Hindawi Publishing Corporation
Research Letters in Ecology
Volume 2007, Article ID 94587, 5 pages
doi:10.1155/2007/94587

Research Letter

Species Diversity Enhances Predator Growth Rates

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Received 20 September 2007; Accepted 10 December 2007

Recommended by Oswald J. Schmitz

Predators can be important top-down regulators of community structure and are known to have both positive and negative effects on species diversity. However, little is known about the reciprocal effects of species diversity on predators. Across a set of 80 lakes in Connecticut, USA, we found a strong positive correlation between prey species diversity (using the Shannon-Weiner Diversity Index) and growth rates of largemouth bass (*Micropterus salmoides*). This correlation was strongest for small predators and decreased with body size. Although the underlying mechanisms are not known, the correlation is not driven by total fish abundance, predator abundance, or productivity.

1. INTRODUCTION

As demonstrated by classic studies of *Pisaster* in the rocky intertidal zone [1] and peacock bass *Cichla temensis* in Lake Gatun [2], predators can be important regulators of community structure. Through both direct predation and indirect effects, such as the modification of the strength or symmetry of competitive interactions among prey species [3], predators can increase or decrease species richness and diversity [4]. However, little is known about the reciprocal effects that species diversity can have on predators. Increasing diversity could potentially have positive effects on predators due to a higher overall abundance or reduced temporal variability in abundance of prey [5]. Alternatively, species diversity could negatively affect predators if the abundance of a preferred prey species is lower in high diversity systems. In addition, foraging strategies that involve prey recognition (e.g., search images) may be less effective in high-diversity systems [6]. Because human activities threaten species diversity in virtually all ecosystems [7], an improved understanding the bottom-up effects of species diversity may prove valuable for efforts to maintain ecosystem function or to conserve predator populations.

To investigate the effects of species diversity on predators, we examined individual growth rates of largemouth bass *Micropterus salmoides* (henceforth bass) in 80 lakes in Connecticut, USA. After their first year, largemouth bass are highly piscivorous and can feed on a variety of fish species [8]. However, individual growth rates can vary widely among systems as a function of the quantity and quality of available prey [9]. Therefore, we hypothesized that fish species diversity could have potentially strong positive or negative effects on bass growth.

2. MATERIAL AND METHODS

The lakes used in this study were sampled as part of a statewide survey conducted between 1988–1995 by the Connecticut Department of Environmental Protection [10]. Physical characteristics of study lakes are summarized in Table 1. Each lake was electrofished by boat on 1–4 occasions at night in spring (April–June) or fall (October-November) for an average of 3.6 hours "on time" (i.e., time when electrical current was running through water) per lake (Range: 0.36–12.56 hrs). Total sampling time was proportional to lake size. Fish were collected using a pulsed DC mode (80 pulses/second, 60% pulse width) with 200–400 volts and 3–9 amps, depending on conductivity. During sampling, the boat traveled parallel to shore in water generally <1.5 m deep. All fish species were collected by two netters for up to one hour, and largemouth bass and less common species were collected for any additional time. Boat electrofishing is known to capture some fish species more effectively than others, leading to potential errors in estimating

Table 1: Physical characteristics of study lakes.

Characteristic	Mean	Minimum	Maximum	Coefficient of variation
Surface area (ha)	132.9	6.1	2193.4	197.3
Maximum depth (m)	11.8	1.5	33.9	70
Conductivity (μmhos/cm^3)	88.3	19	300	70.4
Secchi depth (m)	3.0	0.7	9.0	54.9

abundance [11]. However, largemouth bass can be sampled effectively by boat electrofishing [12]. In addition, boat electrofishing is most effective for collecting fish in the littoral zone [11], which is the primary habitat of bass and the location of most encounters with their prey [13].

All fish collected were identified to species and counted prior to release. We estimated abundance of each species as the total number of individuals caught per hour of electrofishing on time [12]. Data from different sampling dates were combined to estimate abundance each species. For each lake, we quantified species richness and species diversity using the Shannon-Weiner Diversity Index H' [14]. Individual fish that were identified as hybrids were not used in the calculation of diversity or richness, but were included in estimates of total fish abundance.

For each bass collected, total length was measured to the nearest 1 mm and a small number of scales were taken from behind the depressed pectoral fin. These scales were used to determine ages and to back-calculate lengths at each age using the Fraser-Lee method [15]. After converting back-calculated lengths to masses using a standardized length-mass regression, we regressed ln-transformed annual change in mass versus ln-transformed mass at the start of the year for each lake. Sample sizes for regressions averaged 139.3 ± 8.1 ($\overline{X} \pm 1$ SE) estimates of annual growth. We only used fish aged 2–10 years to ensure similar domains for all regressions and to avoid errors associated with aging older fish [16]. These lake-specific regressions were used to predict growth rates of bass that began the year at three different sizes (150, 250, and 350 mm total length). We used individual estimates of annual growth as separate observations in our regressions. Although an individual fish could be used to generate multiple estimates of annual growth, our experimental units were lakes and not fish. Therefore, we used all available observations to generate the most accurate estimates of growth possible for each lake.

We used correlation coefficients to explore relationships between species richness and diversity, and bass growth rates. We also calculated correlations between these variables and bass abundance, total fish abundance, bluegill (*Lepomis macrochirus*) abundance (the primary prey of bass in many systems [17]), lake surface area, and mean conductivity, an estimate of lake productivity [18], to explore mechanisms and rule out alternative explanations. Finally, we used multiple regression to simultaneously evaluate the effects of species diversity, bass abundance, total fish abundance, surface area, and conductivity on bass growth rates.

3. RESULTS

Species richness in our study lakes averaged 12.65 species (range: 4–25) and mean species diversity (H') was 0.68 (range: 0.22–1.01). Bluegill were the most abundant species collected and were found in 79 of the 80 lakes (Table 2). Other common species (in terms of frequency of occurrence and/or relative abundance) were pumpkinseed *Lepomis gibbosus*, yellow perch *Perca flavescens*, golden shiner *Notemigonus chrysoleucas*, yellow bullhead *Ameirus nebulosus*, and black crappie *Pomoxis nigromaculatus* (Table 2). Largemouth bass were the most abundant predator ($\overline{X} =$ 9.2% of total fish abundance). Chain pickerel *Esox niger* were also found in most study lakes, and averaged 1.9% of total fish abundance (Table 2).

Across the study lakes, ln-transformed growth rates of 150 mm bass were positively correlated with fish species diversity (see Figure 1, $r = 0.38$, $P < .0005$) but not species richness ($r = 0.19$, $P > 0.05$). If the lowest diversity lake was removed from the dataset, the correlation was weaker but still significant ($r = 0.33$, $P < .005$). The observed correlation with species diversity does not appear to be driven by total fish abundance or bluegill abundance, because both variables were negatively correlated with species diversity (total abundance: $r = -0.27$, $P < .02$, bluegill abundance: $r = -0.35$, $P < .002$). Similarly, species diversity was not correlated with bass abundance ($r = -0.16$, $P > .15$) or conductivity ($r = -0.16$, $P > .10$). Species diversity was correlated with surface area ($r = 0.32$, $P < .005$), but surface area itself was not correlated with bass growth ($r = 0.11$, $P > .30$). Bass growth was negatively correlated with bass abundance ($r = -0.34$, $P < .005$), but not with potential interspecific competitors chain pickerel ($r = 0.06$, $P > 0.50$) or smallmouth bass *Micropterus dolomieu* ($r = 0.20$, $P > .05$). Correlations between growth rate and species diversity were highest for 150 mm bass and decreased as a function of body size. The correlation was still significant for the 250 mm size class ($r = 0.33$, $P < .005$) but not for the 350 mm size class ($r = 0.14$, $P > 0.20$).

The multiple regression on bass growth rates was also highly significant and included significant coefficients for species diversity and largemouth bass abundance (Table 3). These two variables influenced growth rates in opposite directions. Whereas species diversity had a positive effect on bass growth, bass abundance had a negative effect. In absolute terms, the magnitude of the species diversity coefficient was also much larger than the coefficient for bass abundance.

4. DISCUSSION

Our results suggest that species diversity has a positive effect on growth rates of largemouth bass. This relationship does not appear to be a spurious result of collinear associations between species diversity and other variables such as total fish abundance, bluegill abundance, bass abundance, or system productivity (as measured by conductivity). Species diversity was positively correlated with lake area, but lake area was not directly correlated with bass growth. Therefore, lake area is more likely to influence bass growth indirectly

Table 2: Fish species collected in study lakes. For each species, relative abundance was calculated only for lakes in which a species was present. Therefore, the sum of relative abundances for all species exceeds 100%.

Species	Frequency of occurrence (% of lakes)	Relative abundance when present (% of total abundance)	Maximum relative abundance (% of total abundance)
Alosa pseudoharengus	31.25	6.7	22.6
Ambloplites rupestris	33.75	6.8	29.9
Ameiurus catus	11.25	0.6	3.5
Ameiurus natalis	11.25	0.8	3.1
Ameiurus nebulosus	83.75	2.2	42.2
Anguilla rostrata	65	2.1	11.2
Carassius auratus	6.25	0.4	0.9
Catostomus commersoni	55	5.5	43.7
Cyprinus carpio	16.25	0.8	1.7
Erimyzon oblongus	12.5	0.9	3.1
Esox americanus	2.5	0.2	0.3
Esox lucius	2.5	0.2	0.3
Esox niger	87.5	1.9	9.4
Etheostoma olmstedi	16.25	0.1	0.6
Fundulus diaphanous	36.25	0.5	3.9
Lepomis auritus	37.5	3.4	13.2
Lepomis cyanellis	3.75	0.6	1.2
Lepomis gibbosus	98.75	10	64.9
Lepomis macrochirus	98.75	37.5	89.5
Luxilus cornutus	2.5	0.2	0.4
Micropterus dolomieu	42.5	3.7	20
Micropterus salmoides*	100	9.2	28.1
Morone Americana	30	11.1	64.6
Notemigonus crysoleucas	86.25	2.2	14.7
Notropis hudsonius	12.5	13.2	45.5
Notropis bifrenatus	6.25	0.2	0.9
Onchorhynchus mykiss	28.75	2.1	11.4
Onchorhynchus nerka	3.75	0.1	0.2
Osmerus mordax	1.25	0.1	0.1
Perca flavescens	95	20	69.1
Petromyzon marinus	1.25	0.1	0.1
Pomoxis nigromaculatus	73.75	1.6	8.2
Salmo salar	1.25	0.1	0.1
Salmo trutta	40	1	8.5
Salvelinus fontinalis	10	0.4	2.1
Semotilus corporalis	6.25	0.2	0.4

*Largemouth bass.

through species diversity. Of the two components of species diversity, relative abundance appears to have a stronger effect on bass growth. Species richness alone was not correlated with growth rates of any size class.

We have interpreted the correlation between species diversity and bass growth directionally as a bottom-up effect of diversity on growth. Fish community composition in lakes is strongly affected by physical characteristics such as area and connectivity [19] as well as historical processes such as accidental introductions and deliberate stocking [20]. Within a system, the relative abundance of species is influenced by habitat heterogeneity, particularly the relative proportion of littoral and pelagic habitat [21]. Nevertheless, largemouth bass may play a top-down role in determining community structure as the dominant predator in our study systems. Although bass abundance was not related to species diversity as would be expected if they were structuring prey communities, bass growth could influence species diversity through

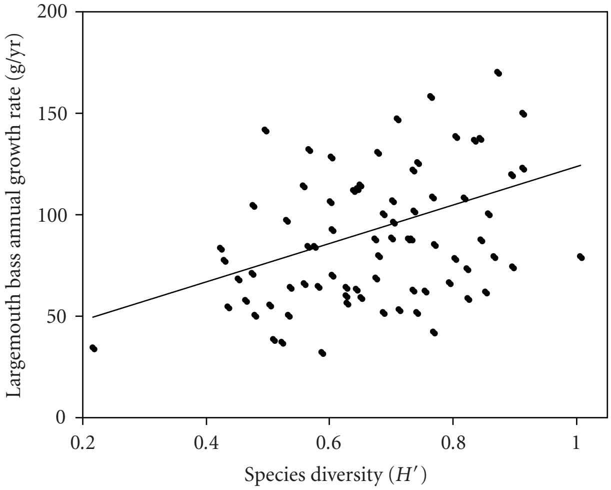

Figure 1: Annual growth rate of largemouth bass (g/year) as a function of prey species diversity H' (measured by the Shannon-Weiner Diversity Index). Each point corresponds to one study lake. Annual growth rate is calculated for 150 mm largemouth bass in each lake using back-calculated lengths from scales.

Table 3: Multiple regression coefficients for annual growth rates (g/year) of largemouth bass in 80 Connecticut lakes. The overall regression was highly significant ($F_{5,74} = 4.80$, $P < .001$, $r^2 = 0.25$). The dependent variable was ln-transformed prior to analysis. Species diversity was calculated using the Shannon-Weiner Diversity Index. Largemouth bass abundance and total fish abundance are calculated from electrofishing catch rates.

Variable	Coefficient (±SE)	P-value
Species diversity (H')*	1.027 ± 0.33	.0022
Largemouth bass abundance (no./h)*	-0.0038 ± 0.0017	.029
Total fish abundance (no./h)	0.00004 ± 0.00020	.85
Surface area (ha)	-0.00003 ± 0.00002	.89
Conductivity (μmhos/cm^3)	-0.0011 ± 0.0008	.19

*Significant coefficients.

its consequent effect on size structure. Because bass are gape-limited predators, the range of prey sizes that can be consumed increases as a function of body size [22]. Therefore, a larger proportion of more species will be vulnerable to predation in systems where bass grow well. In addition, increased vulnerability to predation will likely have a stronger influence on behaviors that can modify interactions among prey species [23]. The relationship between species diversity and predator growth may ultimately reflect a feedback loop wherein each component influences the other.

Mechanisms underlying the relationship between bass growth and species diversity are not currently known. Interannual variability in total fish abundance may be lower in high diversity systems due to interspecific differences in spawning requirements (e.g., temperature, habitat) or early growth rates that could increase the probability of at least some species reproducing successfully in a given year [24]. This increased likelihood of having small prey in high diversity systems could in turn lead to consistently higher growth rates of bass across years, particularly for smaller size classes that rely most heavily on young-of-year prey [25]. Larger size classes may be less dependent on a diverse prey community because their large gape allows them to feed on multiple age classes of a single prey species. Increased growth rates in high diversity systems may also be due to the importance of relative body size in the interaction between predator and prey. Because bass grow continuously, optimal and maximum prey sizes change with body size [26]. Bass in high diversity systems may be able to shift among prey species to maintain optimal size ratios with prey. In contrast, bass in low diversity systems may be forced to feed on a single year class of an abundant prey species for extended periods of time until they are large enough switch to other year classes.

Elucidating the mechanisms underlying variation in bass growth is an important next step in understanding the bottom-up effects of species diversity on predators. Detailed analyses of bass diets will help determine whether bass in more diverse systems feed on a broader range of prey species and sizes as they grow. Repeated sampling of study lakes will yield insights into interannual variation in prey abundance, particularly for small bass, as a function of species diversity. These data could also help explain some of the residual variation in growth rates in Figure 1. Effects of prey species diversity on predator performance should be tested experimentally as well. Although an experimental manipulation involving largemouth bass may be difficult due the relatively slow time scales of prey reproduction (i.e., annually), organisms at lower trophic levels may provide a tractable study system. For example, predatory mosquito larvae in pitcher plant inquiline communities are known to have strong effects on species diversity of lower trophic levels [27, 28]. These prey communities could be experimentally manipulated to create a range of diversities to test for potential effects on mosquito growth and molting rates.

Conservation biologists have long recognized the importance of predators to ecosystem structure and function. In particular, keystone predators are well known to exert strong top-down effects on patterns of species diversity [29]. Our results suggest that species diversity may also influence predators from the bottom-up. As external forces reduce diversity in ecosystems, predator performance (e.g., growth) may decrease, thereby lessening their role in structuring prey communities. Therefore, efforts to conserve ecosystems should be directed at all trophic levels.

ACKNOWLEDGMENTS

This study was supported by the Federal Aid to Sport Fish Restoration Act through the Connecticut Department of Environmental Protection, Project F-57-R-14. We thank Janet Fischer for a constructive review of this manuscript.

REFERENCES

[1] R. T. Paine, “Food web complexity and species diversity,” *The American Naturalist*, vol. 100, no. 910, pp. 65–75, 1966.

[2] T. M. Zaret and R. T. Paine, “Species introduction in a tropical lake,” *Science*, vol. 182, no. 4111, pp. 449–455, 1973.

[3] S. D. Peacor and E. E. Werner, “The contribution of trait-mediated indirect effects to the net effects of a predator,” *Proceedings of the National Academy of Sciences*, vol. 98, no. 7, pp. 3904–3908, 2001.

[4] A. Sih, P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier, “Predation, competition, and prey communities: a review of field experiments,” *Annual Review of Ecology and Systematics*, vol. 16, pp. 269–311, 1985.

[5] S. Naeem, F. S. Chapin, R. Costanza, et al., “Biodiversity and ecosystem functioning: maintaining natural life support processes,” *Issues in Ecology*, vol. 4, pp. 1–12, 1999.

[6] S. J. Shettleworth, *Cognition, Evolution, and Behavior*, Oxford University Press, New York, NY, USA, 1998.

[7] Millennium Ecosystem Assessment, “Ecosystems and Human Well-being: Biodiversity Synthesis,” World Resources Institute, Washington DC, USA, 2005.

[8] J. R. Hodgson, X. He, D. E. Schindler, and J. F. Kitchell, “Diet overlap in a piscivore community,” *Ecology of Freshwater Fish*, vol. 6, no. 3, pp. 144–149, 1997.

[9] R. C. P. Beamsderfer and J. A. North, “Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America,” *North American Journal of Fisheries Management*, vol. 15, no. 3, pp. 688–704, 1995.

[10] R. P. Jacobs and E. B. O’Donnell, “An electrofishing survey of selected Connecticut lakes,” Final Report F-57-R-14, Department of Environmental Protection, Hartford, Conn, USA, 1996.

[11] P. B. Bayley and D. J. Austen, “Capture efficiency of a boat electrofisher,” *Transactions of the American Fisheries Society*, vol. 131, no. 3, pp. 435–451, 2002.

[12] L. E. Miranda, W. D. Hubbard, S. Sangare, and T. Holman, “Optimizing electrofishing sample duration for estimating relative abundance of largemouth bass in reservoirs,” *North American Journal of Fisheries Management*, vol. 16, no. 2, pp. 324–331, 1996.

[13] E. E. Werner, D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk, “Habitat partitioning in a freshwater fish community,” *Journal of the Fisheries Research Board of Canada*, vol. 34, no. 3, pp. 360–370, 1977.

[14] E. C. Pielou, “The measurement of diversity in different types of biological collections,” *Journal of Theoretical Biology*, vol. 13, pp. 131–144, 1966.

[15] F. W. Tesch, “Age and growth,” in *Methods for Assessment of Fish Production in Freshwaters*, W. E. Ricker, Ed., pp. 93–123, Blackwell Science, Oxford, UK, 1968.

[16] M. J. Maceina, J. Boxrucker, D. L. Buckmeier, et al., “Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions,” *Fisheries*, vol. 32, pp. 329–340, 2007.

[17] E. E. Werner and D. J. Hall, “Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk tradeoff,” *Ecology*, vol. 69, no. 5, pp. 1352–1366, 1988.

[18] R. G. Wetzel, *Limnology: Lake and River Ecosystems*, Academic Press, San Diego, Calif, USA, 3rd edition, 2001.

[19] J. J. Magnuson, W. M. Tonn, A. Banerjee, J. Toivonen, O. Sanchez, and M. Rask, “Isolation vs. extinction in the assembly of fishes in small northern lakes,” *Ecology*, vol. 79, no. 8, pp. 2941–2956, 1998.

[20] F. J. Rahel, “Homogenization of freshwater faunas,” *Annual Review of Ecology and Systematics*, vol. 33, pp. 291–315, 2002.

[21] B. J. Benson and J. J. Magnuson, “Spatial heterogeneity of littoral fish assemblages in lakes: relation to species diversity and habitat structure,” *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 49, no. 7, pp. 1493–1500, 1992.

[22] E. E. Werner, “Fish size, prey size, handling time relation in several sunfishes and some implications,” *Journal of the Fisheries Research Board of Canada*, vol. 31, pp. 1531–1536, 1974.

[23] O. J. Schmitz, V. Krivan, and O. Ovadia, “Trophic cascades: the primacy of trait-mediated indirect interactions,” *Ecology Letters*, vol. 7, no. 2, pp. 153–163, 2004.

[24] A. Keast and J. Eadie, “Growth in the first summer of life: a comparison of nine co-occurring fish species,” *Canadian Journal of Zoology*, vol. 62, no. 7, pp. 1242–1250, 1984.

[25] G. G. Mittelbach and L. Persson, “The ontogeny of piscivory and its ecological consequences,” *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 55, no. 6, pp. 1454–1465, 1998.

[26] J. A. Hoyle and A. Keast, “The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*),” *Canadian Journal of Zoology*, vol. 65, no. 8, pp. 1972–1977, 1987.

[27] J. M. Kneitel and T. E. Miller, “Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community,” *Ecology*, vol. 83, no. 3, pp. 680–688, 2002.

[28] H. L. Buckley, T. E. Miller, A. M. Ellison, and N. J. Gotelli, “Reverse latitudinal trends in species rich ness of pitcher-plant food webs,” *Ecology Letters*, vol. 6, pp. 825–829, 2003.

[29] M. E. Power, D. Tilman, J. A. Estes, et al., “Challenges in the quest for keystones,” *BioScience*, vol. 46, no. 8, pp. 609–620, 1996.


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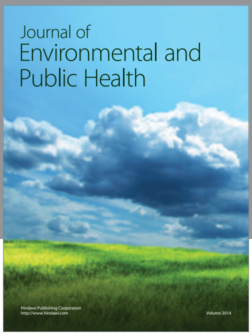
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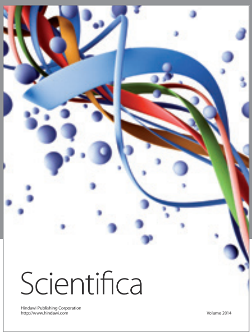
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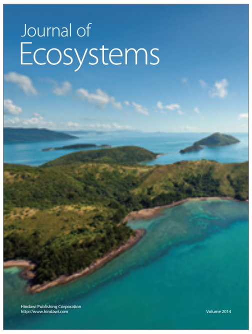
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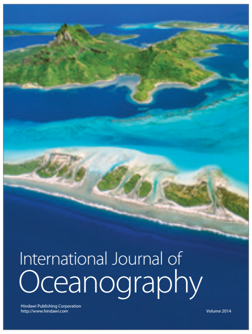
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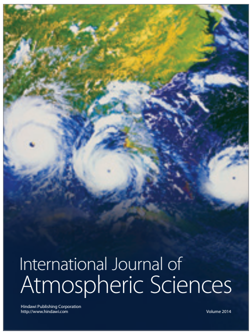
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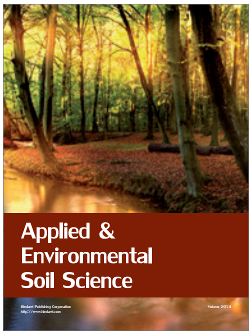
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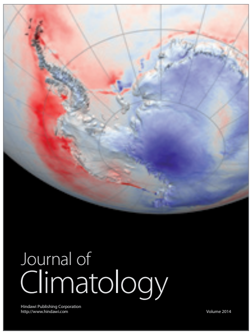
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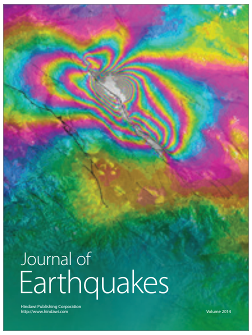
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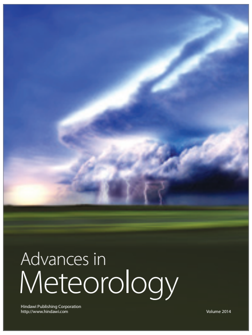
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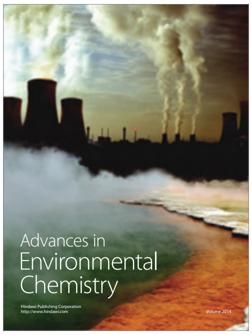
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