannibals (NCa m^{-2}) resulted in a two-variable model ($R^2 = 0.864$ $df = 12$, $P < 0.01$, variables presented in order of integration into the model):

$$NCa\,\mathrm{m}^{-2} = -\,22.517 + 9.109\mathrm{Log}(ISD) + 3.545\ 10^{(SGR-15)},$$

with ISD = initial stocking density (fish m^{-2}) and SGR = specific growth rate (% day^{-1}). The initial availability of live planktonic prey (rotifers) was negatively correlated ($r = -\,0.567$, $P < 0.05$) with the final density of cannibals but did not enter the model at the 0.1 level of significance ($t = 1.09$, $df = 12$, $P = 0.31$), plausibly as a result of its correlation with growth and survival. Larger densities of cannibals were indeed observed at the highest stocking density (e.g. from 2.6 to 14.7 cannibal fish m^{-2}, at 500 and 4 000 fish m^{-2}, respectively). However, the semi-logarithmic nature of the relationship between the two variables suggests that increasing stocking density proportionally reduces the emergence of cannibalism.

This hypothesis is supported by the low survival rates observed at the lowest stocking density: 14.2 and 11.5% after 44 days of rearing, at stocking densities of 500 and 700 fish m^{-2}, respectively. By contrast, perch larvae reared at densities from 1 000 to 2 000 fish m^{-2} had a survival rate above 20%. The survival rate after 44 days (SR, %) was modelled from the stepwise multiple-regression analysis as:

$$(R^2 = 0.727,\ df = 12,\ P < 0.01):$$
$$SR\ (\%) = -\,58.197 + 26.651\mathrm{Log}(ISD) - 1.815\ 10^{(SGR-15)},$$

where ISD and SGR as above. Predictive models of emergence of cannibalism and survival rate depending on stocking density and growth patterns are illustrated in Fig. 3. Such models clearly suggest to increase stocking density as much as possible to reach the optimum growth-survival combinations. Still, it should be reminded that higher stocking densities would probably generate physicochemical conditions beyond the tolerance range of perch larvae: at 4 000 fish m^{-2}, the concentration of nitrites and ammonium averaged 0.50 and 1.17 mg l^{-1}, respectively, and peaked around twice these values. Similarly, the quantitative availability of live natural planktonic prey in the rearing system is limited, resulting in a possible shortage of prey at densities higher than 4 000 fish m^{-2}.

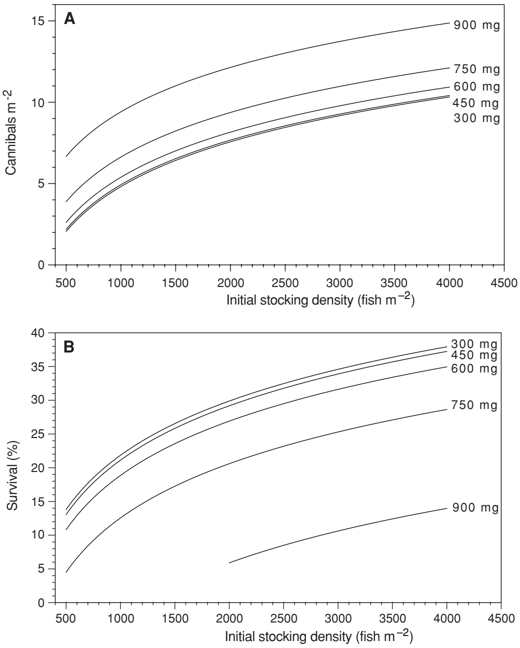

Fig. 3. Predictive relationships between stocking density, growth patterns and emergence of cannibalism (A) and survival (B) in 44-day old perch larvae reared in flow-through plastic tanks (5 × 2 m^2) at 23°C.

3.2. Juvenile stages

Despite size grading at the moment of stocking, cannibalism in juvenile perch took place at all stocking densities (Fig. 4), at least during the first 24 rearing days. Further size-grading proved to be most efficient and to prevent the emergence of cannibal fish beyond this delay. The overall numbers of cannibals collected in each tank ranged from 14 to 127, at 95 and 1 430 fish m^{-2}, respectively. Since densities higher than 1 430 fish m^{-2} produced lower amounts of cannibals, the emergence of cannibalism depending on density was modelled as a second order polynomial equation ($R^2 = 0.995$, $df = 9$, $P < 0.01$):

$$NCa\,\mathrm{m}^{-2} = 0.157 + 6.394 \times 10^{-2}\,ISD - 1.779 \times 10^{-5}(ISD)^2,$$

where ISD = initial stocking density (fish m^{-2}).

The survival rate varied between 75.4 and 92.2%, at 1 430 and 95 fish m^{-2}, respectively. On the average cannibalism caused overall mortality rates of 3.0, 4.5, 6.7, 11.4 and 7.1% at densities from 95 to 2 380 fish m^{-2}. Growth patterns were also strongly influenced by stocking density. At 13 and 24 days,

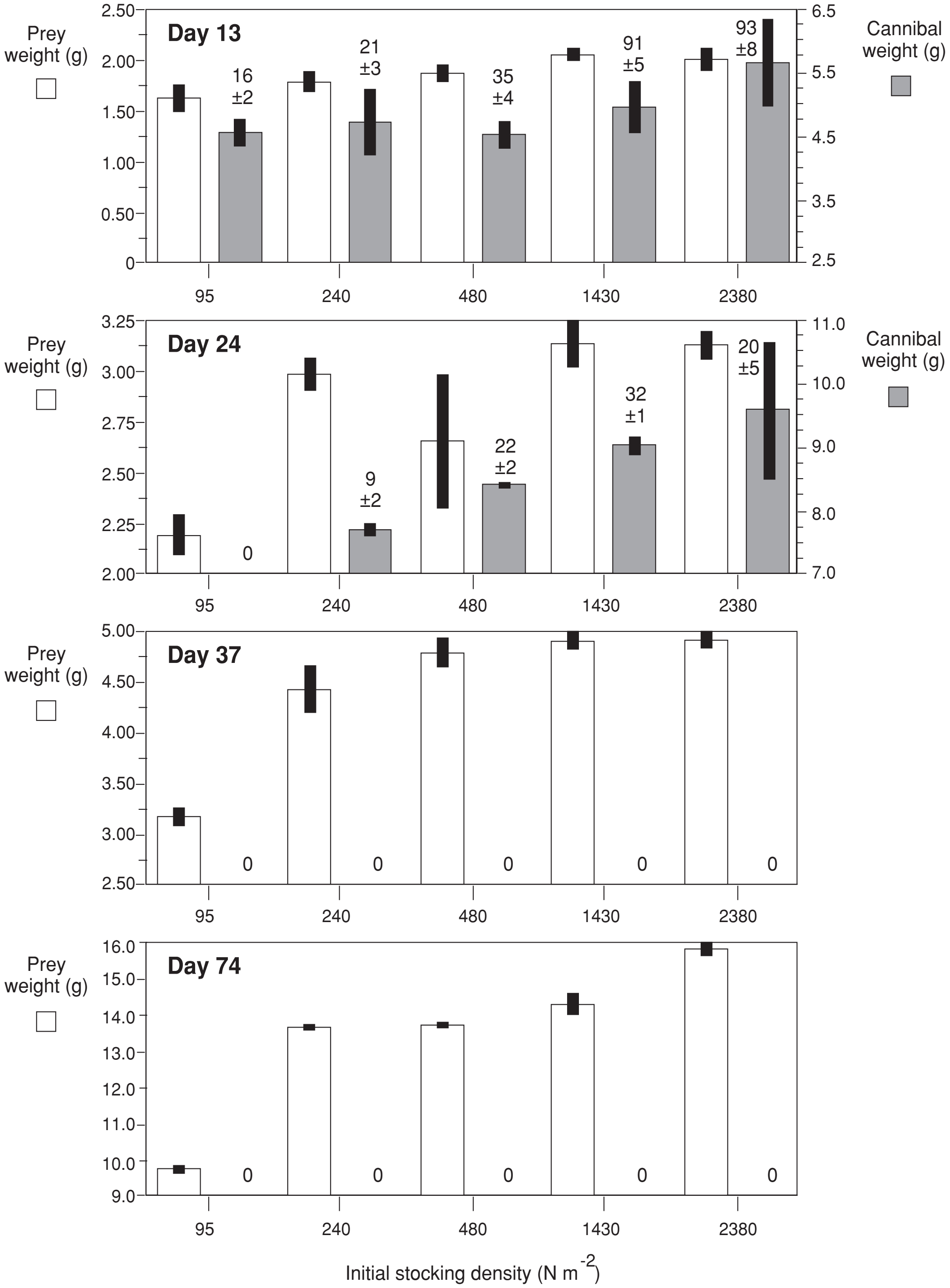

Fig. 4. Effect of stocking density on growth and cannibalism in perch juveniles reared in 2.2 m^2 (0.5 m^3) flow through tanks at 23°C. The experiment started with 45-day old weaned juveniles averaging 0.857 g, with emergent cannibals sorted at each control. Values are means of replicates, with thick dark bars indicating the variability between two replicates. Values above the bars correspond the mean number of cannibals observed at the corresponding density.

the mean weight of cannibal perch was positively correlated with stocking density ($R^2 = 0.405$, $df = 9$, $P < 0.05$) and $R^2 = 0.572$, $df = 7$, $P < 0.05$, respectively). Similarly, the growth of non cannibal juveniles at the end of the 74-day rearing period was dependent on density (semi-log relationship, $R^2 = 0.807$, $df = 9$): perch juveniles reared at 95 and 2 380 fish m^{-2} averaged 9.75 g and 15.83 g, corresponding to mean daily growth increments and specific growth rates of 121 mg d^{-1} and 3.44 % d^{-1}, 202 mg d^{-1} and 3.87% d^{-1}, respectively. Proportionally similar differences between the two extreme densities were observed at each control (Fig. 4). By contrast, the growth patterns of perch juveniles at 1 430 and 2 380 fish m^{-2} were similar (nearest 0.01 g) till day 37 and only differed during the second part of the experiment. As observed during the larval rearing period, high stocking density proportionally reduced the heterogeneity of growth within the population (at least after size-grading and sorting of cannibals): the coefficient of variation of mean individual body weight at the end of the 74-day rearing period ranged from 57.1 to 59.6% at densities from 480 to 2 380 fish m^{-2}, vs. 69.0% at 240 fish m^{-2} and 98.6% at 95 fish m^{-2}.

4. Discussion

This study clearly demonstrated the influence of stocking density on the growth-cannibalism-survival (GCS) dynamics in intensively cultured larvae and juveniles of perch *Perca fluviatilis*. The influence of stocking density on cannibalism at larval stages had already been evidenced by other authors (e.g. Van Damme *et al.* 1989, Smith & Reay 1991, Hecht & Pienaar 1993, for review): in koï carp, Van Damme *et al.* (1989) related the higher mortality rates observed at high stocking density to increased cannibalistic tendencies. In perch larvae, the overall number of cannibals collected at the end of the 44-day rearing period was indeed positively correlated with the initial stocking density. However the semi-logarithmic relationship between the two variables indicated that the impact of cannibalism was proportionally reduced at higher density. This relationship probably emerges as a consequence of territorial tendencies in cannibal fish, assuming that a minimum territory size is necessary for the expression of cannibalistic tendencies. In our experiments on larval stages this limit was probably not overridden since the highest density of cannibal fish was observed at the highest stocking density. Complementary hypotheses on the proportionally lower impact of cannibalism at higher stocking densities refer to prey tactics and escape responses such as shoaling behaviour (review in Fuiman & Magurran 1994).

The key to the understanding of the GCS dynamics plausibly refers to the variability of individual growth patterns, especially at the early stages when growth is allometric and potentially maximal (Appelbaum 1986, Smith & Reay 1991). Huge discrepancies between individual growth patterns during this period would favour the precocious emergence of cannibal fish resulting in lower survival rates. Within this context, the availability of natural planktonic prey (rotifers) plays a key role in the GCS dynamics. Since perch larvae hatch at a small size (around 0.8 mg) with lower yolk reserves than other species, they should quickly find in their culture environment prey of adequate dimensions for their gape width. A shortage in tiny natural prey such as rotifers would thus plausibly cause a size-selective access to larger prey such as *Artemia* nauplii (see comment by Guma'a 1978 on the shift of feeding strategies of wild perch larvae under shortage conditions). This variable access to food resources would result in variable initial survival and growth rates that would directly depend on the size distribution of hatched larvae or, as a corollary, on the delay between the first and last hatching of larvae in the culture environment. Beyond the potential higher initial mortality of larvae unable to feed on small prey (see Tsai 1991 for parallel in *Morone saxatilis*), a shortage in natural prey would favour a higher initial size heterogeneity and thus a more precocious emergence of cannibalism, as proposed by Smily (1952) for wild fish. Cannibalism from the early rearing days would thus cause in the long run the progressive vanishing of smaller prey, resulting into a more homogeneous population with higher mean size. This dynamic interpretation would account for the rather paradoxical negative relationships between the initial availability of natural prey and growth-cannibalism at the end of the larval rearing period.

Since the production of large amounts of weaned juveniles represents the key to intensive perch culture, fish farmers should tune their larval rearing accordingly and favour highest initial survival rates.

Hopefully the predictive models on the trade-off between growth and survival in cultured perch larvae (Fig. 3) provide fish farmers with practical bases for efficiently managing the larval rearing period. From the present experiments and models of larval growth, it is strongly suggested that a saturation in natural prey (rotifers) at a lower thermal regime (20°C vs. 23°C) would proportionally increase the initial survival rate. The precise effect of such rearing conditions at different stocking densities remains to be investigated in future research.

The GCS dynamics of intensively cultured juvenile perch was similar to that observed during the larval rearing period. The polynomial nature of the relationship between stocking density and the emergence of cannibalism at these stages is plausibly accounted for by the saturation of the maximum carrying capacity of rearing tanks for territories of cannibal fish. This difference between the juvenile and larval stages (when no saturation effect was observed even at 4 000 fish m^{-2}) probably originates from a common sense relationship between fish size and territory, but the reduction of aggressive tendencies by increasing density may also be evoked. Despite the proportionally lower emergence of cannibalism at higher stocking density, the impact of cannibalism was slightly higher than at low density. This paradox may reflect the difficulty of numerous prey to escape predator attacks when the whole rearing environment is saturated with cannibals.

These experiments support the relevance of high density rearing for the culture of juvenile perch since maximum growth and minimum size heterogeneity were achieved at the highest stocking densities (1 430 and 2 380 fish m^{-2}) at least when cannibals were sorted on a 10–14 day basis: the impact of cannibalism was indeed reduced to zero beyond the first 24 rearing days (fish ≥ 3–4 g) following two consecutive size-sorting of large juveniles. Similar results were obtained with juveniles of other fish species with cannibalistic tendencies (McIntyre *et al.* 1987) and support the relevance of size-sorting juvenile fish, especially within a standard intensive rearing framework, implying the transfer at regular intervals of fish to larger tanks. The natural progressive decrease of growth potentialities at older stages limits the risks of cannibal emergence in older size-sorted juveniles although the variability of individual growth patterns may be substantial (Mélard *et al.* 1995).

This study on the production dynamics of intensively cultured perch larvae and juveniles proposed preliminary black box models of growth, survival and cannibalism that integrate most environmental variables ruling commercial production. Still, further understanding and analyses are required, especially on the emergence of cannibalism at the early stages and on the precise evolution of cannibalism throughout fish ontogeny. Such fundamental elements of perch biology will be investigated in coming behavioural studies at an experimental scale.

Acknowledgements. This study was supported by the Ministry of Environment of the Walloon Region (D.G.R.N.E.) and by Electrabel s.a. Research of E. Baras on fish behaviour in aquaculture is supported by the Ministry of New Technologies (D.G.T.R.E, FIRST-University programme).

References

Appelbaum, S., Anderson, P. & Mochendorf, C. 1986: Cannibalism in reared Koï carp larvae. 235. — In: Billard, R. & Marcel, M. (eds.), Aquaculture of Cyprinids. INRA, Paris, France.

Brown, M. E. 1957: Experimental studies on growth. — In: Brown, M. E. (ed.), The physiology of fishes: 361–400. Academic Press, New York, N.Y., USA.

Craig, J. F. 1987: The biology of perch and related fish. — Croom Helm, Beckenham, England. 333 pp.

De Angelis, D. L., Cox, D. K. & Coutant, C. C. 1979: Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. — Ecol. Model. 8: 133–148.

Dominey, J. & Blumer, L. S. 1984: Cannibalism and early life stages of fishes. — In: Haustafe, G. & Hardy, S. B. (eds.), Infanticide: comparative and evolutionary perspectives: 43–64. Aldine, New York, N.Y., USA.

Fontaine, P., Tamazouzt, L., Terver, D. & Georges, A. 1993: Actual state of production of perch: problems and prospects. 1. Mass rearing potentialities of the common perch under controlled conditions. — In: Kestemont, P. & Billard, R. (eds.), Workshop on Aquaculture of Freshwater Species (except salmonids): 46–18. EAS Spec. Publ., 20, Ghent, Belgium, 79 pp.

Fuiman, L. A & Magurran, A. E. 1994: Development of predator defences in fishes. — Rev. Fish Biol. Fish. 4: 145–183.

Guma'a, S. A. 1978: The food and feeding habits of young perch, Perca fluviatilis, in Windermere. — Freshwat. Biol. 8: 177–187.

Hecht, T. & Appelbaum, S. 1988: Observations on intraspecific aggression and coeval sibling cannibalism by larval and juvenile Clarias gariepinus (Clariidae: Pisces) under controlled conditions. — J. Zool. (Lond.) 214: 21–44.

Hecht, T. & Pienaar, A. G. 1993: A review of cannibalism and its implication in fish larviculture. — J. World.

Aquacult. Soc. 24: 246–261.

Hokanson, K. E. & Lien, G. G. 1986: Effects of diet on growth and survival of larval walleyes. — Prog. Fish Cult. 48: 250–258.

Lorenz, K. 1966: On aggression. — Bantam Books, New York, N.Y., USA.

McIntyre, D. B., Ward, F. J. & Swanson, G. M. 1987: Factors affecting cannibalism by pond-reared juvenile walleyes. — Prog. Fish Cult. 49: 264–269.

Mélard, C. & Kestemont, P. 1994: Diversification de la pisciculture Wallonne. Mise au point de l'élevage intensif de nouvelles espèces de consommation et de repeuplement: cyprinidés et percidés. — Rapport de recherches à la Région Wallonne, Université de Liège, Facultés Universitaires Notre-Dame de la Paix à Namur, mars 1994. 68 pp.

Mélard, C. & Philippart, J. C. 1984: Essai d'élevage semi-intensif en bassin d'alevins de perche fluviatile (Perca fluviatilis) obtenus par reproduction artificielle. — Cah. Ethol. appl. 4 : 59–66.

Mélard, C., Baras, E. & Kestemont, P. 1995: Preliminary results of European perch (Perca fluviatilis) intensive rearing trials: effect of temperature and size grading on growth. — Bull. Fr. Pêch. Pisc. 336: 19–27.

Mélard, C., Kestemont, P. & Grignard, J. C. 1996: Intensive ongrowing of juvenile perch (Perca fluviatilis): zootechnical parameters and growth. — J. Appl. Ichtyol. (In press.)

Mélard, C., Baras, E., Desprez, D., Philippart, J. C. & Kestemont, P. 1994: Intensive culture of perch (Perca fluviatilis). First results on the effects of stocking density on growth and survival of larvae and juveniles. — In: Measures for Success: 206–207. EAS Spec. Publ. 21, Oostende, Belgium. 352 pp.

Pienaar, A. G. 1990: A study of coeval sibling cannibalism in larval and juvenile fishes and its control under culture conditions. — M.Sc.-thesis, Rhodes University, Grahamstown, South Africa.

Shirahata, S. 1984: On "cannibalism" in the rainbow trout fingerling, Salmo gairdneri irideus. — Jap. J. Ecol. 14: 25–32.

Smily, W. J. P. 1952: Observations on the food of the fry of perch, Perca fluviatilis L. in Windermere. — Proc. Zool. Soc. Lond. 122: 407–416.

Smith, C. & Reay, P. 1991: Cannibalism in teleost fishes. — Rev. Fish Biol. Fish. 1: 41–64.

Tamazouzt, L., Dubois, J. P. & Fontaine, P. 1994: Production et marché actuels de la perche (Perca fluviatilis) en Europe. — Pisc. Franç. 114: 4–8.

Thorpe, J. 1977: Synopsis of biological data on the perch, Perca fluviatilis (Linnaeus, 1758) and Perca flavescens (Mitchill, 1814). — FAO Fish. Synop., N°113. 138 pp.

Tsai, C. 1991: Prey density requirements of the stripped bass, Morone saxatilis (Walbaum), larvae. — Estuaries 14: 207–217.

Valerio, M. & Barlow, G. W. 1986: Ontogeny of young Midas cichlids: a study of feeding, filial cannibalism and agonism in relation to difference in size. — Biol. Behav. 11: 16–35.

Van Damme, P., Appelbaum, S. & Hecht, T. 1989: Sibling cannibalism in koï carp, Cyprinus carpio L., larvae and juveniles reared under controlled conditions. — J. Fish Biol. 34: 855–863.