Succession in a stream invertebrate community: A transition in species dominance through colonization

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A field experiment was conducted using ceramic plates as experimental substrates to describe the colonizing pattern of a stream invertebrate community after disturbance, and to ascertain the importance of colonizing ability for succession in a Japanese stream. We employed the simultaneous removal design in which plates were periodically set in place (1, 2, 4, 8, 16 and 32 days before sampling) and all plates were sampled on the last day of the experiment, to diminish the influence of seasonal change in stream invertebrates. Total abundance and taxon richness reached a plateau after 4–16 days of colonization. In contrast, the relative abundance of six common taxa and community structure changed throughout the 32 days of colonization. Differences in the colonizing ability of the stream invertebrates were evident. Taxa with high mobility, such as the mayflies *Baetis thermicus*, *Paraleptophlebia japonica*, *Cinygmula* sp. and *Drunella sachalinensis*, colonized faster than those with low mobility (e.g. the caddisfly species *Brachycentrus americanus* and the chironomid midge Diamesinae spp.). The abundance of the most common taxon, *Baetis*, decreased at late stages of colonization, possibly because of low periphyton biomass. Consequently, we concluded that a difference in colonization ability among taxa is an important factor causing succession in stream invertebrate communities in local habitats.

Key words: colonization; disturbance; field experiment; mobility; simultaneous removal design.

INTRODUCTION

Ecologists have long been interested in the succession of ecological communities following a physical disturbance that disrupts the community and opens up space for new colonizers (Clements 1916; Pickett & White 1985). Many studies have described temporal patterns of community structure after a disturbance to elucidate the processes determining community organization and these studies have often found that there is a transition in species dominance with time (seeMorin 1999). In these studies, colonizing ability has gained prominence as a possible factor causing transitions in species dominance, such as seed arrival to forest gaps (Walker & Chapin 1987) or settlement of rocky shore and coral reef fish communities (Booth & Brosnan 1995).

In streams, floods often disrupt the stream invertebrate community and create open patches on the stream bed (Resh *et al*. 1988; Lake 2000). A number of field experiments have been conducted, mainly in stream riffles, to describe the colonizing pattern of stream invertebrates on stone surfaces after a flood disturbance (see review by Hayashi 1991). In these studies, disturbed patches were artificially created by introducing substrates, such as bricks, or by physically disturbing the natural stream bed (Sheldon 1984). In general, because stream invertebrates have a high mobility both total abundance and species richness reach a

plateau within a few weeks after the disturbance (see Mackay 1992). Several studies have found that a transition in species dominance occurs during colonization and that particular species typically dominate during the early stage of colonization (e.g. Downes & Lake 1991). This suggests that differences in mobility between species could strongly affect succession in stream invertebrate communities.

Most of the above studies, however, have been criticized because of the experimental design in which all disturbed patches are established at the one time and subsequently sampled according to some predetermined schedule (simultaneous placement design; Ciborowski & Clifford 1985). This design is largely influenced by seasonal changes in the abundance and faunal composition of stream invertebrates and, thus, the effect of colonizing ability on colonization pattern may be confounded with seasonal changes in abundance and faunal composition (Ciborowski & Clifford 1985). Shaw and Minshall (1980) recommended the use of a 'simultaneous removal design', in which disturbed patches are periodically established and all patches are sampled on the last day of the experiment. This design ensures that all samples are exposed to similar seasonal changes and that the invertebrates collected are from the same sampling population, at least immediately prior to sampling (Ciborowski & Clifford 1985). In the present study we conducted a field experiment in the riffles of a Japanese stream using experimental substrates to describe the colonizing pattern of a stream invertebrate community. We used a simultaneous removal design.

METHODS

Study site

The study was conducted in the Horonai Stream, which runs though the Tomakomai experimental forest of Hokkaido University, southwestern Hokkaido, Japan (TOEF: 42°43′N, 141°36′E), during early summer, May to July, 2001. The catchment of this stream is underlain by pyroclastic flow and fall deposits (mainly pumice) originating from the past volcanic activities of Mt Tarumae (Sakuma 1987). The spring-fed stream (14 km long), which discharges directly into the Pacific Ocean, has

small, relatively uniform substrate materials, composed mainly of pebbles, gravel and sand (8 mm mean particle size), with low specific gravity (see Urabe & Nakano 1998). With approximately 90% of the annual flow derived from groundwater discharge, temporal variability in stream flow is relatively small throughout the year (Miyazaki *et al.* 1991). However, the sediments are small and light, resulting in continuous and patchy movement of small substrate materials even during baseflow periods (Miyake & Nakano 2002). Thus, a large portion of the sediment is in motion, particularly during the spring snowmelt and after heavy rain in mid summer, which occurred before and after the period of this study, respectively (Y. Miyake, unpubl. data, 2000). A 500-m stretch was selected as the study reach in a second-order section of the stream (3.2–5.0 m wide, gradient <1%). Discharge was relatively constant (ranging from 0.30 to 0.36 m^3 s^{-1}) and the water temperature was stable (8.1–10.2°C) throughout the study period. The vegetation of the riparian zone consisted of a secondary deciduous broad-leaved forest and approximately 95% of the bankful channel was covered by the forest canopy (see Nakano *et al.* 1999).

Experimental procedure

We established six treatments with different colonization times (1, 2, 4, 8, 16 and 32 days) to test the effect of time following a disturbance on an invertebrate community. For the invertebrate sampling, we used a simultaneous removal design in which experimental substrates were periodically set in place and all substrates were sampled on the last day of the experiment (Shaw & Minshall 1980)

Seventy-two unglazed ceramic plates (19 cm × 19 cm × 1 cm) were used as the experimental substrates to quantitatively evaluate the colonization pattern of stream invertebrates to a stone surface. These plates have a rough surface texture similar to natural stones. We used ceramic bricks (20 cm × 20 cm × 6 cm) as a platform for the plates to ensure that all invertebrates collected came from the upper surface of the plates only. Invertebrates were unable to use the undersurface of the plates because there was no space between the plates and the brick platforms. Experimental plates were placed at least 10 m apart or separated by pools to

minimize accidental disturbance to neighboring plates during the experiment. Each set of 12 platforms was randomly selected and assigned to one of the six treatments.

Two months prior to the start of the experiment, all plates were placed on the stream bed (i.e. under grazing by invertebrates) to establish sufficient periphyton mats at the beginning of the experiment (see Nakano *et al*. 1999). Plates were placed on the platforms on 30 May, 15 June, 23 June, 27 June, 29 June and 30 June for 32, 16, 8, 4, 2 and 1 day treatments, respectively. Immediately before placing the plates, we physically disturbed the stream bed (3×3 m area) around the platforms to simulate natural flood disturbances (Matthaei *et al*. 1997). The experimental disturbance consisted of 5 min of vigorous kicking, followed by raking with a wide-toothed rake in two directions (downstream and across the stream) to redistribute the substrate material evenly over the area. Thus, the experimental setting of this study simulated a flood disturbance that patchily overturns stream bed stones. The experimental plates mimic disturbed stone surfaces where the disturbance has left the periphyton intact, but washed out invertebrates by high shear stress (mild disturbance; see Mackay 1992). Just before and after the disturbance, we sampled invertebrates from the stream bed sediments using a Surber net sampler (25 cm $\times 25$ cm quadrat area, 225 μm mesh, 100 cm long) at 12 locations (two locations for each treatment) to evaluate potential sources of colonization and the effects of the experimental disturbance. Following this we placed the experimental plates on platforms in the center of the disturbed stream bed. Prior to placing the plates all of the invertebrates attached to the plates were removed by gently rubbing the plates by hand and removing individuals with forceps. The initial periphyton biomass estimated from samples taken from two small areas on each plate did not differ significantly among the six treatments (the two samples were pooled for each plate; ANOVA, $F_{5,66} = 0.63$, $P = 0.68$, mean $\pm$ SE $= 27.8 \pm 1.1$ chlorophyll *a* mg m^{-2}).

Sampling

On 1 July 2001, we washed, by gently rubbing the plate surface by hand, all invertebrates from the upper surface of the experimental plates into a Surber net sampler held just downstream of each plate. Invertebrates remaining on the plate surface were picked off with forceps. Samples were preserved in 5% formalin solution for later analysis. Immediately following invertebrate sampling, periphyton was sampled at two locations on each plate following the method of Tanida *et al*. (1999). At each location, a rubber plate with a 24-mm-diameter hole was placed on the plate and the periphyton in the hole was scraped off using an acrylate fiber cloth (Micro-cloth; Koyo Co. Ltd, Tokyo, Japan). After sampling both the invertebrates and periphyton, all plates were returned to their original locations. The velocity of the current 13 mm above each plate was measured using a portable current meter (Model CR-7WP, Cosmo-Riken Inc., Osaka, Japan; see Tanida *et al*. 1985 for a more detailed description). Water depth was measured simultaneously. Current velocities (mean $\pm$ SE, 52.9 ± 0.9 cm s^{-1}) and water depth (11.1 ± 0.3 cm) did not differ significantly among the six treatments (velocity, $F_{5,66} = 0.60$, $P = 0.70$; depth, $F_{5,66} = 0.88$, $P = 0.50$).

Laboratory procedures and data treatment

Invertebrate samples were sorted and identified to the lowest possible taxonomic level, to species where possible, under a binocular microscope. Invertebrates were classified into functional feeding groups according to previous regional studies (e.g. Nakano *et al*. 1999; Merritt & Cummins 1996). To describe the invertebrate assemblage, we used two parameters: (i) total abundance (numbers m^{-2}); and (ii) taxon richness. The relative abundance of each taxon was also calculated for all replicate samples for each colonization-time treatment and for each plate sample.

Chlorophyll *a* concentration (mg m^{-2}) was used as a measure of periphyton biomass. Within 1 day of collection, the acrylate-fiber cloths were placed in 99.5% ethanol at 5°C for 24 h to extract the pigments. Pigments in the solution were measured using a spectrophotometer (Model u-1100, Hitachi Co., Tokyo, Japan). The data were converted to chlorophyll *a* estimates following the procedures outlined in UNESCO (1966). The two samples from each plate were pooled for the statistical analyses.

Statistical analyses

We used one-way ANOVAs to examine periphyton biomass, total abundance and taxon richness of the stream invertebrate community and absolute abundance of the common taxa with colonization time. As independence could not be assumed for the absolute abundance of common taxa, sequential Bonferroni tests were used to correct the significance levels of the one-way ANOVAs (Sokal & Rohlf 1995). Differences among treatments were assessed using the Tukey's method if the effect of colonization time was found to be significant (Sokal & Rohlf 1995). Log_{10} x- or log_{10} (x + 1)-transformations of exact values were done to standardize variances and improve normality. As the plates were arranged along the stream and were potentially affected by artificial disturbances from upstream, relationships between community variables (total abundance and species richness) of invertebrates on plates and the longitudinal order of the plates along stream were tested using a correlation analysis (Kendall's rank correlation coefficient, τ) for each colonization-time treatment. Detrended correspondence analysis (DCA) was used to identify community structure representing variations in taxonomic composition based on the relative abundance of all taxa over the plate samples. Each sample was plotted against the first two axes of a DCA.

RESULTS

Artificial disturbance of the stream bed around the experimental substrates effectively reduced the abundance of stream invertebrates. Surber samples taken from the sediment before and after the experimental disturbance revealed that invertebrates were reduced by $86.3 \pm 3.4\%$ in total abundance (1805 ± 374 to 192 ± 35 m^{-2}). Samples taken before the disturbance, which indicate a potential colonization source, were numerically dominated by gatherers (74%), followed by predators (12%), scrapers (9%), filterers (3%) and shredders (2%). The greatest taxon richness was found for predators (33%), followed by scrapers (21%), gatherers (20%), filterers (13%) and shredders (13%). The dominant taxa (>5% in total abundance) were a riffle beetle (Coleoptera), *Optioservus kubotai* Nomura (Elmidae, 21%, gatherer),

chironomid midges (Diptera), Orthocladiinae spp. (Chironomidae, 20%, gatherer) and Diamesinae spp. (Chironomidae, 11%, scraper), and a mayfly (Ephemeroptera), *Paraleptophlebia japonica* Matsumura (Leptophlebiidae, 17%, scraper).

A total of 4668 individuals and 43 taxa were found on the plate samples. Species dominance of the invertebrate community on the plates was, to some extent, different from the colonization source, indicating that the plates facilitate the colonization of some taxa. When each taxa was assigned to one of the functional feeding groups, invertebrates from the plate samples were numerically dominated by scrapers (71%), followed by filterers (10%), predators (8%), shredders (7%) and gatherers (4%). The greatest taxon richness was found for predators (37%), followed by scrapers (21%), gatherers (18%), filterers (12%) and shredders (12%). Invertebrate taxa that were shredders and gatherers were not included in further analyses because these two functional feeding groups were not considered to use the surface of plates and most individuals are likely to have been accidentally collected from the surrounding substrate. Thus a total of 4144 individuals and 30 taxa were included in further analyses. Six of these taxa colonized the plates in sufficient numbers for analysis. These included four mayflies (Ephemeroptera), *Baetis thermicus* Uéno (Baetidae, relative abundance: 39%, scraper), *Paraleptophlebia japonica* Matsumura (Leptophlebiidae, 28%, scraper), *Cinygmula* sp. (Heptageniidae, 4%, scraper) and *Drunella sachalinensis* Matsumura (Ephemerellidae, 3%, predator), a caddisfly (Trichoptera), *Brachycentrus americanus* (Martynov) (Brachycentridae, 9%, filterer) and a chironomid midge (Diptera), Diamesinae spp. (Chironomidae, 3%, scraper). When combining all plate samples, these six taxa were found to represent 86.5% of the total abundance.

Periphyton biomass sharply decreased in the latter stages of colonization (Fig. 1; one-way ANOVA, $F_{5,66} = 15.38$, $P < 0.001$). Periphyton biomass in the 16 and 32 day treatments was significantly lower than in the 1, 2, 4 and 8 day treatments. One-way ANOVA revealed that the time of colonization was significant on both total abundance ($F_{5,66} = 41.20$, $P < 0.001$) and taxon richness ($F_{5,66} = 23.53$, $P < 0.001$). Both parameters increased as colonization time increased up to
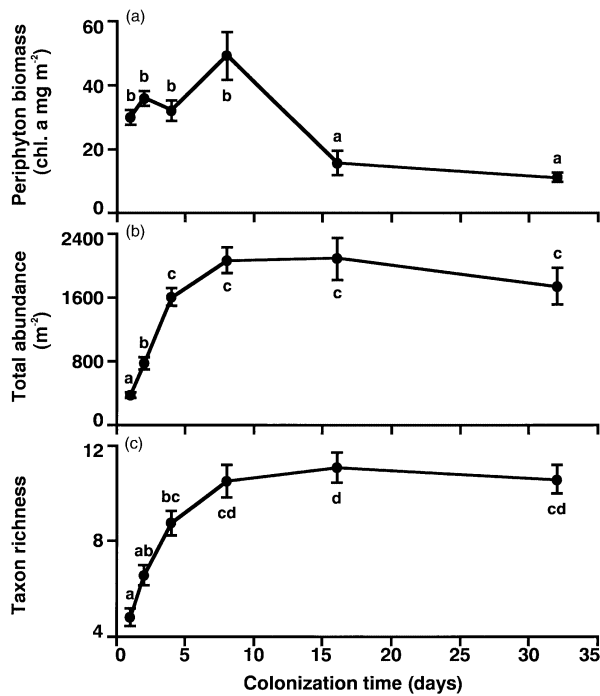
Fig. 1. (a) Periphyton biomass, (b) total abundance and (c) taxon richness of stream invertebrates on the experimental plates with colonization time. Means ± 1SE are shown. Different letters indicate significant differences ($P < 0.05$) among treatments as assessed using the Tukey method.

4–16 days and then leveled off (Fig. 1). The longitudinal order of the plates along the stream was not significantly correlated with total abundance ($n = 12$, $\tau = 0.09$–0.35, $P > 0.114$) or with species richness ($n = 12$, $\tau = -0.03$–0.35, $P > 0.114$) in any of the disturbance frequency treatments.

Fluctuations in absolute abundance with colonization time differed considerably among the six common taxa (Fig. 2). One-way ANOVAS with sequential Bonferroni tests revealed significant effects of colonization time on all six common taxa (Table 1). Absolute abundance of four mayflies, *Baetis*, *Paraleptophlebia*, *Cinygmula* and *Drunella* increased as colonization time increased up to the 4 or 8 day treatments (Fig. 2). Subsequently, the absolute abundance of *Baetis* and *Drunella* decreased as colonization time increased to 32 days and numbers of *Paraleptophlebia* and *Cinygmula* leveled off. In contrast, the absolute abundance of *Brachycentrus* and Diamesinae moderately increased with colonization time and tended to increase throughout the experiment.

Relative abundance, including all replicated samples in each treatment, also differed considerably with colonization time (Fig. 3). *Baetis* dominated during the first 8 days of colonization, but its relative abundance decreased during the remainder of the 32-day experimental period. In contrast, the relative abundance of *Brachycentrus* increased with colonization time. The relative abundance of *Paraleptophlebia*, *Cinygmula*, *Drunella* and Diamesinae did not change clearly with colonization time.

The taxonomic compositions of the invertebrates continuously changed with colonization time. Detrended correspondence analysis biplots showed that treatments with short colonization times occurred in domains in which the values for axis 1 were low (Fig. 4). The domains then gradually shifted in the direction of higher values on axis 1 as colonization time increased and, consequently, the 32-day treatment occurred in the domain in which values for axis 1 were the highest among all treatments.

DISCUSSION

Rapid colonization by stream invertebrates was demonstrated in the present study. Total abundance reached a plateau after 4 days of colonization. Mackay (1992) found in her review of colonization by stream invertebrates under various conditions that total abundance and taxon richness usually leveled off after 10–30 days of colonization, which was relatively slower than in the present study. A possible reason for the rapid colonization observed in the present study is that we used a substrate with intact periphyton, whereas previous studies often used substrates in which periphyton was initially reduced or removed to simulate severe disturbance (e.g. Doeg *et al.* 1989; Mackay 1992). Stream invertebrates are known to aggregate in patches that contain high resource levels and, consequently, the colonization rate of each species increases with the quality of the patch (Lake & Doeg 1985). We suggest that a less intense disturbance that leaves periphyton intact should result in faster colonization by stream invertebrates. Rapid colonization may also be attributed to the artificial substrates used in this study, which enhanced the colonization of some
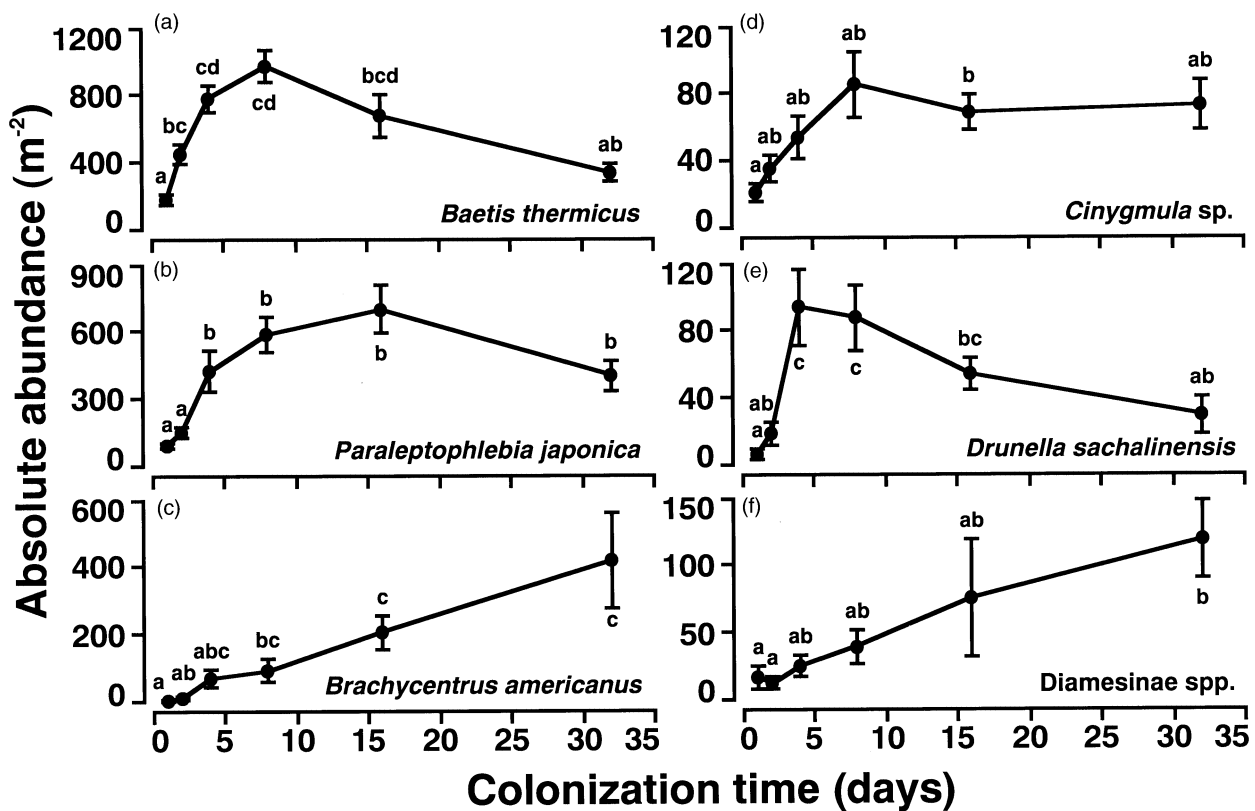
Fig. 2. (a–f) Effect of colonization time on the absolute abundance of six common taxa on the experimental plates. Means ± 1SE are shown. Different letters indicate significant differences ($P < 0.05$) among treatments as assessed using the Tukey method.

taxa with high mobility, such as *Baetis* (well-known highly mobile species; see Mackay 1992). *Baetis* was the most common taxon on the plates, but was rare in the surrounding areas (i.e. the colonizing source).

Continuous changes in community composition were evident even after total abundance and taxon richness reached a plateau, indicating that succession proceeded throughout the 32 days of colonization. The relative abundance of common taxa, particularly *Baetis* and *Brachycentrus*, changed with colonization time. Furthermore, the domain occupied by each colonization-time treatment in the DCA biplots shifted continuously. We will discuss possible mechanisms that may explain the colonizing pattern of stream invertebrates observed in the present study.

Differences in colonizing ability among stream invertebrate taxa were evident. Absolute abundance of four mayflies, *Baetis*, *Paraleptophlebia*, *Cinygmula* and *Drunella*, reached a plateau after 4 or 8 days of colonization, whereas the abundance of

the caddisfly, *Brachycentrus*, and the midge, Diamesinae, continued to increase throughout the 32-day study period, indicating that mayflies were more rapid colonizers than the caddisfly and the midge. Mayflies are known to have a relatively high mobility and can rapidly colonize open substrates (Wiley & Kohler 1981; Otto & Sjöström 1986). In contrast, the mobility of *Brachycentrus* and Diamesinae are assumed to not be as high because they are relatively sedentary taxa. *Brachycentrus* larvae build portable cases and temporarily attach the front lip of their case to the substrate while feeding (Voelz & Ward 1996). Likewise, Diamesinae, mainly composed of *Diamesa* in the Horonai stream (see Miyake & Nakano 2002), is a tube builder adhering to the substrate (Y. Miyake, pers. obs., 2000). Such differences in colonizing ability among community members, resulting from differences in mobility, were suggested to contribute to the succession of the stream invertebrate community throughout the colonization period.

Table 1 Results of ANOVAs examining the effects of colonization time on the absolute abundance of six common invertebrate taxa on the experimental plates

Taxon	F	P	Associated α
Baetis thermicus	13.65	<0.001	0.010
Paraleptophlebia japonica	14.39	<0.001	0.009
Brachycentrus americanus	7.67	<0.001	0.017
Cinygmula sp.	2.84	0.022	0.050
Drunella sachalinensis	8.48	<0.001	0.013
Diamesinae spp.	3.62	0.006	0.025

Degrees of freedom was 5, 66 for all ANOVAs. The associated α for each taxon was calculated using a sequential Bonferroni test. Note that the effects of colonization time are significant when $P < \alpha$.
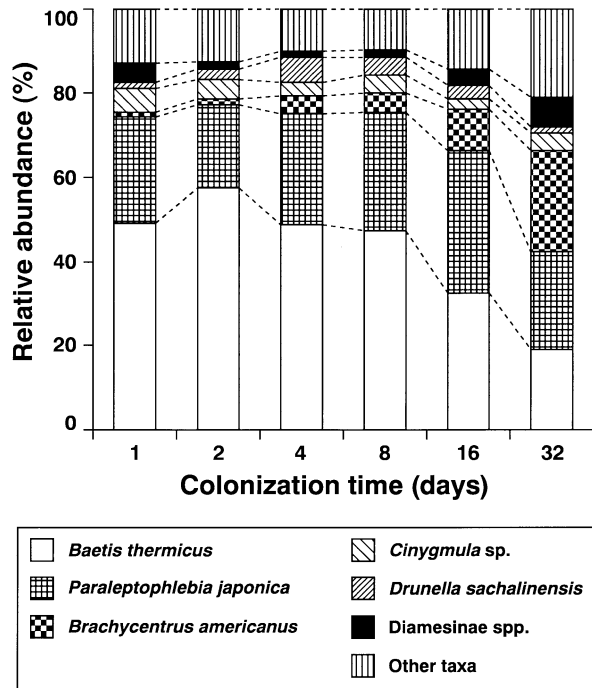

Fig. 4. Plots of the first two axes for the detrended correspondence analysis (DCA) on the relative abundance of stream invertebrates on each experimental plate. Numerals correspond to each colonization-time treatment. The domain occupied by each treatment is indicated with lines.

Fig. 3. Relative abundance of six common taxa, including all replicated samples in each colonization-time treatment.

The absolute abundance of the most common taxon, *Baetis*, decreased towards the end of the colonization experiment. Several previous experiments have also demonstrated this pattern (Shaw & Minshall 1980; Doeg *et al*. 1989; Matthaei *et al*. 1996), although the mechanism causing this pattern has not been explained. In the present study, periphyton biomass decreased simulta-
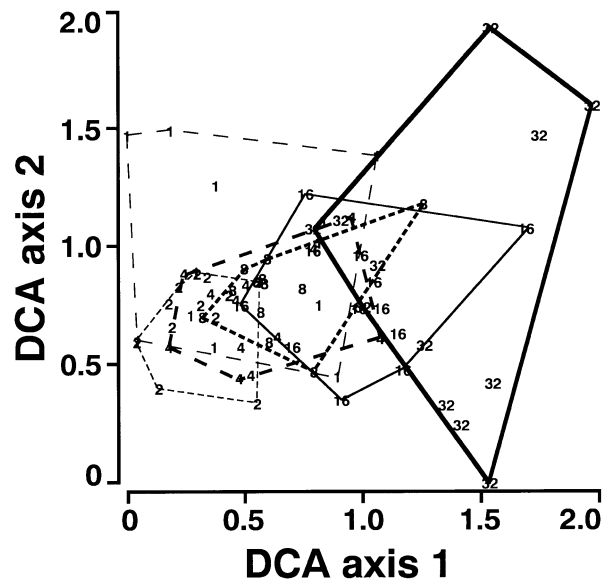
neously with the absolute abundance of *Baetis*. This implies that resource depression by grazers, including large numbers of *Baetis*, caused resource limitation and, then, enhanced emigration of *Baetis*. It is known that there is strong intraspecific competition among *Baetis* (Kohler 1992) and that they abandon habitats when resources are depressed (Kohler 1985). Although threshold levels for *Baetis* and other grazers abandoning habitats have not been established at present, this may be one possible explanation for the decrease in the absolute abundance and relative abundance of *Baetis*. Thus, we suggest that changes in resource conditions might contribute to the transition in species dominance during the colonization of stream invertebrates. The predatory mayfly, *Drunella*, exhibited a similar pattern in absolute abundance with colonization time. The abundance of invertebrate predators is known to be strongly affected by the abundance of invertebrate prey (e.g. Townsend & Hildrew 1976), suggesting that there may be a shortage of some prey taxa on the experimental substrates in the late stages of colonization in the present study. Although there is little information about the preferred food of *Drunella*, it is possible that the

synchronous reduction in the abundance of *Baetis* influenced the abundance of *Drunella*.

In summary, our results show that there was a transition in species dominance throughout the colonization period in the stream invertebrate community. A difference in colonization ability was suggested to contribute to this succession, both at early and late stages of colonization. Taxa with high mobility established dominance during the early stages of colonization. In contrast, taxa with low mobility dominated later because of a slow increase in their abundance and, also, a decrease in the abundance of highly mobile taxa, possibly caused by changes in resource conditions. Consequently, we concluded that a difference in colonization ability among taxa is an important factor resulting in succession of stream invertebrate communities in local habitats.

ACKNOWLEDGEMENTS

REFERENCES

BOOTH D. J. & BROSNAN D. M. (1995) The role of recruitment dynamics in rocky shore and coral fish communities. *Advances in Ecological Research* **26**: 309–385.

CIBOROWSKI J. J. H. & CLIFFORD H. F. (1985) Short-term colonizing pattern of lotic macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* **41**: 1626–1633.

CLEMENTS F. E. (1916) *Plant Succession: Analysis of the Development of Vegetation.* Publication No. 242. Carnegie Institute of Washington, Washington.

DOEG T. J., LAKE P. S. & MARCHANT R. (1989) Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. *Australian Journal of Ecology* **14**: 207–220.

DOWNES B. J. & LAKE P. S. (1991) Different colonization patterns of two closely related stream insects (*Austrosimulium* spp.) following disturbance. *Freshwater Biology* **26**: 295–306.

HAYASHI F. (1991) Dynamic relations within and between populations of stream insect communities. *Biological Science* **43**: 1–13 (in Japanese).

KOHLER S. L. (1985) Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* **66**: 1749–1761.

KOHLER S. L. (1992) Competition and the structure of a benthic stream community. *Ecological Monographs* **62**: 165–188.

LAKE P. S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**: 573–592.

LAKE P. S. & DOEG T. J. (1985) Macroinvertebrate colonization of stones in two upland southern Australian streams. *Hydrobiologia* **126**: 199–211.

MACKAY R. J. (1992) Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 617–628.

MATTHAEI C. D., UEHLINGER U. & FRUTIGER A. (1997) Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology* **37**: 61–77.

MATTHAEI C. D., UEHLINGER U., MEYER E. & FRUTIGER A. (1996) Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. *Freshwater Biology* **35**: 23–248.

MERRITT R. W. & CUMMINS K. W. (eds) (1996) *An Introduction to the Aquatic Insects of North America*, 3rd edn. Kendall/Hunt Publishing Co, Dubuque.

MIYAKE Y. & NAKANO S. (2002) Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. *Freshwater Biology* **47**: 219–230.

MIYAZAKI T., TANAKA Y., ARAYA T. (1991) Discharge stability by large storage of groundwater in the Horonai basin of the Tarumae volcanic area. *Transactions of the Meeting in Hokkaido Branch of Japanese Forestry Society* **39**: 181–184 (in Japanese).

MORIN P. J. (1999) *Community Ecology.* Blackwell Science, Oxford.

NAKANO S., MIYASAKA H. & KUHARA N. (1999) Terrestrial–aquatic linkages: riparian arthropod alter trophic cascades in a stream food web. *Ecology* **80**: 2435–2441.

OTTO C. & SJÖSTRÖM P. (1986) Behaviour of drifting insect larvae. *Hydrobiologia* **131**: 77–86.

PICKETT S. T. A. & WHITE P. S. (eds) (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.

RESH V. H., BROWN A. V., COVICH A. P., GURTZ M. E., LI H. W., MINSHALL G. W., REICE S. R., SHELDON A. L., WALLACE J. B. & WISSMAR R. C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society* **7**: 433–455.

SAKUMA T. (1987) Characterization of soil in the Tomakomai Experimental Forest: especially on the characteristics of the organic horizons and their alteration following the partial cutting. *Research Bulletins of the Hokkaido University Forests* **44**: 749–760 (in Japanese with English summary).

SHAW D. W. & MINSHALL G. W. (1980) Colonization of an introduced substrate by stream macroinvertebrates. *Oikos* **34**: 259–271.

SHELDON A. L. (1984) Colonization dynamics of aquatic insects. In: *The Ecology of Aquatic Insects* (ed. V. H. Resh & D. M. Rosenberg) pp. 401–429. Praeger Publishers, New York.

SOKAL R. R. & ROHLF F. J. (1995) *Biometry*, 3rd edn. Freeman, New York.

TANIDA K., MITSUHASHI H. & FUJITANI T. (1999) A simple acrylate fiber sampler for stream periphyton. *Japanese Journal of Limnology* **60**: 619–624 (in Japanese with English summary).

TANIDA K., YAMASHITA K. & ROSSITER A. (1985) A portable current meter for field use. *Japanese Journal of Limnology* **46**: 219–221.

TOWNSEND C. R. & HILDREW A. G. (1976) Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology* **45**: 759–772.

UNESCO (1966) The SCOR–UNESCO working group on photosynethetic pigments. In: *Monograph on Oceanographic Methodology*, No.1, Report of SCOR–UNESCO working group 17. p 69. UNESCO, Paris.

URABE H. & NAKANO S. (1998) Contribution of woody debris to trout habitat modification in small stream in secondary deciduous forest, northern Japan. *Ecological Research* **13**: 335–345.

VOELZ N. J. & WARD J. V. (1996) Microdistributions of filter-feeding caddisflies (Insecta: Trichoptera) in a regulated Rocky Mountain river. *Canadian Journal of Zoology* **74**: 654–666.

WALKER L. A. & CHAPIN F. S. III (1987) Interactions among processes controlling successional change. *Oikos* **50**: 131–135.

WILEY M. J. & KOHLER S. L. (1981) An assessment of biological interactions in an epilithic stream community using time-lapse cinematography. *Hydrobiologia* **78**: 183–188.