

Long-term changes in the abundance of *Jesogammarus annandalei* (Tattersall) in Lake Biwa

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Abstract

Changes in the abundance of an endemic amphipod, *Jesogammarus annandalei*, that inhabits the profundal zone of Lake Biwa were examined from 1966 to 1999. The abundance of *J. annandalei* increased suddenly during the mid-1980s and thereafter stayed at a level that was sevenfold higher than that before 1980. Compared with the amphipod in the 1960s, both the clutch and body size of the matured individuals decreased during the 1990s, which suggests that per capita food supply decreased. Thus, the increase in the abundance of *J. annandalei* appeared to be due largely to an increase in their survival rate and not their growth or reproduction rates. In accord with the increase in amphipod abundance, the fishery catch of an endemic gobiid fish species that is dominant in the profundal zone and preys on this amphipod as a major food, decreased dramatically during the mid-1980s. These results suggest that long-term changes in abundance of *J. annandalei* in Lake Biwa are mainly regulated by fish predation rather than by food supply.

Amphipods are common benthic animals in many lakes and are one of the most important food items for fish (Gardner et al. 1990; Johnson and Widerholm 1992). Because they live mainly on the sediment surface of the lake bottom where organic matter accumulates, amphipods play a crucial role in channeling sedimented organic matter to organisms at higher trophic levels in lakes (Gardner et al. 1990). Thus, amphipods are a potentially important component of material flows in lake ecosystems. However, their abundance is not necessarily stable, and it sometimes exhibits large temporal changes (McDonald et al. 1990; Johnson and Widerholm 1992; Jorgenson et al. 1992). Several studies have suggested factors that might cause such changes. For example, Jorgenson et al. (1992) found that, in Canadian Arctic lakes, an amphipod species increased its abundance after artificial fertilization, which suggests that an increase in food supply caused by increased primary production can stimulate amphipod production. A similar phenomenon was also found by Johnson and Widerholm (1992) in Lake Vänern. In Lake Michigan, however, large changes in the composition and abundance of macrobenthic species, including amphipods, occurred in parallel with a shift in the fish community (McDonald et al. 1990). These results suggest that amphipod populations are highly vulnerable to both bottom-up (food

supply) and top-down forces (fish predation) in lake ecosystems. However, the relative importance of these forces in determining long-term changes in amphipod abundance has seldom been assessed.

The amphipod *Jesogammarus annandalei* (Tattersall) is an endemic species in Lake Biwa, the largest lake in Japan. This amphipod lives in the profundal zone and is a semelparous species with a 1-yr life cycle that begins in early autumn (Narita 1976; Ishikawa and Urabe 2002). As in several amphipods, such as *Gammarus lacustris* (Wilhelm and Schindler 1999), *J. annandalei* shows diel vertical migration and ascends to just below the thermocline during the night (Trevorrow and Tanaka 1997). According to Yamada et al. (1998), $\delta^{13}\text{C}$ values are found between those of large phytoplankton and fresh organic matter on the lake sediment and the $\delta^{15}\text{N}$ values of this species are equivalent to or higher than those of *Daphnia*. Indeed, the results of gut content analysis have indicated that *J. annandalei* feed mainly on phytoplankton and zooplankton at night, when they ascend to layers below the thermocline (Ishikawa unpubl. data). Thus, this species relies not only on fresh organic matter in the lake sediment but also on plankton for its diet. In a previous study, we showed that biomass of *J. annandalei* in terms of carbon is comparable to, and sometimes higher than, those of zooplankton and benthic oligochaetes in Lake Biwa (Ishikawa and Urabe 2002). This result implies that this species is a quantitatively dominant species in the profundal zone of this lake. However, fragmental evidence suggests that the abundance of *J. annandalei* was much lower 30 yr ago than it is now (Narita 1976; Ishikawa and Urabe 2002). Unfortunately, however, it is not clear whether its abundance has increased gradually for the past 30 yr or suddenly at some point during this period.

In Lake Biwa, biotic and abiotic conditions have been changing for the past 30 yr. At the lake bottom, the minimum oxygen concentration in fall was $>7\text{ mg L}^{-1}$ before 1965 but has been sometimes $<4\text{ mg L}^{-1}$ during recent years (Kalff 2002). The composition and abundance of plankton have also been changing for the past 30 yr (Tezuka 1984;

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Tsugeki et al. 2003). These changes are thought to be a result of eutrophication (Nakanishi and Sekino 1996). Furthermore, according to fishery statistics, the abundance and composition of fish in Lake Biwa have changed considerably (Yuma et al. 1998). Thus, in addition to abiotic conditions, it is most likely that both bottom-up and top-down forces on *J. annandalei* may have changed during the past 30 yr.

In the present study, therefore, we examined long-term temporal changes in the abundance of *J. annandalei* using benthic samples collected routinely since 1966 in Lake Biwa (Mori et al. 1967). We also examined the relative importance of factors affecting *J. annandalei* by comparing annual changes in its abundance with those of some abiotic and biotic parameters that reflect trophic conditions and fish abundance in the lake. To examine whether the increase in the abundance of *J. annandalei* was caused mainly by an increase in reproduction or survival rates, we also analyzed the clutch and body size of the amphipod using samples collected intensively in 1964 (Narita 1976) and 1997 (Ishikawa and Urabe 2002) for the study of the seasonal dynamics of the amphipod population.

Materials and methods

Long-term data—The abundance of *J. annandalei* was estimated using samples collected during a long-term monitoring program that started in 1966 (Mori et al. 1967). In this program, samples were obtained from a fixed station located in the north basin of Lake Biwa (35°12'58"N, 135°59'55"E, ~75 m in depth). The amphipods were collected using an Ekman-Birge grab sampler (225 cm²) in the daytime, sieved with a 500- μ m mesh screen, fixed with 5% formalin, and stored in 70% ethanol. From 1966 to 1988, triplicate samples were collected monthly. From 1989 to 1999, samples were collected in duplicate in February and August, except for 1993, 1996, and 1997, when duplicate samples were collected monthly. All amphipod individuals in these samples were enumerated under dissecting microscopes. When mature individuals were found in the samples (mainly August), the body size was measured under a dissecting microscope at 0.1 mm, as described by Ishikawa and Urabe (2002). At the time of sampling, water transparency, the dissolved oxygen concentration, and water temperature at 1 m above the lake bottom were recorded. Water transparency was measured using a Secchi disk 25 cm in diameter. Water temperature was measured with an electric thermometer (ET-5; Toho-Dentan) before 1994 and with a conductivity-temperature-depth profiler (SBE 25; Sea-Bird Electronics) thereafter. The dissolved oxygen concentration was determined by the Winkler method, using water samples collected with a 3-liter van Dorn water sampler. Data on the amount of total phosphorous in the surface water in the north basin of Lake Biwa was obtained from the *White Paper on the Environment of Shiga Prefecture* (Shiga Prefecture 1966–2001).

Life history parameters—Because the number of *J. annandalei* individuals collected by the grab sampler was limited, we examined additional samples collected intensively in 1964 and 1997 to analyze the life history and seasonal

changes in population structures of *J. annandalei* (Narita 1976; Ishikawa and Urabe 2002). These samples were used to measure amphipod clutch and body size. Details of the sampling methods have been described elsewhere (Narita 1976; Ishikawa and Urabe 2002). In short, the samples were collected by a sledge at 60 m depth in 1964 and by a nighttime vertical tow of plankton net in 1997. In the present analysis, we examined *J. annandalei* individuals collected during their reproductive season, from August to October. In each sample, we first randomly selected >100 individuals, and their body length was measured as described above. From these individuals, 20 females carrying eggs were randomly selected during each year, and the number of eggs in the brood pouch was counted after the eggs were removed using needles and tweezers. We also measured the body length of small individuals (neonates) that appeared in September. In August 1997, a further sampling was made using the same sledge as described in Narita (1976). The sample was used to examine whether the body size of matured individuals differed between different sampling methods (i.e., vertical tow sampling in night vs. sledge sampling in day).

Predatory fish—Data on annual catches of fish species during the study period were obtained from the fishery statistics for Lake Biwa (Shiga Statistics Information Office 1966–2001). In the present study, special attention was paid to two fish species—Biwa-masu, a trout (*Oncorhynchus masou* subsp.) and isaza, a gobiid fish (*Gymnogobius isaza*)—because they inhabit mainly the pelagic and profundal zone and are known to feed on *J. annandalei* (Miura 1966b; Nakanishi and Nagoshi 1984).

Data analyses—To examine density-dependent effects on population size of *J. annandalei*, autocorrelation analysis was performed using the annual mean abundance at year t and $t + 1$ after log transformation to stabilize the variances. To examine whether the abundance level of *J. annandalei* differed between different periods, we used the Mann-Whitney U test, because distribution of data within each period did not necessarily satisfy normality. Temporal trends of the body size of matured individuals were first analyzed by the simple linear regression analysis and then by “hockey-stick” model analysis (Barrowman and Myers 2000). In short, the hockey-stick model analysis decides slope and a breakpoint on the regression line using maximum-likelihood fitting with Akaike’s information criterion (AIC; Akaike 1974). We used AIC to determine which is the better fitting model, the simple linear regression model or the hockey-stick model. Differences in the body sizes of the mature individuals and neonates and clutch sizes obtained between 1964 and 1999 with different sampling methods were examined by either analysis of variance (ANOVA) with Scheffe’s post hoc test or t test. In addition, analysis of covariance (ANCOVA) was performed to examine difference in the clutch size relative to the maternal size between these 2 yr.

Results

Throughout the study period, egg-carrying females of *J. annandalei* always appeared in July–September but were not

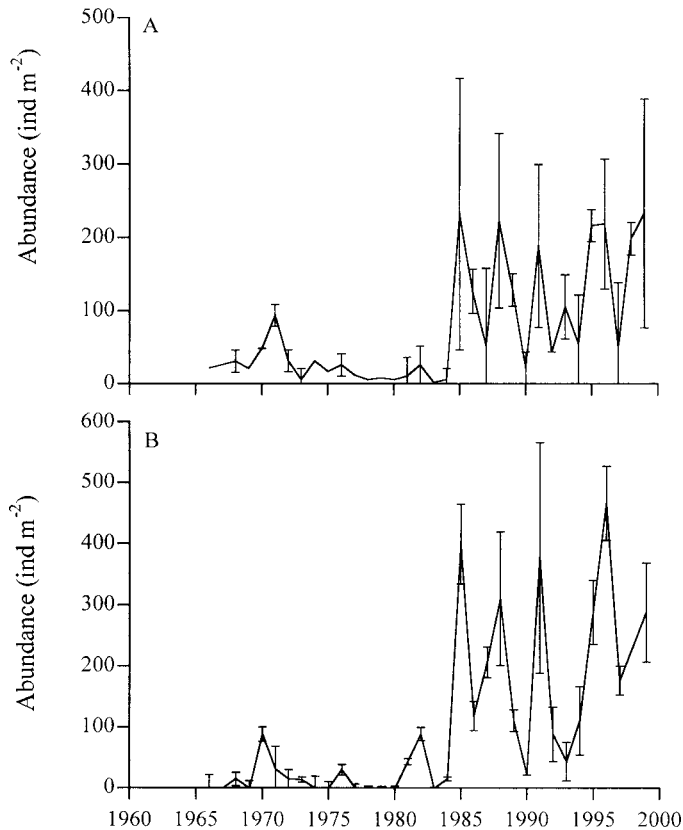


Fig. 1. Long-term changes in the abundance of *J. annandalei* at the north basin of Lake Biwa. (A) Annual mean abundance and (B) abundance in August. Vertical bars represent the SE.

collected thereafter, whereas small juveniles were collected only in September–early October. Thus, the reproduction of this amphipod was limited to late summer, as was shown by Narita (1976) and Ishikawa and Urabe (2002). This implies that no major shift in the reproductive seasons occurred during the study period. Because *J. annandalei* were not collected in some months by the grab sampler, their density highly varied even within single year (Fig. 1A). However, the annual mean abundance of the amphipod changed considerably during the study period. From 1966 to 1984, it ranged from <1 to 94 ind m⁻², with an average of 21 ind m⁻². In 1985, the abundance suddenly increased to 230 ind m⁻² and ranged 50–250 ind m⁻², with an average of 140 ind m⁻² thereafter. Through the study period, the annual mean abundance at year *t* was positively correlated with those at year *t* + 1 ($r = 0.445$, $n = 33$, $p < 0.01$). This positive correlation was largely due to a sudden increase in the amphipod abundance at 1985. Indeed, when the same analyses were repeated separately for the periods before and after 1985, no significant relationship was detected between amphipod abundances during successive years. Instead, the amphipod abundance differed significantly between these periods (Mann-Whitney *U* test, $p < 0.001$) and was, on average, sevenfold higher during the period after 1985 than that before 1985. Note that, because the sampling frequency differed somewhat among the years, one may suspect that there is an artificiality in the long-term trend of the estimated

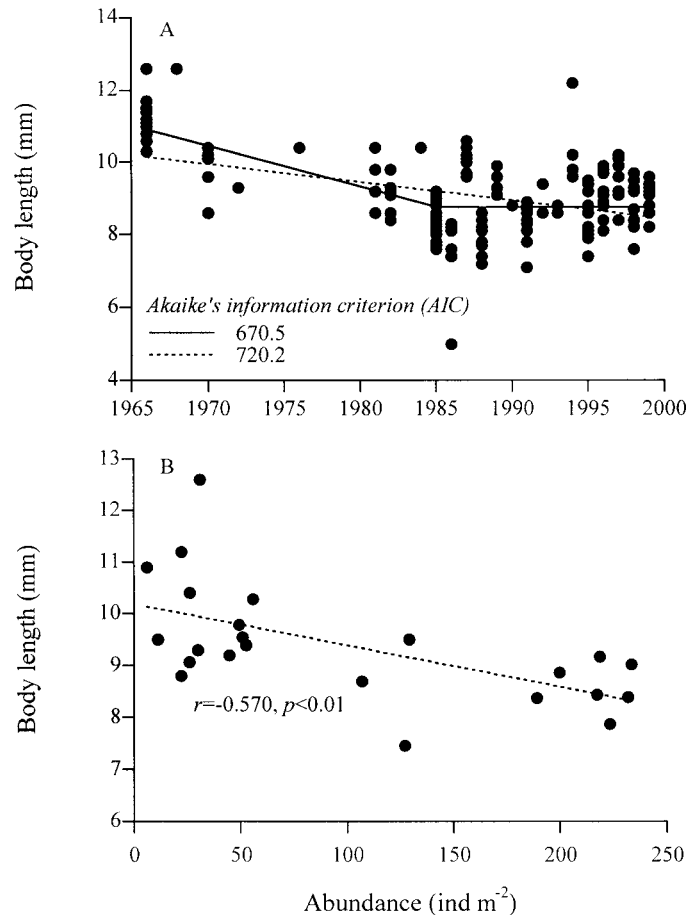


Fig. 2. (A) Long-term changes in the body length of mature *J. annandalei* individuals in August at the north basin of Lake Biwa. Solid and dashed lines show hockey-stick fitting and linear regression, respectively. (B) The relationship between the body length of mature individuals and the mean annual abundance of *J. annandalei*. The dashed line shows linear regression.

annual abundance of *J. annandalei*. Fortunately, throughout the study period, we collected *J. annandalei* commonly in August—the reproductive season of this species. The abundance of *J. annandalei* in August showed the same trends as the annual mean abundance (Fig. 1B). Thus, it was clear that the abundance of *J. annandalei* did increase substantially after 1985.

Because the number of *J. annandalei* individuals collected by the grab sampler was limited, we could not examine the long-term trends of changes in various aspects of life history parameters of this species, except for the body size of mature individuals. When the body length of the mature individuals found in the grab samples was plotted against the year of collection, there was a decreasing trend from 1964 to 1999 (Fig. 2A); the body size of the amphipods seems to have changed during the study period. Although a significant linear relationship from 1964 to 1999 was detected by regression analysis ($r = 0.564$, $p < 0.01$; AIC = 720.2), the hockey-stick model with a breakpoint in 1985 (AIC = 670.5) was selected as the better fitting model because of its lower AIC value (Fig. 2A). In addition, the body length correlated

Table 1. Body length and clutch size of mature individuals in August and neonate size in September (mean \pm SD) in 1964 and 1997. The number of specimens measured is shown in parentheses.

Body size	1997			Statistical test
	1964 sledge	plankton net	1997 sledge	
Matured individual (mm)	11.0 \pm 0.81 ^a (100)	10.1 \pm 0.79 ^b (132)	10.0 \pm 0.68 ^b (100)	ANOVA with Scheffé's post hoc <i>t</i> test
Neonates (mm)	1.90 \pm 0.48 ^c (49)	1.94 \pm 0.27 ^c (108)		
Clutch size (eggs female ⁻¹)	107.6 \pm 27.5 ^d (20)	58.2 \pm 10.1 ^e (20)		<i>t</i> test

Significant differences at the 5% level, as determined by ANOVA or *t* test, are denoted by different letters.

negatively with the mean annual abundance (Fig. 2B). To confirm such changes for the past 30 yr, we examined mature individuals and neonates of this amphipod that had been collected intensively in the late summer in 1964 and 1997 (Table 1). According to the results of ANOVA with Scheffé's post hoc test, the mean body length of mature individuals in August 1997 did not significantly differ between samples collected by the sledge and the nighttime vertical tows but was smaller than those in the sample collected by the sledge in 1964 ($F_{2,329} = 47.9, p < 0.001$). Unfortunately, most mature females in the sledge sample collected in August 1997 dropped their eggs from the brood pouch, probably because we fixed the sample several hours after sampling. Thus, we could not estimate clutch size of *J. annandalei* collected by the sledge in August 1997. However, the clutch size per gravid female collected by the plankton net in 1997 was significantly smaller than those collected by the sledge in 1964 ($t = 7.54, p < 0.01$).

In 1997, the clutch size increased significantly with the body length of gravid females (Fig. 3). A significant increase in the clutch size relative to the body length of gravid females was also found in 1964. In this analysis, we excluded data from three anomalous individuals, because their brood

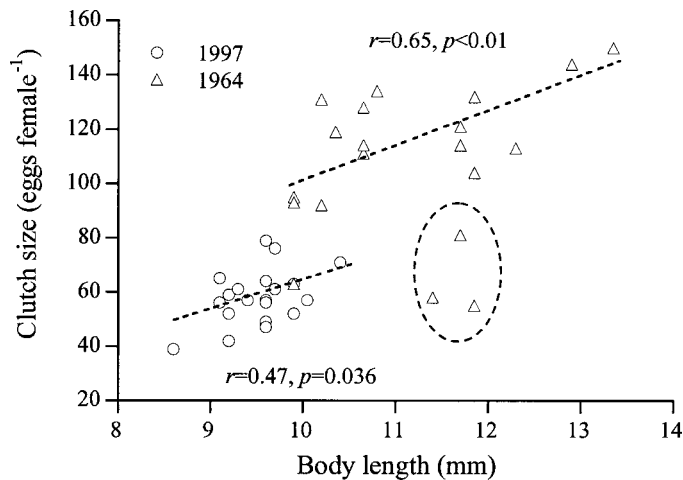


Fig. 3. Clutch size of *J. annandalei*, plotted against the body length of maternal individuals in 1964 and 1997. The regression line between the clutch size and maternal size is inserted. Note that data enclosed by a dashed circle are not included in the regression line of 1964. See text for explanation.

pouch was widely opened, which suggests that these individuals dropped eggs during storage. The results of ANCOVA showed that the elevation of least-squares regressions was significantly different between 1997 and 1964 ($F_{1,34} = 34.7, p < 0.0001$), but the slope was not ($F_{1,33} = 0.013, p = 0.914$). Thus, not only the size of gravid females but also the size-specific clutch size was smaller in 1997 than in 1964. Because the reproduction of *J. annandalei* was limited to late summer, we defined small individuals appearing in September as neonates (Table 1). The mean body length of the neonates did not differ between these 2 yr ($t = 0.509, p = 0.66$).

Unlike the abundance of the amphipod, no marked shift during the mid-1980s was found in chemical and physical conditions of the lake water during the study period (Fig. 4). Although water transparency has become seasonally more varied during recent years, the annual mean fell within the range of 5–7 m. Total phosphorus in the surface mixing layer ranged 12–8 $\mu\text{g L}^{-1}$ and tended to decrease in recent years. Water temperature above the lake bottom (70 m depth) changed seasonally and varied from 5.5° to 8.5°C. From 1985 to 1990, the water temperature increased, but this variation was within the range found in other years. The con-

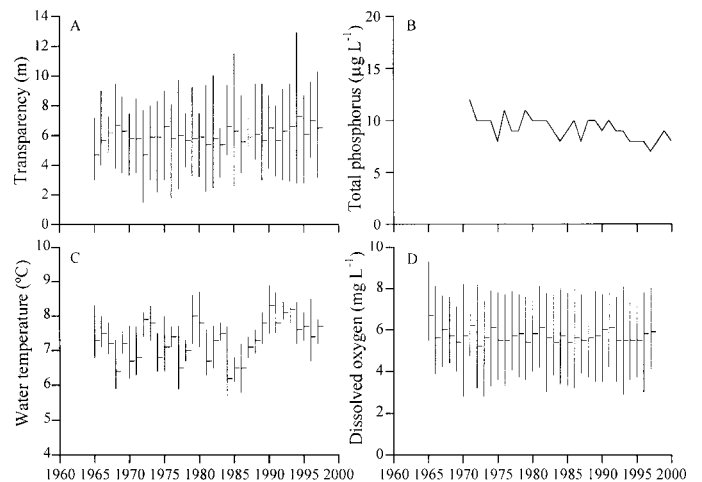


Fig. 4. Long-term changes in annual mean of (A) water transparency, (B) total phosphorus in the surface lake water, (C) water temperature, and (D) dissolved oxygen concentration in water at 1 m above the lake bottom. In panels A, C, and D, vertical bars indicate annual range of the observed values.

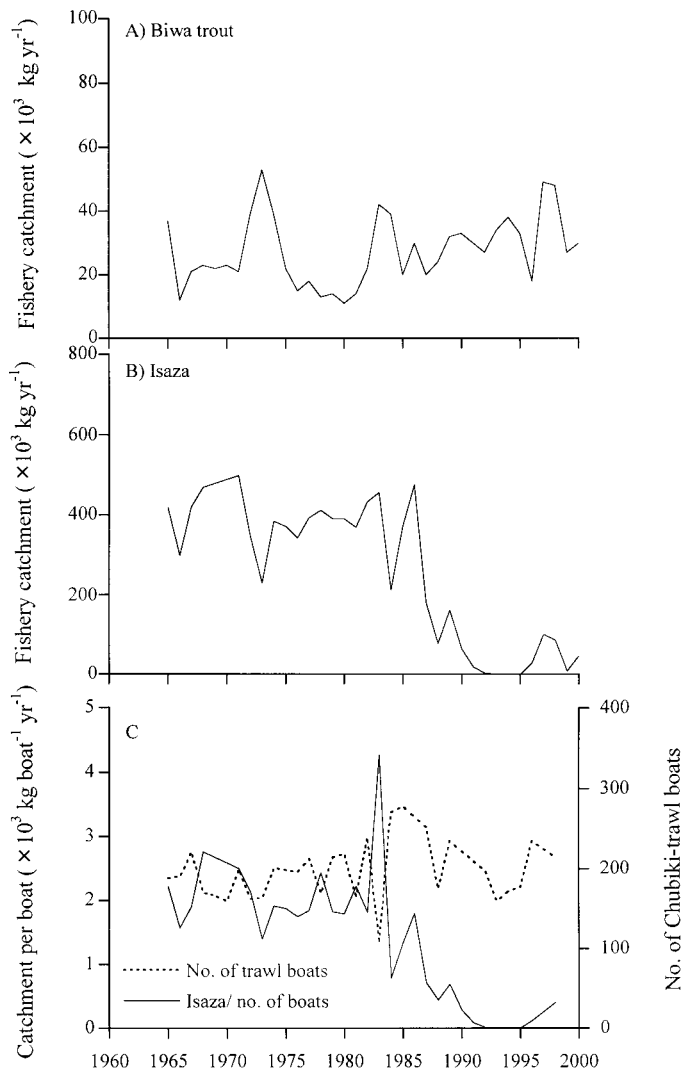


Fig. 5. Changes in the total annual fishery catch of (A) Biwa trout and (B) isaza. (C) Number of Chubiki-trawl boats and annual catch of isaza per Chubiki-trawl boat.

centration of dissolved oxygen in the bottom water also varied seasonally and was highest in winter and lowest in fall for all of the years examined. The lowest concentration of dissolved oxygen was >5.5 mg L⁻¹ in 1965, and it tended to decrease toward 1970, when it reached 3 mg L⁻¹. Thereafter, however, no major changes in both seasonal pattern and absolute value of the oxygen concentration were found.

The annual catch of Biwa trout (*O. masou* subsp.) increased once during the early 1970s but was relatively stable thereafter, being $\sim 30 \times 10^3$ kg (Fig. 5A). However, the annual catch of the gobiid fish isaza (*G. isaza*) showed large changes during the study period (Fig. 5B). In Lake Biwa, $>90\%$ of isaza harvest was obtained by Chubiki-trawl nets (trawl net fishing offshore) during winter (Shiga Statistics Information Office 1966–2001). Before the mid-1980s, $>300 \times 10^3$ kg of this fish were, on average, harvested annually by Chubiki trawling. In 1984, the annual catch of isaza decreased to 50% of that in the previous year, but it recovered to a high level in the following 2 yr. In 1987,

however, the annual catch decreased and reached almost zero in 1992. After 1995, the annual catch recovered to some extent but never reached the level before 1985. It was noteworthy that, after 1983, the number of fishing boats operating the Chubiki trawl increased from ~ 180 to >250 . As a result, although the total annual catch of isaza did not decrease until 1986, the annual catch per Chubiki-trawl boat decreased to a low level after 1984 (Fig. 5C).

Discussion

The present results show that the abundance of *J. annandalei*, an endemic amphipod in Lake Biwa, has increased for the past 30 yr and that this increase occurred suddenly in 1985. Judging from chemical and physical conditions, the north basin of Lake Biwa was oligotrophic, although the lake is now classed as mesotrophic because of eutrophication (Tezuka 1984; Nakajima and Nakai 1994; Nakanishi and Sekino 1996). However, the sudden increase in abundance of *J. annandalei* cannot be explained by changes in the trophic conditions of Lake Biwa. The eutrophication of this lake progressed most rapidly between the 1960s and 1970s because of an increase in the human population and urbanization in the watershed (Nakajima and Nakai 1994; Ogawa et al. 2001). Indeed, the dissolved oxygen concentration at the lake bottom of our sampling site decreased to <3 mg L⁻¹ in 1970. However, after 1970, total phosphorus in the surface layer of this lake tended to decrease, probably because of legal regulation of nutrient loading and the development of sewerage systems in the surrounding areas. In Lake Biwa, algal growth and primary production are limited mainly by the P supply (Urabe et al. 1999). Therefore, it is unlikely that primary production, and, thus, the sinking flux of organic matter to the lake bottom, increased suddenly in 1985. In support of this inference, no marked changes were found in the absolute concentration and seasonal pattern of dissolved oxygen at the lake bottom, which suggests that the discharge of organic matter to the lake bottom did not change markedly after the 1970s, at least at our sampling site. Tsugeki et al. (2003) showed that the abundance of crustacean zooplankton, especially *Daphnia*, increased from 1960 to 1970, in parallel with progress of eutrophication, but that it decreased in the early 1980s and was relatively low until the mid-1990s. During the study period, the water temperature at the lake bottom varied but did not show a consistent difference before and after the mid-1980s. These results suggest that no large changes occurred either to the food supply of *J. annandalei* or the physical conditions of its habitat in the 1980s. However, we could not rule out the possibility that food conditions for *J. annandalei* had changed during the eutrophication, simply because we have no data that directly quantify the supply of their food items in the profundal zone.

Our results show that both the clutch and body size of the gravid females were significantly smaller in 1997 than in 1964. In addition, a comparison of body length between maternal individuals suggests that the somatic growth rate of this amphipod was lower in 1997. The long-term changes in body length of the matured amphipods were better fitted by

the hockey-stick model with the breakpoint at 1985 than by the simple linear model. These results indicate that the decrease in the body size of the amphipod occurred before 1985. This decrease might have related with changes in food condition related to eutrophication. However, we could not ascribe the increase in abundance of *J. annandalei* to an overall increase in supply of their food. It is well known for a variety of organisms that the maturation size decreases with decreasing food supply (Urabe 1991; Johnson and Widderholm 1992; Urabe and Sterner 2001). Thus, the maturation size of *J. annandalei* suggests that per capita food supply was kept low after 1985. If food conditions do not change greatly, an increase in the survival rate would reduce the per capita food supply. It is most likely that the increase in *J. annandalei* abundance was not caused by increase in food supply but largely by an increase in its survival rate.

Because amphipods are one of major food sources for fish species, changes in fish abundance would affect their survival rates. McDonald et al. (1990) showed that the abundance of benthic amphipod in Lake Michigan changed dramatically because of changes in the fish community. In Lake Biwa, two endemic fish, isaza (*G. isaza*) and Biwa trout (*O. masou* subsp.), are known to prey on *J. annandalei* (Miura 1966b). Nagoshi (1966) and Nakanishi and Nagoshi (1984) examined stomach contents of isaza in various seasons and showed that this fish relies heavily on *J. annandalei* as a major food item. Biwa trout, however, mainly feeds upon other fish (Miura 1966b). The annual fishery catch of Biwa trout increased once in the 1970s but did not change largely in the 1980s. According to fishery statistics, however, isaza, which was much more abundant than Biwa trout, decreased dramatically in the mid-1980s. The first symptom of the decline of isaza abundance appeared in 1984, when the annual Chubiki-trawl catch decreased to 50% of that in the previous year. In the succeeding 2 yr (1985 and 1986), the annual catch of this fish increased. However, the increase was caused largely by an increase in fishing efforts. During the mid-1980s, the number of Chubiki-trawl boats increased, because fishermen were trying to catch juvenile ayu (*Plecoglossus altivelis altivelis*), which has a high market value (Iwasaki 1987), although the annual catch of juvenile ayu by Chubiki trawling was <10% of that of isaza (Iwasaki 1987). Thus, the annual catch of isaza per fishing boat decreased after 1984, coinciding almost exactly with the time when *J. annandalei* increased abundantly.

To assess the potential impact of isaza on the *J. annandalei* population, the predation rate of isaza is required. In Lake Biwa, there are basic data to estimate roughly the predation rate of isaza. According to Nagoshi (1966), isaza has a 2-yr life span, and the net growth rate is ~ 1.8 g wet weight $\text{ind}^{-1} \text{yr}^{-1}$. The value corresponds to 0.23 g C $\text{ind}^{-1} \text{yr}^{-1}$ (Ishikawa unpubl. data). From changes in the body size along their life history (Nagoshi 1966) and the allometric equation of respiration rate for isaza at 9°C (Suzuki 1967), the annual carbon loss rate due to respiration is, on average, estimated to be 4.7 g C $\text{ind}^{-1} \text{yr}^{-1}$ if the respiration quotient is 1 (Schmidt-Nielsen 1997). In this estimation, no correction by water temperature is needed, because isaza grows in the profundal zone that *J. annandalei* inhabit (Nagoshi 1966). Thus, we can expect that one isaza individual assimilates,

on average, 4.9 g C yr^{-1} . If we assume arbitrarily an assimilation efficiency of 0.4 (Wootton 1998), the annual ingestion rate is 12.3 g C $\text{ind}^{-1} \text{yr}^{-1}$. In isaza fishing, 0+ and 1+ individuals have been caught in almost equal numbers; thus, the average individual body weight in the fish harvest would be 2.3 g wet weight (Nagoshi 1969). Therefore, $300\text{--}400 \times 10^3$ kg of the fishery's catchments implies that isaza population in Lake Biwa ingested a total of $1.6\text{--}2.1 \times 10^9$ g C yr^{-1} before 1985. Because this fish inhabits the deep cold layers (Nagoshi 1966), we assumed that their distribution area of the fish covers 60% of the surface area of the northern basin (613 km^2) of Lake Biwa. Thus, the ingestion rate of isaza population is estimated to be $4.4\text{--}5.7$ g C $\text{m}^{-2} \text{yr}^{-1}$. It is likely that this value underestimates the ingestion rate in situ, because the commercial fishing harvests a part of isaza population. Nonetheless, the estimated value is comparable to the net production rate of *J. annandalei* estimated in 1997 (11.5 g C $\text{m}^{-2} \text{yr}^{-1}$; Ishikawa and Urabe 2002). These rough estimations suggest that isaza were abundant enough to depress *J. annandalei* abundance before 1985. Considering the fact that isaza preys on *J. annandalei* as a major food item and has been the most abundant fish in the profundal zone of Lake Biwa, it is most likely that predation pressure to the *J. annandalei* population was relieved by the decrease in the standing stock of isaza at the mid 1980s, which has resulted in an increase in the amphipod abundance.

Several studies have reported that a decrease in abundance of predatory fish leads to an increase in the body size of prey amphipods because the fish usually prefer large individual prey (McDonald et al. 1990; Wellborn 1994). Studies of the stomach contents of isaza have shown that this fish tends to prey preferentially on large food items in Lake Biwa (Nakanishi and Nagoshi 1984). In the present study, however, increases in body size of mature *J. annandalei* individuals were not found when isaza decreased. As was mentioned earlier, an increase in the abundance of consumers would result in a decrease in the per capita food supply unless their food condition changed greatly. Under such conditions, we can expect a negative-density dependence of the maturation size of consumers under a limited food supply. Indeed, we observed the negative relationship between the abundance of *J. annandalei* and their maturation size throughout the study period (Fig. 2B). According to the results of Ishikawa and Urabe (2002), the net production of *J. annandalei* from 1997 to 1998 was comparable to the amount of particulate organic carbon transported from the epilimnion to the hypolimnion in Lake Biwa, which suggests that the population density of *J. annandalei* reached a level near the carrying capacity in terms of food supply after 1985. Thus, it is likely that the decrease in the abundance of predatory fish decreased the maturation size of the prey amphipod indirectly by increasing the prey population density and thus intensifying the intraspecific competition under the limited food supply.

It is not clear why isaza decreased suddenly in the 1980s. Overfishing caused by an increase in trawl boats is one possibility, although there was no sign of overfishing, because the body size of isaza, including mature individuals, tended to increase during the 1980s (Nagoshi pers. comm.). In the

1950s, isaza also experienced a dramatic decrease in the number of standing stock (Nagoshi 1969). Unfortunately, we were unable to determine whether this decrease was accompanied by an increase in the abundance of *J. annandalei*, because no samples were available during that time. Miura (1966a) suggested that the decrease in isaza in the 1950s was a result of exploitative competition with ayu, because the annual catch of the former species correlated negatively with that of the latter species, and young isaza individuals share the same food with small individuals of the latter species. Alternatively, Nagoshi (1969) suggested that the isaza population might have been suppressed by ayu in the 1950s, because adult individuals of the latter species can feed directly on larvae of the former species. According to Yuma et al. (1998), the relative abundance of fish species in Lake Biwa has changed during the past 30 yr. Although numbers of most of the cyprinid fish species have decreased, the annual catch of ayu increased from the 1960s to the 1990s (Yuma 1998). However, there is no sign that the standing stock of ayu increased dramatically during the mid-1980s. Because isaza spawn in the littoral zone of Lake Biwa, environmental alternations in the nearshore areas or an invasion of exotic carnivore fish such as large-mouth bass (*Micropterus salmoides*) to this lake might have induced a decrease in the standing stock of isaza in the 1980s, as has been suggested by some researchers (Nakanishi and Sekino 1996; Yuma 1998). In any event, these possibilities suggest that the sudden increase in abundance of *J. annandalei* reflects lakewide changes that occurred in the community structures in Lake Biwa around the 1980s.

In conclusion, the timing of the sudden increase in abundance of *J. annandalei* was not matched by environmental changes induced by eutrophication. Changes in the clutch and body size of *J. annandalei* during the past 30 yr suggest that the per capita food supply of this amphipod has decreased somewhat. Thus, the increase in abundance is due largely to an increase in survival rate and not in the growth and reproduction rates. In accord with the timing of the increase in *J. annandalei* abundance, the standing stock of the dominant predator fish isaza decreased dramatically during the mid-1980s. This suggests that long-term changes in the abundance of this endemic amphipod are regulated mainly by top-down forces rather than bottom-up forces.

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