

Glacial clay affects foraging performance in a Patagonian fish and cladoceran

Mikael Jönsson · Lynn Ranåker · Alice Nicolle · Peter Ljungberg ·
Tony Fagerberg · Samuel Hylander · Therese Jephson ·
Karen Lebret · Jessica von Einem · Lars-Anders Hansson ·
P. Anders Nilsson · Esteban Balseiro · Beatriz Modenutti

Received: 17 September 2010 / Revised: 29 October 2010 / Accepted: 13 November 2010 / Published online: 30 November 2010
© Springer Science+Business Media B.V. 2010

Abstract Climate change is altering temperatures and precipitation patterns all over the world. In Patagonia, Argentina, predicted increase in precipitation together with rapidly melting glaciers increase the surface runoff, and thereby the transport of suspended solids to recipient lakes. Suspended solids affect the visual conditions in the water which in turn restricts visual foraging. The native fish *Aplochiton zebra* Jenyns, and its filter-feeding cladoceran prey, *Daphnia commutata* Ekman, were subjected to foraging experiments at three turbidity levels. *A. zebra* foraging rate was substantially reduced at naturally occurring turbidity levels and the filtering rate of *D. commutata* was reduced at the highest turbidity level. This indicates that *Daphnia* may be partly released from predation from *A. zebra* at the same time as it can maintain relatively high feeding rates as turbidity increases. Lower foraging rates at the same time as the

metabolic demand increases, through increased temperatures, may result in larger effects on *A. zebra* than could be expected from increases in turbidity or temperature alone. Turbidity may, as an indirect effect of climate change, decrease planktivore foraging rates and thereby alter the interaction strength between trophic levels.

Keywords Turbidity · Glacial melting · Foraging · Filtering rate · Visual conditions

Introduction

Foraging success is of fundamental importance for most organisms as it governs growth, survival and reproductive success, all important life history traits. Environmental factors, such as amount of suspended solids, are known to affect foraging in organisms in aquatic environments at several different trophic levels, making it an important environmental variable for the biota (Utne-Palm, 1999; Kirk, 1992). These suspended solids are transported to aquatic ecosystems by surface runoff. Increases in surface runoff, as predicted by the IPCC (2007) for many regions through altered precipitation patterns, may result in increased transport of suspended solids to recipient lakes. Increased temperatures also melt continental glaciers which in many cases also results in increased transport of suspended solids from glacial forefields and subglacial environments (Moore et al., 2009).

Handling editor: M. Power

M. Jönsson (✉) · L. Ranåker · A. Nicolle ·
P. Ljungberg · T. Fagerberg · S. Hylander ·
T. Jephson · K. Lebret · J. von Einem ·
L.-A. Hansson · P. A. Nilsson
Limnology, Ecology Building, Lund University,
SE223 62 Lund, Sweden
e-mail: mikael.jonsson@limnol.lu.se

E. Balseiro · B. Modenutti
Laboratorio de Limnología, INIBIOMA,
CONICET-Universidad Nacional del Comahue,
Quintral 1250, 8400 Bariloche, Argentina

Increased load of suspended solids and thereby increased turbidity may be a secondary effect of climate change increasing turbidity levels in glacier fed aquatic ecosystems.

There are different types of suspended solids: organic and inorganic. Organic suspended solids include phytoplankton and plant material, while inorganic suspended solids (ISS) are mainly particles from weathering of rock and soil. The suspended material in water scatters and absorbs light and creates a turbid environment. Changes in turbidity affect aquatic organisms at different trophic levels, but through different mechanisms. Filter-feeding zooplankton are affected through mechanical disturbance of the filtering apparatus (Kirk, 1991a), while visually foraging fish experience reduced prey detection distance due to higher turbidity (Chesney, 1989; Utne-Palm, 1999). Higher levels of ISS may even be lethal for fish by physically affecting gill function (Bruton, 1985). For filter-feeding zooplankton, increased amounts of ISS will result in an intake of a mixture of food, normally phytoplankton, and non-food items (Kirk, 1991b). If this mixture is inappropriate as food, collected particles may be rejected as pseudofaeces reducing intake rates (Kirk, 1991a). However, organic compounds or bacteria that are a suitable source of nutrients for zooplankton may adhere to the surface of ISS making digestion of the particles beneficial for zooplankton (Lind & Davalosind, 1991). ISS may also clog the filtering appendages, making them less efficient, and reduce the beat rate of the filtering appendages due to gut fullness, even if the material filling the gut is not food (Kirk, 1991a). Further, assimilation efficiency may decrease when food is mixed with ISS (Arruda et al., 1983). All these mechanisms may result in reduced growth and fitness in zooplankton even if phytoplankton are abundant in the water (Kirk, 1992). For fish, ISS degrades the visual conditions by increasing turbidity, which is the main mechanism affecting foraging at naturally occurring levels of turbidity. Many fish species depend on vision as their primary sense when locating and capturing prey (Utne-Palm, 1999), but suspended material alter the visual conditions in different ways, through attenuation of light and through image degradation and altered background contrast from scattering. Attenuation of light in turbid water is primarily facilitated by the scattering of light on particles, increasing the distance the light travels in the

water and thereby the probability of absorption. In highly turbid water, parts of the water column may be very dark and therefore not allow for visual detection of prey. But even at the surface, where light levels are sufficient, image degradation through scattering may affect visual detection. Moderate levels of turbidity have been shown to increase detection distances in water because back-scattering increases the contrast between background and prey indicating the importance of background irradiance and color (Gregory & Northcote, 1993; Vinyard & O'Brien, 1976). However, in general, higher turbidity reduces the detection distance for predators by decreasing the visual range through scattering. Planktivorous fish are generally assumed to be less affected by turbidity than larger piscivorous fish that detect prey at longer distances (Chesney, 1989; Utne-Palm, 1999). However, foraging of several planktivores has been shown to be affected by turbidity (Vinyard & O'Brien 1976; Gregory & Northcote 1993; Utne, 1997). Removal of prey through predation does not only affect prey density but also prey size structure (Northcote, 1988) and behavior (Lima, 1998) and by inducing consequences for foraging rates in fish, increased turbidity may alter both community structure, individual behavior and the strength of trophic interactions (Fryxell & Lundberg, 1998). As planktivory is important in structuring zooplankton communities and for the timing of seasonal plankton succession (Modenutti et al., 1993; Hansson et al., 2007), the dynamics of the entire system may be altered by addition of ISS.

In Patagonia, South America, global warming is predicted to have a larger effect on temperature compared to global means (Gille, 2002) and the presence of rapidly melting glaciers are well documented (Rignot et al., 2003). The region is also predicted to suffer increased surface runoff due to global warming (IPCC, 2007). Hence, the rationale for this experimental study is to assess the indirect effects of climate change through increased turbidity on an indigenous planktivorous fish (*Aplocheilichthys zebra* Jenyns) with poor cover in the ecological literature (Cussac et al., 2004) and its cladoceran prey (*Daphnia commutata* Ekman). *A. zebra* has a very restricted distribution range (Baigun & Ferriz, 2003) and most studies conducted after its discovery and description (Jenyns, 1842) are in the fields of taxonomy (Chapman, 1944; McDowall, 1969; McDowall &

Nakaya, 1987; McDowall & Nakaya, 1988), reproduction (Lattuca et al., 2008), biogeography (Piacentino, 1999; Baigun & Ferriz, 2003; Cussac et al., 2004) and diet (Lattuca et al., 2007). Experimental work on *A. zebra* is rare (but see Young et al., 2009) underlining the importance of basic ecological research on the species. Effects of glacial retreat on these organisms are therefore assessed together with a measure of differences in effect size of turbidity on the two trophic levels. It is hypothesized that foraging rate of both *A. zebra* and *D. commutata* decreases with increasing turbidity. For *A. zebra*, foraging success decrease as an effect of impaired vision and increasing difficulty in finding prey when the water gets more turbid. For *Daphnia*, decreased foraging rate is expected to result from mechanical disturbance of the filtering apparatus.

Methods

Fish foraging experiment

In January 2009, juvenile *A. zebra* (total length: 27.7 ± 2.1 mm, mean \pm SD), were caught using beach seine in Lake Mascaradi ($41^{\circ}19'S$, $71^{\circ}34'W$) in Patagonia, Argentina. Fish were transported to the Limnological Laboratory at San Carlos de Bariloche, National University of Comahue, and kept for 4 days in a 100-l holding tank and fed flake food prior to experiments. *A. zebra* were kept in a light regime consistent with the local daily rhythm and in lake water (initial temperature of $17.5^{\circ}C$) which was slowly allowed to increase in temperature over the 4 acclimatization days, to the experimental temperature (22 – $23^{\circ}C$). *D. commutata*, caught in the same lake with a 50- μ m plankton net, was used as experimental prey.

Trials were conducted at three different turbidity levels where turbidity (LaMotte TC-3000i turbidity meter) and visual range were measured. The visual range in the water was defined as the horizontal distance between the human eye and a secchi disc at which the contrast between the disc's black and white fields disappeared. This measure relates more directly to visual conditions than turbidity (Steel & Neuhauser, 2002) and the method has been thoroughly evaluated in the lab where reaction distance of a visual forager (pike, *Esox lucius*) to fish prey

corresponds tightly with the measured visual range (Ran aker et al., unpublished). The turbid conditions were obtained by mixing bentonite clay with lake water and letting it settle for 1 h. After sedimentation, the upper layers of the clay slurry were removed and allowed to settle for an additional 24 h. Once again, the upper layer of this slurry was removed and used in the experiments. The first sedimentation period removed the particles with the highest sedimentation rate and after the longer sedimentation, only clay particles that would remain suspended in the water for 24 h remained. This clay slurry was diluted with lake water to obtain the experimental turbidity levels and the procedure ensured constant turbidity levels throughout the duration of the trials. Experiments were conducted in circular arenas with a diameter of 0.30 m filled with 3.5 l of water to a depth of 0.05 m. Water temperature was monitored and kept at $22.7 \pm 2.1^{\circ}C$ (mean \pm SD) and turbidity levels were low turbidity (clear water, 0.74 ± 0.62 NTU, no ISS added), intermediate turbidity (visual range of 0.2 m, 40.7 ± 2.3 NTU, 0.300 ± 0.156 g l⁻¹ of ISS) and high turbidity (visual range of 0.05 m, 209.3 ± 10.3 NTU, 1.618 ± 0.016 g l⁻¹ of ISS). Arenas were illuminated from above by two halogen lights (500 W each) situated 1 m above the arena. Halogen was used to ensure that a broad spectrum of wavelengths were present and two light sources created arenas with even light conditions without shadows, similar to daylight conditions (5200 lux, INS DX-100 Digital lux meter).

One *A. zebra* was introduced into the experimental arena and was acclimatized for 2 min before the trial was started by adding 15 *D. commutata*. Trials were terminated after 2 min by removing the *A. zebra*, after which the water was filtered through a 50 μ m net and the remaining *Daphnia* was counted. For each treatment, 12 replicate trials were performed. The trial time was established in pre trials where it was evident that *A. zebra* did not require longer acclimatization periods, and that trial time was enough for the fish to feed efficiently but not get satiated with prey under clear conditions. Also, the short trial time compensated for the small size of the experimental arena. The effect of turbidity (low, intermediate and high turbidity) on the dependent variable consumption (arcsin \sqrt{x} -transformed proportions of *Daphnia* eaten) was evaluated by ANOVA. After transformation, the dependent variables met the assumptions of

normality as well as homoscedasticity. The origin of significant ANOVA effects was analyzed with post-hoc Tukey tests. No differences in size of *A. zebra* between turbidity treatments ($F_{2,33} = 1.41$, $P = 0.258$) was detected.

Daphnia grazing experiment

Grazing experiments with *D. commutata* caught in Lake Mascardi January 2009, were performed according to a Lehman-Sandgren design in the same turbidity levels as in the previous experiment (Lehman & Sandgren, 1985). Trials were performed in 60-ml glass containers in an incubator at 17.0°C and in fluorescent light. A known volume of phytoplankton inoculum (*Chlamydomonas reinhardtii* Dangeard) from a laboratory culture was added to each of the containers and trials were started by adding *Daphnia* in eight different densities (2, 3, 4, 5, 6, 8, 10, and 12 *Daphnia*/container). One extra container with experimental water for each treatment was prepared and analysed for initial phytoplankton concentration. The experiment was terminated after 4 h by preservation in Lugol's solution. Biomass of *Daphnia* in each container was calculated from individual *Daphnia* lengths (Bottrell et al., 1976). Both the initial concentration of phytoplankton and the concentration after experiments were determined by counting phytoplankton in a microscope at 200× magnification along three transects through a 1-ml Sedgwick-Rafter chamber (19 × 58 × 1 mm). The equation used for calculating the change in phytoplankton density is:

$$r = \ln(N_t/N_0)/\Delta t \quad (1)$$

where r is the net change in phytoplankton density (phytoplankton net growth), N_t is the phytoplankton density at time t , N_0 is the phytoplankton density at the start of the trial and Δt is the duration of the trial (Lehman & Sandgren, 1985). A negative r indicates that *Daphnia* consume phytoplankton faster than phytoplankton growth or that phytoplankton have increased mortality for other reasons, and a positive r that phytoplankton growth is greater than *Daphnia* consumption rate.

The effect of the main factor, turbidity (low, intermediate and high turbidity), on the dependent variable, phytoplankton net growth (r), was evaluated using ANCOVA with biomass of *Daphnia* as the covariate. An ANCOVA design was used to evaluate

if turbidity reduced filtering rate to close to zero which can be detected if filtering rate is independent from biomass of the consumer in any of the treatments. The origin of significant ANCOVA results was analyzed with pairwise comparisons with Bonferroni corrections and P values were validated using the sequential Bonferroni method (Rice, 1989). The residuals for the dependent variable met the assumption of normality and homoscedasticity. All statistics were performed in SPSS for Windows, version 15.

Results

Fish foraging experiment

The consumption rate of *A. zebra* on *D. commutata* was affected by turbidity ($F_{2,33} = 26.39$, $P < 0.001$) and *A. zebra* consumption rate differed between all three turbidity levels (low-intermediate turbidity: $P = 0.026$, low-high turbidity: $P < 0.001$ and intermediate-high turbidity: $P < 0.001$) and higher turbidity resulted in reduced consumption rates (Fig. 1).

Daphnia grazing experiment

In trials where *D. commutata* were feeding on phytoplankton there was an effect of turbidity ($F_{2,20} = 14.331$, $P < 0.001$) as well as of *Daphnia* biomass ($F_{1,20} = 9.905$, $P = 0.005$) on phytoplankton net growth. The interaction term was not significant and was therefore removed from the analysis ($F_{2,18} = 2.652$, $P = 0.098$). Pairwise comparisons with Bonferroni corrections showed that high turbidity differed from intermediate ($P = 0.006$) and low turbidity ($P < 0.001$), but there was no difference between intermediate and low turbidity ($P = 0.295$). Phytoplankton net growth increased when turbidity increased, meaning decreasing *Daphnia* consumption rates at high turbidity. Phytoplankton net growth was positive (phytoplankton growth greater than *Daphnia* consumption rate) only in the high turbidity treatment (Fig. 2).

Discussion

Here, we demonstrate that foraging in the planktivorous fish, *A. zebra*, is substantially impaired by the

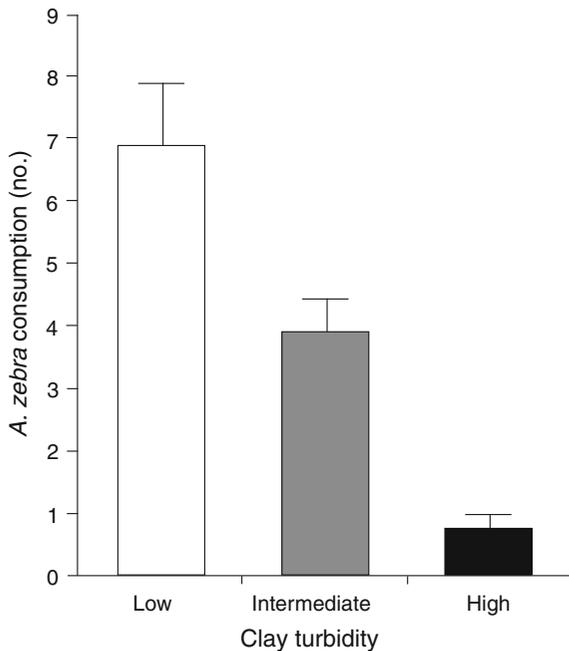


Fig. 1 Absolute consumption of zooplankton, *Daphnia commutata*, by juvenile fish, *Aplochiton zebra*, in low (0 NTU, open bar), intermediate (40 NTU, grey bar) and high turbidity (200 NTU, black bar). Statistics were performed on transformed proportional consumption to satisfy assumptions of normality and homoscedasticity. Bars show mean consumption and error bars denote one SE

short visual range at naturally occurring turbidity levels (Granqvist & Mattila, 2001; Liljendahl-Nurminen et al., 2008). Their filter-feeding cladoceran prey is also affected by turbidity, but only at extremely high turbidity. The consumption rate of *Daphnia* was only reduced at the highest turbidity level and *A. zebra* therefore seem to be more affected by increased turbidity earlier than its cladoceran prey.

In previous studies, effects of turbidity are reported to be both beneficial (Boehlert & Morgan, 1985; Gregory & Northcote, 1993) and detrimental to planktivorous foragers (Vinyard & O'Brien 1976; Chesney, 1989; Granqvist & Mattila, 2001). Especially interesting is the lack of effects in *Galaxias maculatus* (Stuart-Smith et al., 2007) which is a member of the same family as *A. zebra*, Galaxiidae. *G. maculatus* have a wider geographical distribution which may indicate that they are more adaptive and/or have lower environmental demands, but they may also be stronger competitors in turbid water. The

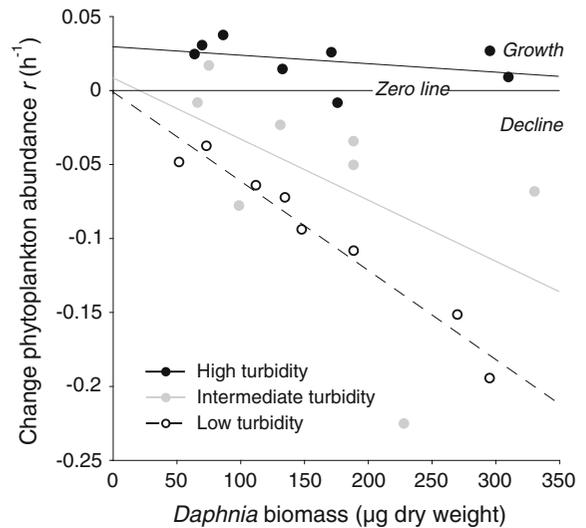


Fig. 2 Phytoplankton net growth (*Chlamydomonas reinhardtii*) as a function of grazer biomass (*Daphnia commutata*) in low (0 NTU, open circles and dashed line), intermediate (40 NTU, grey dots and grey line) and high turbidity (200 NTU, black dots and black line). Positive phytoplankton net growth (above the zero-line) means that phytoplankton growth is larger than *Daphnia* consumption rate and negative phytoplankton net growth (below the zero-line) means that *Daphnia* consumption is larger than phytoplankton growth. Regression lines are added to visualize the difference between treatments even if differences are tested with ANCOVA

strong effects of turbidity found on the foraging by *A. zebra* may be explained if *A. zebra* is adapted predominantly to clear water. This is supported by field studies where eye-size growth-trajectories in *A. zebra* differ between turbid and clear water environments (McDowall & Pankhurst, 2005; Lattuca et al., 2007). The relative eye size to body-size increases in less transparent environments, possibly as a response to the harsh visual conditions (McDowall & Pankhurst 2005). However, the change in relative eye size may also be caused by different diets (Lattuca et al., 2007). The strong effects on both foraging and morphology indicate that *A. zebra* is more sensitive to increasing turbidity than other planktivorous fish. Even though the direct effects of increasing turbidity on foraging of *A. zebra* are negative, there may be positive effects of turbidity as well. In turbid water, predation from piscivores may be reduced (Gregory & Northcote, 1993; Utne-Palm, 1999) as they are generally more dependent on visual conditions for foraging (Chesney,

1989; Utne-Palm, 1999) and Patagonian waters are inhabited not only by the indigenous piscivore Creole perch (*Percichthys trucha* Valenciennes) (Baigun & Ferriz, 2003) but also by several non-native salmonids (Pascual et al., 2007). The use of open habitats in prey fish may also increase as the turbid water functions as a refuge from visual predation (Miner & Stein, 1996; Engström-Öst & Mattila, 2008). This increases the time *A. zebra* can spend on foraging, counteracting the direct negative effects on encounter rate in turbid environments.

The suspension feeding zooplankton, *D. commutata*, was also negatively affected by increased turbidity. At the highest turbidity level, phytoplankton growth rate exceeded *Daphnia* filtering rate across *Daphnia* biomasses (regression slope close to zero), and produced no changes in phytoplankton abundance (Fig. 2). This indicates that high turbidity levels severely reduce *Daphnia* filtering rates. In the two lower turbidity levels, the filtering rate of *Daphnia* did exceed the growth rate of phytoplankton, while our results do not indicate different levels of filtering capacities between the intermediate and low turbidity levels. *Daphnia* filtering rate is thus not significantly impaired at naturally occurring intermediate and low turbidities. Gradients in turbidity should hereby affect the trophic interaction strength between *Daphnia* and phytoplankton. It should be noted, however, that the intermediate turbidity level resulted in higher variation in phytoplankton abundance change from *Daphnia* filtering (Fig. 2) that may explain why we did not find a difference between low and intermediate turbidity levels.

From single species experiments it is difficult to accurately predict effects on the ecosystem level as there are many trophic links missing. However, *A. zebra* are affected at lower turbidity levels than *Daphnia* and they may therefore experience a lower predation pressure from *A. zebra* with increasing turbidity. At the same time, *Daphnia* is able to uphold a relatively high level of feeding. The effects on the strengths of the trophic interactions may therefore be different for the two interactions. The strength of the interaction between *Daphnia* and phytoplankton may remain unaffected during the turbidity increase and zooplankton may even benefit from increased turbidity as turbid water lowers the compensation depth thereby concentrating phytoplankton in the surface layer. Organic material and bacteria also adhere to

ISS making it beneficial for zooplankton to ingest the clay–bacteria aggregates; these aggregates may even subsidize the zooplankton population providing an efficient way of energy transfer to higher trophic levels, circumventing phytoplankton. The interaction strength between *A. zebra* and *Daphnia* decrease through decreased foraging rate of *A. zebra*. *Daphnia* is thereby, at least partly, released from predation, resulting in increased growth if environmental conditions allow it.

The focus of this article is effects of turbidity, but the main effect of climate change is increased temperatures. Increased temperatures increase the metabolic demand of organisms like fish (Clarke & Johnston, 1999). To increase the metabolic need at the same time as foraging efficiency is decreased, through increased turbidity, may lower individual growth potential. Following decreases in population densities may result in more pronounced effects of climate change than could be expected from turbidity or temperature increases alone. Also, the effects shown here may to some extent underestimate the real effects due to both low volume of water during trials and short duration of the trials. Low volumes make the prey denser and increase encounter rates. Also, in short trials, handling time restricts the foraging rates, making it possible that *A. zebra* reached its maximum foraging rate in clear water. However, they were still not able to reach this high level of foraging in turbid treatments, making it possible that effects were underestimated.

The effect of global warming, such as glacier melt-off and altered precipitation patterns, is nowadays a fact (IPCC, 2007). To understand the consequences on lake ecosystems, it is of crucial importance not only to evaluate temperature effects. In order to grasp the full extent of the effects, both direct and indirect effects need to be considered. As the response to changes in turbidity is very different, even in closely related fish species, predictions on community responses to increased turbidity should not be based on single species experiments but rather on the response of an array of relevant species inhabiting lakes receiving glacial run-off. By performing experimental work, we do not only add to the knowledge of the indirect effects of global warming, but also to the knowledge on relative differences in sensitivity between trophic levels to increased levels of ISS and thereby turbidity.

Acknowledgments This work was financed by Helge Ax:son Johnsons foundation, Sweden, Laboratorio de Limnología, INIBIOMA, CONICET-Universidad Nacional del Comahue, Argentina, and the Limnology section at the Department of Ecology, Lund University, Sweden. All experiments were in compliance with local law.

References

- Arruda, J. A., G. R. Marzolf & R. T. Faulk, 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. *Ecology* 64: 1225–1235.
- Baigun, C. & R. Ferriz, 2003. Distribution patterns of native freshwater fishes in Patagonia (Argentina). *Organisms Diversity & Evolution* 3: 151–159.
- Boehlert, G. W. & J. B. Morgan, 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasii*. *Hydrobiologia* 123: 161–170.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. Review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24: 419–456.
- Bruton, M. N., 1985. The effect of suspensoids on fish. *Hydrobiologia* 125: 221–241.
- Chapman, W. M., 1944. On the osteology and relationships of the South American fish, *Aplochiton zebra* Jenyns. *Journal of Morphology (Philadelphia)* 75: 149–165.
- Chesney, E. J., 1989. Estimating the food-requirements of striped bass larvae *Morone saxatilis*: effects of light, turbidity and turbulence. *Marine Ecology-Progress Series* 53: 191–200.
- Clarke, A. & N. M. Johnston, 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* 68: 893–905.
- Cussac, V., S. Ortubay, G. Iglesias, D. Milano, M. E. Lattuca, J. P. Barriga, M. Battini & M. Gross, 2004. The distribution of South American galaxiid fishes: the role of biological traits and post-glacial history. *Journal of Biogeography* 31: 103–121.
- Engström-Öst, J. & J. Mattila, 2008. Foraging, growth and habitat choice in turbid water: an experimental study with fish larvae in the Baltic Sea. *Marine Ecology-Progress Series* 359: 275–281.
- Fryxell, J. M. & P. Lundberg, 1998. Individual behavior and community dynamics. Chapman & Hall, New York.
- Gille, S. T., 2002. Warming of the Southern Ocean since the 1950s. *Science* 295: 1275–1277.
- Granqvist, M. & J. Mattila, 2001. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). In 17th Baltic Marine Biologists Symposium. Kluwer Academic Publisher, Stockholm: 93–101.
- Gregory, R. S. & T. G. Northcote, 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 233–240.
- Hansson, L. A., A. Nicolle, J. Brodersen, P. Romare, P. A. Nilsson, C. Brönmark & C. Skov, 2007. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. *Limnology and Oceanography* 52: 696–706.
- IPCC, 2007. Climate Change 2007: synthesis report. In Pachauri, R. K. & A. Reisinger (eds), Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change: 104.
- Jenyns, L., 1842. Fish, Part 4. In Darwin, C. (ed.), *The Zoology of the Voyage of H.M.S. Beagle, under the command of Captain Fitzroy, R. N. during the years 1832 to 1836*. Smith, Elder, and Co, London.
- Kirk, K. L., 1991a. Suspended clay reduces *Daphnia* feeding rate - Behavioral mechanisms. *Freshwater Biology* 25: 357–365.
- Kirk, K. L., 1991b. Inorganic particles alter competition in grazing plankton—the role of selective feeding. *Ecology* 72: 915–923.
- Kirk, K. L., 1992. Effects of suspended clay on *Daphnia* body growth and fitness. *Freshwater Biology* 28: 103–109.
- Lattuca, M. E., S. Ortubay, M. A. Battini, J. P. Barriga & V. E. Cussac, 2007. Presumptive environmental effects on body shape of *Aplochiton zebra* (Pisces, Galaxiidae) in northern Patagonian lakes. *Journal of Applied Ichthyology* 23: 25–33.
- Lattuca, M. E., D. Brown, L. Castineira, M. Renzi, C. Luizon, J. Urbanski & V. Cussac, 2008. Reproduction of landlocked *Aplochiton zebra* Jenyns (Pisces, Galaxiidae). *Ecology of Freshwater Fish* 17: 394–405.
- Lehman, J. T. & C. D. Sandgren, 1985. Species-specific rates of growth and grazing loss among fresh-water algae. *Limnology and Oceanography* 30: 34–46.
- Liljendahl-Nurminen, A., J. Horppila & W. Lampert, 2008. Physiological and visual refuges in a metalimnion: an experimental study of effects of clay turbidity and an oxygen minimum on fish predation. *Freshwater Biology* 53: 945–951.
- Lima, S. L., 1998. Nonlethal effects in the ecology of predator-prey interactions: what are the ecological effects of anti-predator decision-making? *Bioscience* 48: 25–34.
- Lind, O. T. & L. Davaloslind, 1991. Association of turbidity and organic carbon with bacterial abundance and cell size in a large, turbid, tropical lake. *Limnology and Oceanography* 36: 1200–1208.
- McDowall, R. M., 1969. A juvenile of *Aplochiton* Jenyns. *Copeia* 1969: 631–632.
- McDowall, R. M. & K. Nakaya, 1987. Identity of the Galaxioid fishes of the genus *Aplochiton* Jenyns from Southern Chile. *Japanese Journal of Ichthyology* 34: 377–383.
- McDowall, R. M. & K. Nakaya, 1988. Morphological divergence in the two species of *Aplochiton* Jenyns (Salmoniformes: Aplochitonidae): a generalist and a specialist. *Copeia* 1988: 233–236.
- McDowall, R. M. & N. W. Pankhurst, 2005. Loss of negative eye-size allometry in a population of *Aplochiton zebra* (Teleostei : Galaxiidae) from the Falkland Islands. *New Zealand Journal of Zoology* 32: 17–22.
- Miner, J. G. & R. A. Stein, 1996. Detection of predators and habitat choice by small bluegills: Effects of turbidity and

- alternative prey. *Transactions of the American Fisheries Society* 125: 97–103.
- Modenutti, B. E., E. G. Balseiro & P. M. Cervellini, 1993. Effect of the selective feeding of *Galaxias maculatus* (Salmoniformes, Galaxiidae) on zooplankton of a South Andes lake. *Aquatic Sciences* 55: 65–75.
- Moore, R. D., S. W. Fleming, B. Menounos, R. Wheate, A. Fountain, K. Stahl, K. Holm & M. Jakob, 2009. Glacier change in western North America: influences on hydrology, geomorphic hazards and water quality. *Hydrological Processes* 23: 42–61.
- Northcote, T. G., 1988. Fish in the structure and function of fresh-water ecosystems—a top-down view. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 361–379.
- Pascual, M. A., V. Cussac, B. Dyer, D. Soto, P. Vigliano, S. Ortubay & P. Macchi, 2007. Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change. *Aquatic Ecosystem Health & Management* 10: 212–227.
- Piacentino, G. L. M., 1999. New geographic localities of *Aplochiton* species (Salmoniformes : Aplochitonidae) in the Argentinian Patagonia. *Cybium* 23: 209–211.
- Rice, W. R., 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- Rignot, E., A. Rivera & G. Casassa, 2003. Contribution of the Patagonia Icefields of South America to sea level rise. *Science* 302: 434–437.
- Steel, E. A. & S. Neuhausser, 2002. Comparison of methods for measuring visual water clarity. *Journal of the North American Benthological Society* 21: 326–335.
- Stuart-Smith, R. D., J. F. Stuart-Smith, R. W. G. White & L. A. Barmuta, 2007. The effects of turbidity and complex habitats on the feeding of a galaxiid fish are clear and simple. *Marine and Freshwater Research* 58: 429–435.
- Utne, A. C. W., 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *Journal of Fish Biology* 50: 926–938.
- Utne-Palm, A. C., 1999. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. In *Conference on Vision and the Behavior of Marine Animals*. Taylor & Francis Ltd, Oristano: 111–128.
- Vinyard, G. L. & W. J. O'brien, 1976. Effects of light and turbidity on reactive distance of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33: 2845–2849.
- Young, K. A., J. Stephenson, A. Terreau, A. F. Thailly, G. Gajardo & C. G. de Leaniz, 2009. The diversity of juvenile salmonids does not affect their competitive impact on a native galaxiid. *Biological Invasions* 11: 1955–1961.