

Diel and seasonal variations in brown trout (*Salmo trutta*) feeding patterns and relationship with invertebrate drift under natural and hydropeaking conditions in a mountain stream

Thierry Lagarrigue ^a, Régis Céréghino ^{b,*}, Puy Lim ^c, Patricia Reyes-Marchant ^d, Rémi Chappaz ^e, Pierre Lavandier ^b, Alain Belaud ^c

^aCabinet d'études IMAG'O (Ichtyologie, Milieux aquatiques et Gestion des Eaux), 26 rue Dels-Pibouls, Labastide Falgarde, 31120 Lacroix Falgarde, France

^bCentre d'Ecologie des Systèmes aquatiques continentaux, UMR C5576, 118 route de Narbonne, 31062 Toulouse cedex 4, France

^cLaboratoire Environnement aquatique, ENSAT, 1 avenue de l'Agrobiopôle, BP 107 Auzeville-Tolosane, 31326 Castanet-Tolosan, France

^dCabinet d'études EMA (Etudes milieux aquatiques), La Croix Cadet, 63460 Joserand, France

^eUPRES Biodiversité, 1 place Victor Hugo, 13331 Marseille cedex 3, France

Received 14 May 2001; accepted 14 January 2002

Abstract

The abundance of prey ingested by brown trout (*Salmo trutta*) were compared with the abundance of drifting invertebrates in a mountain stream managed by hydropeaking, upstream (site A) and downstream (site B) of a hydroelectric power plant. During power generation, flow and temperature were the two main environmental factors modified. The natural flow in the river below the outlet may be enhanced several times a day from 1 to 11 m³.s⁻¹ in summer and winter, and from 5 to 15 m³.s⁻¹ during spring spates. During hydropeaking, the water was cooled by an average of 6 °C in summer and warmed by an average of 2 °C in winter. Overall drift density was higher at site B than at site A. There was a clear diel pattern of drift at site A, with low drift density during the day and high drift density at night, whereas no clear diel pattern was observed at site B. Below the plant, at site B, drift pattern appeared to be influenced most by hydropeaking. The flushing action of peaking flows caused a catastrophic drift, which was highest in autumn when the difference between natural and peak flows was greatest. Juvenile trout were adversely affected by hydropeaking conditions and subsequently their density and biomass were reduced by 30% from site A to site B, whereas no significant difference was noticed for adults. Gut contents analysis showed that brown trout chiefly fed on the most available prey items at both sites. Fish did not seem to feed in response to diel drift patterns above the plant, whereas they chiefly used drift pulses generated by peaking flows below the outlet. Under natural conditions, fullness indices increased from autumn to summer, suggesting they may be related to prey availability and changes in water temperature. In the regulated section, fullness indices were the lowest in spring, i.e. the season when peak flows added to snowmelt floods, suggesting a prominent role of high current velocities through habitat suitability, position maintenance, and ability to capture preys. Although hydropeaking is known to disturb trout population dynamics in this and other rivers, this kind of river regulation (natural discharge except during periods of power generation, and intermittent hydropeaking from a separate reservoir) allowed the maintain of brown trout below the outlet, probably because the river returned to natural conditions when the plant was inoperative, and because daily artificial fluctuations in flow and temperature remained within the limits of natural seasonal variations. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Variations journalières et saisonnières de la nutrition chez la truite (*Salmo trutta*) et relation avec la dérive des invertébrés en conditions naturelles et en régime d'éclusées dans une rivière de montagne. Nous comparons l'abondance des proies ingérées par la truite commune (*Salmo trutta*) avec l'abondance de la dérive des invertébrés dans une rivière de montagne, en amont (station A) et en aval (station B) d'une usine hydroélectrique gérée par éclusées. Débit et température de l'eau sont les deux principaux facteurs environnementaux affectés par les éclusées. Le débit naturel de la rivière peut être augmenté plusieurs fois par jour, passant de 1 à 11 m³.s⁻¹ en été et

* Corresponding author.

E-mail address: cereghin@cict.fr (R. Céréghino).

en hiver, et de 5 à 15 m³.s⁻¹ pendant la crue printanière. Pendant les éclusées, l'eau de la rivière est refroidie de 6 °C en moyenne en été, et réchauffée de 2 °C en moyenne en hiver. La densité totale de la dérive des invertébrés est la plus importante en aval de l'usine. Il existe un rythme journalier de dérive à la station A, avec de faibles densités de dérive le jour, et de fortes densités la nuit, tandis qu'aucun rythme n'apparaît clairement à la station B. L'action érosive des éclusées provoque une dérive de type catastrophique, d'autant plus forte que la différence débit naturel – débit d'éclusée est élevée. Les truites juvéniles sont également affectées par ces conditions ; leur densité et leur biomasse est réduite de 30 % de la station A à la station B, tandis qu'aucune différence significative n'est constatée pour les adultes. L'analyse des contenus stomacaux montre que les truites se nourrissent principalement des proies les plus disponibles aux deux stations. En amont, les poissons ne semblent pas se nourrir en réponse aux variations journalières de la dérive. En aval, ils utilisent principalement les pics de dérive générés par les éclusées. A la station A, les indices de réplétion augmentent de l'automne à l'été, suggérant une relation avec la disponibilité des proies et avec les variations de température de l'eau. A la station B, les indices de réplétion sont les plus bas au printemps, lorsque les éclusées se surimposent aux forts débits de crue, suggérant un rôle prépondérant des fortes vitesses de courant au travers de la disponibilité des habitats, du maintien des poissons, et des possibilités de capture des proies. Bien que la gestion par éclusées soit connue pour perturber la dynamique des populations de truite en rivière, le type d'aménagement étudié (débit naturel en dehors des périodes d'éclusées, prise d'eau dans un réservoir séparé de la rivière) permet le maintien des truites en aval de l'usine, probablement parce que la rivière retourne à des conditions naturelles lorsque l'usine ne fonctionne pas, et parce que les variations artificielles journalières du débit et de la température restent dans les limites des variations naturelles saisonnières. © 2002 Ifremer/CNRS/Inra/Cemagref/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Feeding patterns; Drift; Invertebrates; Hydropeaking; Brown trout; *Salmo trutta*

1. Introduction

Many ecological studies have dealt with the impact of river regulation, including hydropeaking, on fish in mountain rivers (e.g., Kraft, 1972; Cushman, 1985; Bain et al., 1988; Mann, 1988; Gore et al., 1989; Weisberg and Burton, 1993; Gore et al., 1994). Most have pointed out that salmonid population structure - particularly for brown trout (*Salmo trutta* L.) - is highly dependent on habitat conditions (Gorman and Karr, 1978; Haury et al., 1991; Baran et al., 1995; Greenberg and Dahl, 1998). However few studies have dealt with the biological implications of hydropeaking such as feeding patterns or growth (Brusven and MacPhee, 1976; Garcia de Jalon et al., 1988; Fraley et al., 1989). Hydropeaking usually results in the following types of impact on the lotic ecosystem: i) modification of physical and chemical conditions below the outlet (reviewed in Ward and Stanford, 1979; Gore et al., 1989; Gore et al., 1994); ii) reduction in density, modification of population structures and catastrophic drift of benthic invertebrates (Moog, 1993; Céréghino and Lavandier, 1998); and iii) reduced abundance and/or alteration of population structure of fish (Casado et al., 1989; Moog, 1993; Valentin et al., 1994) with the youngest life stages being the most affected (Liebig et al., 1999).

In France, 144 hydroelectric plants involving 80 rivers are managed by hydropeaking (Lauters, 1995). The stream-water below most hydroplants consists entirely of reservoir water. In the present study, we examined a different situation in which the power plant did not disrupt the natural flow of the river, and was fed by hypolimnetic water from a nearby high-altitude reservoir. Therefore, the natural discharge and temperature regimes were preserved when the plant was inactive, and both invertebrate and trout populations are alternatively subjected to natural followed by highly varying flow and temperature regimes. Considering

previous studies, the expected effects on river biota could be periodic catastrophic drift (Garcia de Jalon et al., 1988; Weisberg et al., 1990), i.e. an increased food availability for drift feeding fish, and as a consequence a modification of their diel and/or seasonal feeding patterns of fish (Weisberg and Burton, 1993). Therefore, the aim of our study was to determine the influence of intermittent hydropeaking on invertebrate drift abundance, and the implications for brown trout feeding. In order to verify whether our observations were consistent with postulated effects of regulation, we focused on the differences observed between a reference site and a downstream site (700 m below the plant). We discuss possible mechanisms explaining these differences.

1.1. Study area

The River Oriège is a torrential stream in the French Pyrénées (latitude N 42° 43', longitude E 1° 50', Fig. 1). A detailed description of the study area has been given by Céréghino et al. (1997). The natural daily mean flow of the Oriège varied from 1 m³.s⁻¹ in winter and summer to 15 m³.s⁻¹ during the spring thaw (Fig. 1). Flow in the Oriège River – 912 m above sea level (a.s.l.) – is supplemented by discharge from the Orlu hydroelectric power plant (flow being supplemented by 5 m³.s⁻¹ in spring to 10 m³.s⁻¹ in winter or summer), which is fed by hypolimnetic water from a high-altitude reservoir (Lake Naguilles, 1 855 m a.s.l.). Two sampling sites were selected, a reference site 700 m upstream of the hydrostation's discharge point (site A), and a regulated site 700 m below the outlet (site B) (Table 1). During hypolimnetic releases, the water was cooled by an average of 6 °C in summer (i.e. from 2.5 to 7 °C) and warmed by an average of 2 °C in winter (from 0.5 to 3.5 °C) (Fig. 2). Degree-days (dd) accumulated at sites B were observed to be 109 dd lower than at site A from August to October 1991, and 61 dd higher from November 1991 to

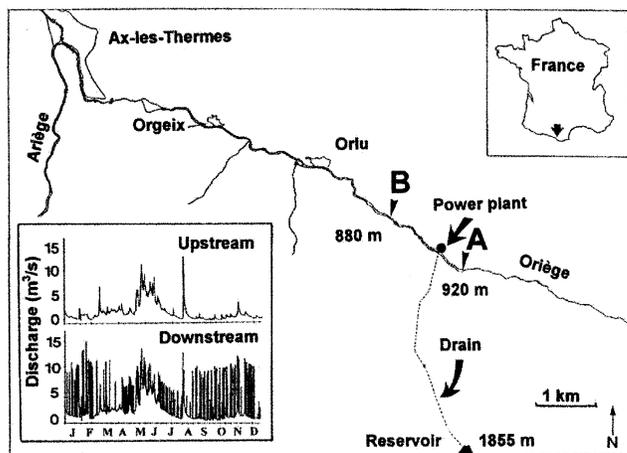


Fig. 1. Map of the River Oriège, location of the two sampling sites (A, B) and hourly discharge ($\text{m}^3\cdot\text{s}^{-1}$) recorded upstream at site A and 1 500 m downstream from the Orlu power plant. The elevations correspond to sampling sites A and B.

July 1992 (Fig. 2). During winter, hypolimnetic releases accentuated the natural increase of temperature at downstream sites (Fig. 2). As a result, site B had the lowest total number of degree-days calculated for the June 1991–July 1992 period, but the annual thermal sums were similar (Table 1).

2. Material and methods

2.1. Invertebrate drift

Invertebrate drift was collected for 24 h on 26 June and 1 October 1991, i.e., during spring spates and low flow periods respectively, at sites A and B. Drift samples were collected using a 30×50 cm drift net (net length 1.50 m, mesh size 0.3 mm) at 1-h intervals. Because of net clogging, the sampling period was reduced to 30 min during hydro-peaking. Bottom, middle and surface water velocities were measured hourly immediately in front of the net using an OTT® portable flowmeter, to allow calculation of the volume of water filtered. Invertebrates were preserved in the field in 5% formalin, identified in the laboratory and preserved in 70% ethylalcohol. Drift abundance was expressed as number of individuals per volume of water filtered ($\text{ind}\cdot 100\text{ m}^{-3}$).

Table 1
Main morphological and thermal characteristics of the study sites (River Oriège, Pyrénées)

	A (upstream)	B (downstream)
Distance from the outlet (m)	700	700
Elevation a.s.l. (m)	920	880
Stream width (m)	8	17
Mean slope (%)	2.56	2.57
Water temperature (min-max, °C)	0–13.5	0.4–13.8
Total degree days (June 1991–July 1992)	2 917	2 877

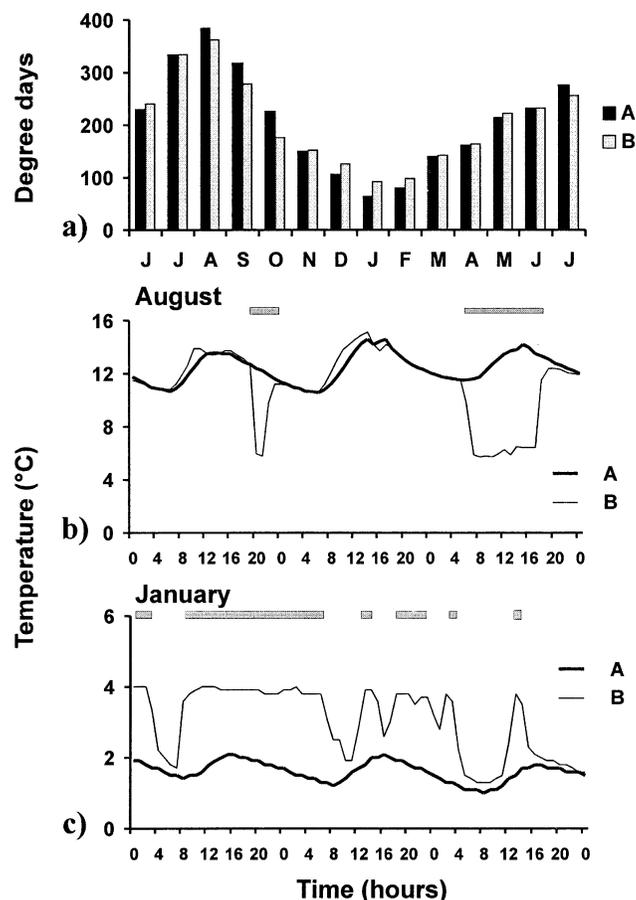


Fig. 2. Thermal regime of the River Oriège and influence of hypolimnetic releases (June 1991–July 1992). a) Total number of degree-days monthly accumulated at the two sites. Examples of diel fluctuations in stream water at the two sites over 3 days: b) in summer (1–3 August 1991) and c) in winter (3–5 January 1992). Grey bars at the top of the graph indicate periods of power generation.

2.2. Trout sampling

Brown trout (*Salmo trutta*) were the only fish in the study section. Density and biomass of brown trout populations were estimated by electrofishing at both sites on 26 June 1991, 1 October 1991, 6 February 1992, and 14 April 1992, using a two-pass removal method (De Lury, 1951). The length of the sampled reach was 80 and 100 m at sites A and B respectively. Block nets were not necessary because the sampled reaches were delimited by two cascades. All collected fish were immediately anaesthetised using tricaine methanesulfonate (MS-222), weighed to the nearest gram and measured to the nearest mm (total length). The density of trout was calculated using the method of Carle and Strub (1978), and separate calculations were performed for 0+ (total length < 110 mm) and older fish (1+ from 110 to 160 mm, and 2–5+ above 160 mm). Trout biomass was evaluated from the length to weight relationships established for each site and for each season.

Table 2

Mean total lengths (\pm SE), mean weights (\pm SE) and sample size (n) of trout (*Salmo trutta*) used for gut content analysis at sites A and B. Between sites, means are significantly different at $P < 0.05$ (*), $P < 0.01$ (**), or not significantly different (ns)

Season	Site	n	Length (mm \pm SE)	p	Weight (g \pm SE)	p
June 1991	A	104	157 \pm 3	ns	44 \pm 2	ns
	B	100	165 \pm 3		48 \pm 3	
October 1991	A	115	178 \pm 2	ns	61 \pm 2	ns
	B	112	173 \pm 3		56 \pm 2	
February 1992	A	119	200 \pm 3	**	80 \pm 4	*
	B	118	184 \pm 3		60 \pm 3	
April 1992	A	119	178 \pm 3	ns	57 \pm 2	ns
	B	121	169 \pm 2		47 \pm 2	

2.3. Trout diet

At both sites, trout feeding habits were assessed over four 24-hour cycles on 26 June 1991, 1 October 1991, 6 February 1992, and 14 April 1992. The former two dates being the same as when drift was sampled. During each cycle, we caught (by electrofishing) approximately 20 trout every four hours (total length > 120 mm) at each site, i.e. a total of 457 and 451 individuals at sites A and B respectively. Gut contents were collected using a non-destructive stomach flushing method (Meehan and Miller, 1978) and preserved in 4% formaldehyde for analyses later in the laboratory. We estimated the wet weights of fresh stomach contents to the nearest 0.1 mg on a micro-precision balance. Consumption was estimated by the fullness index: $FI = \text{weight of fresh stomach content} / \text{weight of the fish}$ (mg.g^{-1}) (Frankiewicz et al., 1993). This index allowed site-to-site and/or seasonal comparisons of consumption without bias caused by differences in trout size or weight. The mean individual size and weight of trout used for gut content analysis are shown in Table 2. With the exception of February, the size-class and weight-class distributions of captured fish for diet and FI analysis did not differ significantly ($p > 0.05$) from one site to another.

2.4. Statistical analyses

Differences in drift composition (upstream vs. downstream) at each date were assessed using Kolmogorov-Smirnov two-sample tests. For each 4-hour sampling period at one site on one date, differences in FI values were assessed using one-way Kruskal-Wallis tests. For each site,

we compared FI among seasons using one-way Kruskal-Wallis tests. Between-site differences of FI (site A vs. site B at each period) were assessed using Mann-Whitney tests. A level of $P < 0.05$ was accepted as significant throughout all analyses.

3. Results

3.1. Population structure of brown trout

Above the hydroelectric power plant, total trout density and biomass (including young-of-the-year, juvenile, and adult stages) ranged from 1 200 to 2 100 fish.ha⁻¹ and from 47 to 76 kg.ha⁻¹ respectively, depending on the season (Table 3). Below the outlet, we observed a reduction in density and biomass (900–1 300 ind. ha⁻¹ representing 34–52 kg.ha⁻¹). From the upstream to the downstream site, the overall fish density was thus reduced by 25 to 38%, and biomass from 28 to 32%, depending on the season, chiefly to the detriment of young-of-the-year and juvenile stages (40 mm < total length < 160 mm).

3.2. Fullness Indices (FI)

At the reference site (site A), trout feeding exhibited a slight diel periodicity (Fig. 3), except in June (snowmelt floods) where FI variations were not significant. FI values generally decreased during the day, and increased during the night to reach their maximum at dawn and/or in the morning. At the regulated site (site B), no clear diel pattern could be identified. Maximum FI values were observed

Table 3

Abundance by size-class of trout (*Salmo trutta*) captured at the two sites and at each sampling period (YOY = young-of-the-year)

Season	Site	Total abundance (ind.ha ⁻¹)	Size class		
			< 110 mm YOY (ind.ha ⁻¹)	110–160 mm 1+ (ind.ha ⁻¹)	160 mm 2+ - 5+ (ind.ha ⁻¹)
June 1991	A	1 200	180	600	420
	B	900	207	378	315
October 1991	A	1 400	238	686	476
	B	1 050	210	388	452
February 1992	A	1 100	132	484	484
	B	900	18	396	486
April 1992	A	2 100	525	756	819
	B	1 300	364	325	611

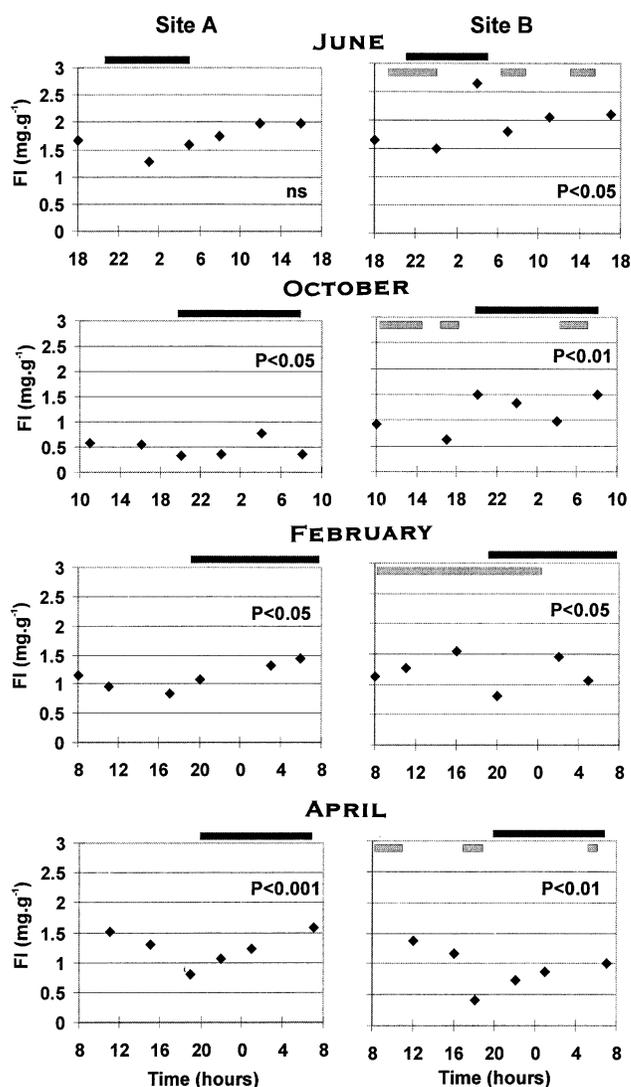


Fig. 3. Diel variations of Fullness indices (FI) over 24 hours, at the two sites and for the four seasons. At the top of the graphs, black solid bars indicate night and grey solid bars indicate periods of power generation. For each 4-hour sampling period at one site on one date, differences in FI values were assessed using one-way Kruskal-Wallis tests (values of p are given; ns = non significant).

during the day (e.g., in April), during the night (e.g., in June), or both during night and day hours (e.g., in October and February).

At each site, seasonal variations in FI were significant ($P < 0.01$) (Fig. 4). At both sites, the highest FI values were observed in June (i.e., during snow melt floods). The lowest FI values were observed in October (i.e., during the low flow period) at site A and in April (i.e., at the beginning of snow melt floods) in site B. FI values were significantly higher in the regulated site in June ($P < 0.05$) and in October ($P < 0.01$) and significantly lower in the regulated site ($P < 0.05$) in April. FI values did not differ significantly from the upstream to the downstream site ($P > 0.05$) in February.

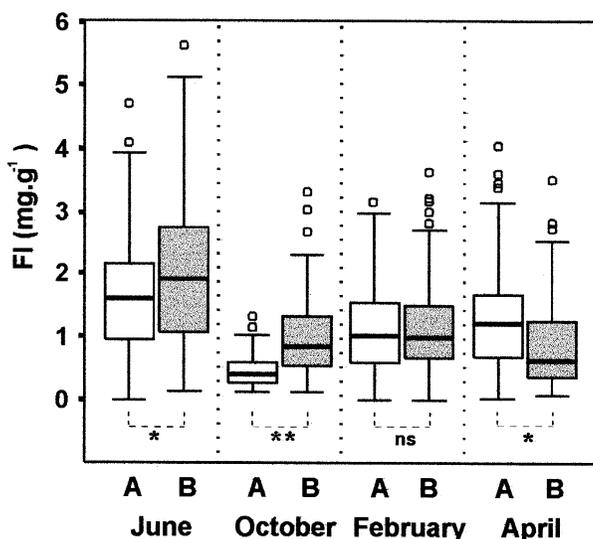


Fig. 4. Box-plots for Fullness indices (FI) at the two sites for each season. Between sites, FI are significantly different at $p < 0.05$ (*), $p < 0.01$ (**) or not significantly different (ns). Open circles represent outlier points.

3.3. Diel feeding patterns vs invertebrate drift

Drift composition at upstream and downstream sites (Fig. 5) did not differ significantly (Kolmogorov-Smirnov two-sample tests, $P > 0.05$) for each sampling date (June and October). In June, the mean number of drifting invertebrates per 24 h were 77 and 185 individuals per 100 m³ at sites A and B, respectively. The dominant drifting taxa were Chironomidae and Blephariceridae (Diptera), *Protonemura* (Plecoptera Nemouridae) and Baetidae (Ephemeroptera). In October, the mean number of drifting invertebrates per 24 h were 305 and 600 individuals per 100 m³ at sites A and B, respectively. Above the hydroplant, Baetidae and Simuliidae were the dominant drifting taxa, while Chironomidae was dominant below. Oligochaeta were only found in high numbers in the drift at site B, and only during hydropeaking.

Gut contents analysis showed that at both sites, brown trout fed chiefly on Baetidae and Chironomidae, which were dominant taxa in the drift, whatever the site and/or flow patterns (Fig. 5). The comparison of upstream vs downstream diel feeding patterns in June and in October (Fig. 6) showed that fish did not seem to feed in response to drift patterns above the plant, whereas they chiefly used catastrophic drift below the outlet. Above the plant, invertebrate drift exhibited a clear diel periodicity and was almost exclusively nocturnal, particularly during low-flow periods in October. In June, drift abundance was about twice as high during the night than during the day, but was at moderate levels when averaged over the 24 h period. Such nocturnal drift can be considered as “behavioural”, sensu Bournaud and Thibault (1973), i.e., influenced by variations in luminosity. FI values were about 3.5 times higher in June, i.e., during spring spates, than in October. However, FI values did not seem to vary in relation to drift abundance over the 24h cycle at each period (Fig. 6). Below the plant, each peak

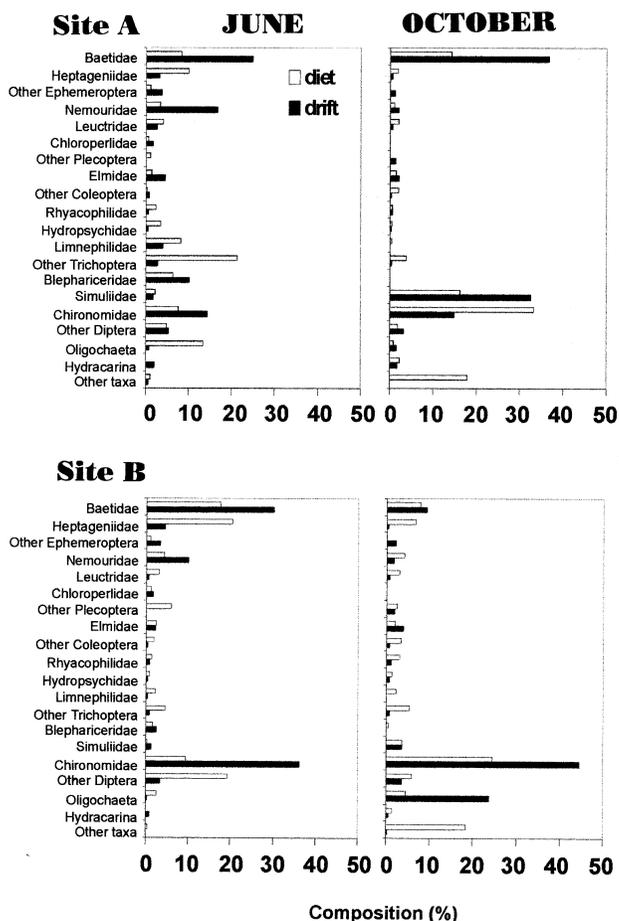


Fig. 5. Composition (%) of the drift and gut contents (*Salmo trutta*) in June and October, at sites A and B.

flow added catastrophic drift (sensu Culp et al., 1985, i.e., generated by any disturbance) to the daily pattern. Most larvae were flushed at the beginning of peak flows, and the disturbance was higher when the difference between natural and peak flow was greatest. Hence, in October, the natural diel periodicity disappeared and drift was chiefly due to hydropower generation. Natural levels of drift during the day were low, so the impact of hydropeaking (elevated drift) was easily detected. Observed FI values for brown trout below the plant were 1.7 times higher than above the plant in June ($P < 0.05$, average 1.96 to 1.71 $\text{mg}\cdot\text{g}^{-1}$) and in October ($P < 0.01$, average 1.14 to 0.49 $\text{mg}\cdot\text{g}^{-1}$). Moreover, hydropeaking modified diel feeding patterns: the highest FI values were observed after peak flow periods with a 2–4 hours time lag (4 h, 11 h, 17 h in June, and 19 h, 8 h in October, see Fig. 6).

4. Discussion

As hypolimnetic releases cause no chemical pollution or oxygen depletion (Liebig et al., 1999), flow and temperature were the two main environmental factors modified by hydropeaking in the river Oriège, as it has been observed in most flow regulation schemes (Ward and Stanford, 1979; Saltveit et al., 1994). Effects of variations in temperature and flow on the habitat of aquatic organisms (particularly fish and invertebrates) have been reported by many authors (e.g., Bain et al., 1988; Garcia de Jalon et al., 1988; Gore et al., 1989; Weisberg et al., 1990; Moog, 1993). Peak flows are known to decrease both the density and biomass of aquatic insects downstream from hydroplant outlets (Ger-sich and Brusven, 1981; Cushman, 1985; Moog, 1993) by

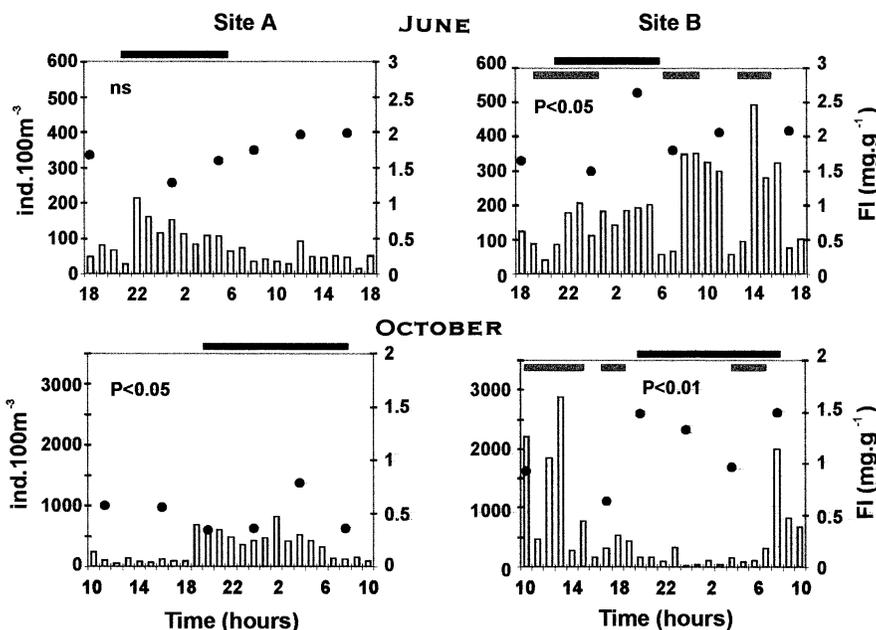


Fig. 6. Diel variations of total invertebrate drift (open bars) and trout Fullness indices (FI, dark points) over 24 hours at the two sites in June and October 1991. On the top of the graphs, black solid bars indicate night and grey solid bars indicate periods of power generation. For each 4-hour sampling period at one site on one date, differences in FI values were assessed using one-way Kruskal-Wallis tests (values of p are given ; ns = non significant).

increasing the frequency and intensity of bed scour (Rader and Ward, 1988; Gore et al., 1994), which causes catastrophic drift (Gore et al., 1989; Poff and Ward, 1991). We also recorded catastrophic drift pulses associated with hydropeaking in the river Oriège. Catastrophic drift was highest in autumn when the difference between natural and peak flows was the greatest. Nocturnal drift almost disappeared at the hydropeaking site, suggesting a density-dependent relationship (Waters, 1965; Ciborowski, 1987).

Below the outlet, we observed a reduction in trout density and biomass, chiefly to the detriment of young-of-the-year and juvenile stages (Table 3), consistent with a hydropeaking impact. One may argue that brown trout may exhibit large upstream- and/or downstream-oriented movements (Ovidio et al., 1998; 2000), and this would give low reliability to our abundance estimates. However, in a previous study, Lauters (1995) used radiotracking experiments (in summer and autumn) to show that in the River Oriège longitudinal movements by brown trout were less than 60 m during periods of natural flow, and less than 10 m during hydropeaking. These results were explained by the high density of cover and the steep slope (about 2.5%) in this river section. Similar observations were reported by Bunt et al. (1999) below a pulsed discharge hydroelectric generating station. Liebig et al. (1999) have already reported that in the Oriège, hydropeaking was primarily responsible for the reduction of the young-of-the-year population downstream of the outlet due to a reduction of the carrying capacity of the stream, i.e., the suitable habitat available. Intermittent hypolimnetic releases also increased the range of daily thermal fluctuations and reduced the annual ones below the outlet. Liebig et al. (1996) have previously found that the thermal regime below this plant remained within the thermal tolerance limits for brown trout (Elliott, 1994) despite strong summer cooling of the streamwater. However, Garcia de Jalon et al. (1988) suggested that summer cooling of stream temperature was responsible for reductions in trout productivity, and this could partially explain the reduction in trout abundance below the outlet in the River Oriège.

Trout density and biomass also depend on food availability (Cada et al., 1987; Mortensen et al., 1988; Ensign et al., 1990). Brown trout are known to feed chiefly on drifting invertebrates (Hayes and Jowett, 1994; Rader, 1997; Young et al., 1997), although stream-dwelling salmonids can adjust their feeding behaviour in response to changes in the abundance of prey (Fausch et al., 1997; McLaughlin et al., 1999), and can also use benthic preys (Forrester et al., 1994; Amundsen et al., 1999). However, there does appear to be some variations in the feeding patterns of salmonid in the wild. For example, whilst Elliott (1973) found rainbow trout to have a peak in feeding at dusk, Angradi and Griffith (1990) found rainbow trout to feed throughout the day. At the unregulated site of the river Oriège (this study), about 45 to 51% of ingested prey were caught at night during spring and winter respectively. This observation suggests that trout are not actually feeding in response to drift patterns,

otherwise we could expect that more than 50% of their food would be caught during the night. Below the outlet (site B), the highest levels of food consumption were observed within 2–4 hours after hydropeaking. These patterns could be explained by the high densities of drifting invertebrates due to hydropeaking (e.g., high numbers of Oligochaeta were flushed downstream and found in gut contents in October). This result also suggests that trout did not (or could not) feed during peaking flows, possibly because of the high energetic cost required to withstand harsh hydraulic conditions (Frankiewicz et al., 1993; Wootton, 1999), and/or because invertebrate prey could not be captured at high water velocities (Hill and Grossman, 1993; Braaten et al., 1997). Finally, under both natural and regulated conditions, brown trout chiefly fed on the most available prey items.

This study complements previous findings of Liebig et al. (1999), who reported that scouring flows in the Oriège reduced the suitable habitats available (i.e., the carrying capacity) for juveniles, which indirectly affected the standing stock. By comparing the abundance by size-class of trout captured above and below the hydroplant, we specified that hypolimnetic discharges primarily reduced the density of juveniles, whereas no significant difference was noticed for adults. These results suggest that under this kind of regulation scheme, the structural attributes of trout population (i.e., density, biomass, size-class structure) were first governed by habitat and hydraulic features. Then, when fish were able to withstand harsh hydrological conditions, their feeding patterns were mainly influenced by invertebrate drift pulses generated by peaking flows. This was particularly true when the difference between natural and peaking flow was the highest, i.e., in the autumn. We may assume that enhanced (catastrophic) invertebrate drift would act as a visual stimulus for trout feeding (Robinson and Tash, 1979). Conversely, diel variations in drift abundance (i.e., low drift density during the day and high drift density at night) did not influence significantly trout feeding patterns in the unregulated section. Seasonal variations in fullness indices were observed at both sites. Under natural conditions, fullness indices were the lowest in autumn, then increased from winter to summer. Several authors have linked such seasonal variations in salmonid feeding activity to prey availability (Frost and Brown, 1967; Bridcut and Giller, 1993; Alanära and Bränäs, 1997) and to changes in water temperature, which influence fish metabolism (Mortensen et al., 1988; Elliott and Hurley, 2001). Elliott (1973) emphasised that the weight of ingested food increased with the seasonal rise in temperature in a Pyrenean stream. In the regulated section, fullness indices were also the highest in summer. However, the lowest FI values were observed in spring, i.e. the season when peak flows added to snowmelt floods, underlining the prominent role of high current velocities through habitat suitability, position maintenance, and ability to capture preys. Nevertheless, despite a reduction in YOY and juvenile density, hypolimnetic hydropeaking allowed the maintain of brown trout below

the outlet, probably because the river returned to natural conditions when the plant was inoperative, and because daily artificial fluctuations in flow and temperature remained within the limits of natural seasonal variations.

Acknowledgements

We wish to thank Electricité De France for financing this study, and two anonymous referees for their helpful comments on an earlier version of this paper.

References

- Alanärä, A., Brännäs, E., 1997. Diurnal and nocturnal feeding activity in Arctic char (*Salvelinus alpinus*) and rainbow trout (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* 54, 2894–2900.
- Amundsen, P.A., Bergersen, R., Huru, H., Heggberget, T.G., 1999. Diel feeding rhythms and daily food consumption of juvenile Atlantic salmon in the River Alta, northern Norway. *J. Fish. Biol.* 54, 58–71.
- Angradi, T.R., Griffith, J.S., 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. *Can. J. Fish. Aquat. Sci.* 47, 199–209.
- Bain, M.B., Finn, J.T., Booke, H.E., 1988. Streamflow regulation and fish community structure. *Ecology* 69, 382–392.
- Baran, P., Delacoste, M., Dauba, F., Lascaux, J.M., Belaud, A., 1995. Effects of reduced flow on brown trout (*Salmo trutta* L.) populations downstream dams in French Pyrenées. *Regul. Rivers: Res. Manage.* 10, 347–361.
- Bournaud, M., Thibault, M., 1973. La dérive des organismes dans les eaux courantes. *Anns. Hydrobiol.* 4, 11–49.
- Braaten, J.P., Dey, P.D., Annear, T.C., 1997. Development and evaluation of bioenergetic-based habitat suitability criteria for trout. *Regul. Rivers: Res. Manage.* 13, 345–356.
- Bridcut, E.E., Giller, P.S., 1993. Diet variability in relation to season and habitat utilisation in brown trout (*Salmo trutta* L.) in a southern Irish stream. In: Gibson, R.J., Cutting, R.E (Eds.), Production of juvenile Atlantic salmon *Salmo salar* in natural waters. *Can. Spec. Publ. Fish. Aquat. Sci.*, 118, pp. 17–24.
- Brusven, M.A., MacPhee, C., 1976. The effects of river fluctuations resulting from hydroelectric peaking on selected invertebrates and fish. Idaho Water Resources Research Institute, University of Idaho, Moscow, Idaho, USA, Project A-035-IDA. pp. 46.
- Bunt, C.M., Cooke, S.J., Katopodis, C., McKinley, R.S., 1999. Movement and summer habitat of brown trout (*Salmo trutta*) below a pulsed discharge hydroelectric generating station. *Regul. Rivers: Res. Manage.* 15, 395–403.
- Cada, G.F., Loar, J.M., Sale, M.J., 1987. Evidence of food limitation of Rainbow and Brown trout in southern Appalachian soft-water streams. *Trans. Am. Fish. Soc.* 116, 692–702.
- Carle, F.L., Strub, M.R., 1978. A new method for estimating population size from removal data. *Biometrics* 34, 621–630.
- Casado, C., Garcia de Jalon, D.G., Del Olmo, C.M., Barcelo, E., Menes, F., 1989. The effects of an irrigation and hydroelectric reservoir on its downstream communities. *Regul. Rivers: Res. Manage.* 4, 275–284.
- Céréghino, R., Boutet, T., Lavandier, P., 1997. Abundance, biomass, life history and growth of six Trichoptera species under natural and hydropeaking conditions with hypolimnetic releases in a Pyrenean stream. *Arch. Hydrobiol.* 138, 307–328.
- Céréghino, R., Lavandier, P., 1998. Influence of hypolimnetic hydropeaking on the distribution and population dynamics of Ephemeroptera in a mountain stream. *Freshwater Biol.* 40, 385–399.
- Ciborowski, J.J.H., 1987. Dynamics of drift and microdistribution of two Mayfly populations: a predictive model. *Can. J. Fish. Aquat. Sci.* 44, 832–845.
- Culp, J.M., Wrona, F.J., Davies, R.W., 1985. Response of stream benthos and drift to fine sediment deposition versus transport. *Can. J. Zool.* 64, 1345–1351.
- Cushman, R.H., 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. *N. Am. J. Fish. Manage.* 5, 330–339.
- De Lury, D.B., 1951. On the planning of experiments for the estimation of fish populations. *J. Fish. Res. Board Can.* 18, 281–307.
- Elliott, J.M., 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. *Oecologia* 12, 329–347.
- Elliott, J.M., 1994. Quantitative Ecology and the Brown Trout. Oxford Univ. Press, Oxford, pp. 286.
- Elliott, J.M., Hurley, M.A., 2001. Modelling growth of brown trout, *Salmo trutta*, in terms of weight and energy units. *Freshwater Biol.* 46, 679–692.
- Ensign, W.E., Strange, R.J., Moore, S.E., 1990. Summer food limitation reduces Brook and Rainbow trout biomass in a southern Appalachian stream. *Trans. Am. Fish. Soc.* 119, 894–901.
- Fausch, K.D., Nakano, S., Kitano, S., 1997. Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. *Behav. Ecol.* 8, 414–420.
- Forrester, G.E., Chace, J.G., McCarthy, W., 1994. Diel and density-related changes in food consumption and prey selection by brook charr in a New Hampshire stream. *Environ. Biol. Fish.* 39, 301–311.
- Fraleigh, J., Marotz, B., Decker-Hess, J., Beattie, W., Zubik, R., 1989. Mitigation, compensation, and future protection for fish populations affected by hydropower development in the upper Columbia system, Montana, USA. *Regul. Rivers: Res. Manage.* 3, 3–18.
- Frankiewicz, P., Zalewski, M., Thorpe, J.E., 1993. Feeding pattern of brown trout (*Salmo trutta* L.) from the river Earn (Scotland), in relation to invertebrate drift. *Pol. Arch. Hydrobiol.* 40, 15–29.
- Frost, W.E., Brown, M.E., 1967. The trout. Collins, St James Place, London, pp. 286.
- Garcia de Jalon, D., Montes, C., Barcelo, E., Casado, C., Menes, F., 1988. Effects of hydroelectric scheme on fluvial ecosystems within the Spanish Pyrenees. *Regul. Rivers: Res. Manage.* 2, 479–491.
- Gersich, F.M., Brusven, M.A., 1981. Insect colonisation rates in near shore regions subjected to hydroelectric power peaking flows. *J. Freshwater Ecol.* 1, 231–236.
- Gore, J.A., Nestler, J.M., Layzer, J.B., 1989. Instream flow predictions and management options for biota affected by peaking-power hydroelectric operations. *Regul. Rivers: Res. Manage.* 3, 35–48.
- Gore, J.A., Niemela, S., Resh, V.H., Stutzner, B., 1994. Near-substrate hydraulic conditions under artificial floods from hydropower operation: a preliminary analysis of disturbance intensity and duration. *Regul. Rivers: Res. Manage.* 9, 15–34.
- Gorman, O.T., Karr, J.R., 1978. Habitat structure and fish communities. *Ecology* 59, 507–515.
- Greenberg, L.A., Dahl, J., 1998. Effect of habitat type on growth and diet of brown trout (*Salmo trutta* L.) in stream enclosures. *Fish. Manage. Ecol.* 5, 331–348.
- Haurly, J., Ombredane, D., Baglinière, J.L., 1991. L'habitat de la truite commune (*Salmo trutta* L.) en eaux courantes. In: Baglinière, J.L., Maisse, G (Eds.), La truite, biologie et écologie. INRA, Paris, pp. 47–96.
- Hayes, J.W., Jowett, I.G., 1994. Microhabitat models of large drift-feeding brown trout in three New Zealand Rivers. *N. Am. J. Fish. Manage.* 14, 710–725.
- Hill, J., Grossman, G.D., 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* 74, 685–698.
- Kraft, M.E., 1972. Effects of controlled flow reduction on a trout stream. *J. Fish. Res. Board Can.* 29, 1405–1411.

- Lauters, F., 1995. Impacts sur l'écosystème aquatique de la gestion par éclusées des ouvrages hydroélectriques. PhD thesis. Université Paul Sabatier, Toulouse. pp. 188.
- Liebig, H., Lim, P., Belaud, A., Lek, S., 1996. Study of the juvenile community in the Brown trout (*Salmo trutta fario* L., 1758) in hydropeaking situations. In: Leclerc, M., Capra, H., Valentin, S. (Eds.), Proceedings of the 2nd IAHR Symposium on Habitat Hydraulics, Ecohydraulics 2000 Inst. Nat. Rech. Scient. Eau, St Foy, Québec, Canada, vol. A, pp. 673–684.
- Liebig, H., Céréghino, R., Lim, P., Belaud, A., Lek, S., 1999. Impact of hydropeaking on the abundance of juvenile brown trout in a Pyrenean stream. *Arch. Hydrobiol.* 144, 439–454.
- Mann, R.H.K., 1988. Fish and fisheries of regulated rivers in the UK. *Regul. Rivers: Res. Manage.* 2, 411–424.
- McLaughlin, R.L., Ferguson, M.M., Noakes, D.L.G., 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. *Behav. Ecol. Sociobiol.* 45, 386–395.
- Meehan, W.R., Miller, R.A., 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. *J. Fish. Res. Board Can.* 135, 1359–1363.
- Moog, O., 1993. Quantification of daily peak hydropower effects on aquatic fauna and management to minimize environmental impacts. *Regul. Rivers: Res. Manage.* 8, 5–14.
- Mortensen, E., Geertz-Hansen, P., Marcus, E., 1988. The significance of temperature and food as factors affecting the growth of brown trout (*Salmo trutta* L.) in four Danish streams. *Pol. Arch. Hydrobiol.* 35, 533–544.
- Ovidio, M., Philippart, J.C., Baras, E., 2000. Methodological bias in home range and mobility estimates when locating radio-tagged trout, *Salmo trutta*, at different time intervals. *Aquat. Living Resour.* 13, 449–454.
- Ovidio, M., Baras, E., Goffaux, D., Birtles, C., Philippart, J.C., 1998. Environmental unpredictability rules the autumn migration of brown trout. *Hydrobiologia* 372, 263–274.
- Poff, N.L., Ward, J.V., 1991. Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Can. J. Fish. Aquat. Sci.* 48, 1926–1936.
- Rader, R.B., 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Can. J. Fish. Aquat. Sci.* 54, 1211–1234.
- Rader, R.B., Ward, J.V., 1988. Influence of regulation on environmental conditions and the invertebrate community in the upper Colorado River. *Regul. Rivers: Res. Manage.* 2, 597–618.
- Robinson, R.W., Tash, J.C., 1979. Feeding by Arizona trout (*Salmo apache*) and brown trout (*Salmo trutta*) at different light intensities. *Environ. Biol. Fish.* 4, 363–368.
- Saltveit, S.J., Bremnes, T., Brittain, J.E., 1994. Effect of a changed temperature regime on the benthos of a Norwegian regulated river. *Regul. Rivers: Res. Manage.* 9, 93–102.
- Valentin, S., Souchon, Y., Wasson, J.G., 1994. Evaluation of hydropeaking effects on fish community and habitat. In: Cowx, I.G. (Ed.), Rehabilitation of Freshwater Fisheries, Fishing News Books. Blackwell Scientific Publications, Oxford, pp. 138–151.
- Ward, J.V., Stanford, J.A., 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. The ecology of regulated streams. Plenum Press, New York, pp. 698.
- Waters, T.F., 1965. Interpretation of invertebrate drift in streams. *Ecology* 46, 327–334.
- Weisberg, S.B., Janicki, A.J., Gerritsen, J., Wilson, H.A., 1990. Enhancement of benthic macroinvertebrates by minimum flow from a hydroelectric dam. *Regul. Rivers: Res. Manage.* 5, 265–277.
- Weisberg, S.B., Burton, W.H., 1993. Enhancement of fish feeding and growth after an increase in minimum flow below the Conowingo Dam. *N. Am. J. Fish. Manage.* 13, 103–109.
- Wootton, R.J., 1999. Ecology of Teleost Fishes. 2nd edn. Kluwer Academic Publishers, Dordrecht, pp. 364.
- Young, M.K., Rader, R.B., Belish, T.A., 1997. Influence of invertebrate drift and light on the activity and movement of Colorado River cutthroat trout. *Trans. Am. Fish. Soc.* 126, 428–437.