

The reproductive biology of a Central American cichlid *Neetroplus nematopus* in Lake Xiloá, Nicaragua

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Abstract This study was conducted to provide a five-year database on the breeding seasonality and breeding biology of a Central American cichlid fish *Neetroplus nematopus*, a biparental substratum-spawning cichlid that cares for its eggs, wrigglers, and fry for up to six weeks. A total of 503 breeding pairs were monitored for breeding success. Breeding pairs of *N. nematopus* are sexually dimorphic in size, with females averaging 39% of male body mass. Fry emerged from 85% of nesting cavities. After three weeks, only 30% of the broods were present in the nesting cavity; these broods had a 30% survival rate, giving a 9% overall survival rate. Nineteen percent of the successful parents with three-week-old broods adopted foreign fry. A consistent unimodal breeding peak in December was observed for five years. This breeding peak differed dramatically from the bimodal breeding season 20 years found in the 1970s. The effects of extensive grenade fishing practices during the 1980s might have played a substantial role in the observed change. Grenade fishing stopped in 1991, and the number of *N. nematopus* pairs increased by 136% from 1990 to 1995. With increased density of breeding fish, the breeding season for this species also expanded. The balance between divergent selection due to competition for breeding sites and stabilizing selection due to predation pressure on offspring is likely to mold the breeding season for *N. nematopus* and other cichlids of Lake Xiloá. We suggest that brood adoption and synchrony of breeding is a strategy to reduce predation on the parent's own young [*Current Zoology* 56 (1): 43–51 2010].

Key words Nicaragua, Cichlids, Breeding, Reproduction, Synchrony, Seasonality

Over the past three decades, an increasing amount of *in situ* information on the reproductive biology of cichlids has become available (Fryer and Iles, 1972; McKaye, 1984; Keenleyside, 1991; Coleman, 2001). Much of this research has focused on African cichlids due to the remarkable radiations within the Rift Lakes as well as the deleterious effects of species introductions (e.g., the Nile perch *Lates nilotica*), fishery practices, and deforestation (Witte et al., 1992; McKaye et al., 2008). Despite the fact that Asian and Latin American cichlid populations face similar threats, limited information exists on their reproductive biology (but see Lowe-McConnell, 1969; Ward and Wyman, 1977; Winemiller, 1989), including a Central American cichlid fish *Neetroplus nematopus*.

Neetroplus nematopus, like most Central American cichlids, is a monogamous substratum-spawning cichlid that provides biparental care (McKaye, 1986). This species breeds primarily in rocky habitats throughout the year, and pair formation usually occurs prior to the es-

tablishment of a breeding territory (McKaye, 1986). Sand is excavated from spaces between the rocks to form a nesting cavity. Adhesive eggs are laid on the ceiling and/or walls within the nest. The process of fertilization is not yet understood, as males are unable to enter the nesting cavity due to a sexual size dimorphism (McKaye, 1986). The eggs hatch 3–4 days after fertilization and remain in the wriggler (larvae with yolk sac) stage for approximately 5–6 days (Konings, 1989). Free-swimming fry emerge from the nest 8–10 days after fertilization. The fry are guarded for up to six weeks by both parents (McKaye, 1977). This species, like other cichlids, is known to provide alloparental care (McKaye and McKaye, 1977), which occurs when a breeding pair adopts and cares for foreign fry along with their own offspring (Keenleyside, 1991).

Neetroplus nematopus is the most abundant and second smallest of the cichlid species inhabiting Lake Xiloá (McKaye, 1977; Waid et al., 1999). In Lake Xiloá (Jiloá), the size range of breeding *N. nematopus* males

Received Nov. 28, 2009; accepted Jan. 20, 2010

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and females is 57 – 108 mm and 31 – 80 mm standard length (SL), respectively (McKaye, 1986). Breeding pairs of *N. nematopus* are distinguished from nonbreeders by a dramatic change in body coloration (Fig. 1). Both sexes transform from a pale gray body color with one black mid-body vertical bar when not breeding, to a black body with one white mid-body vertical bar during breeding (Konings, 1989).

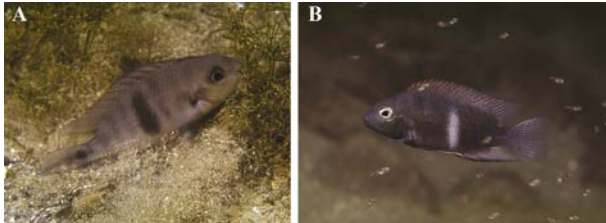


Fig.1 The dramatic change in coloration between a non-breeding (A) and breeding (B) *N. nematopus* (Photo by Ad Konings).

Studies on the reproductive biology of tropical organisms are frequently restricted to short time periods, covering a few months to a year (e.g., McKaye, 1977; Abindin, 1986). McKaye (1977) studied the reproductive biology of the cichlid species in Lake Xiloá, Nicaragua for a total of eight months (February to September). He described a bimodal breeding season within this cichlid assemblage. The *Amphilophus citrinellus* (Meek, 1907) species complex (see Stauffer and McKaye, 2002) and *Neotroplus nematopus* (Günther, 1869) bred at high densities during July and August, while the remaining seven cichlid species and *N. nematopus* (for a second time) bred at high densities during February and March 1974. *N. nematopus* was observed breeding at similar densities during both peak seasons. McKaye (1977) quantified one sharp decrease in the breeding activity of Lake Xiloá cichlids from April to June. A second decrease in breeding activity was hypothesized to occur from October through January. In 1990, we obtained funding to conduct the first continuous, long-term study of these fishes *in situ* in order to accurately describe their reproductive behavior. In the study here-in, we examine the breeding seasonality, reproductive success and pair formation of *N. nematopus* over a five-year period and compare the results to those of McKaye's (1977, 1986) studies. The study was complicated by the heavy grenade fishing by unauthorized members of the Nicaraguan army when we arrived at Laguna de Xiloá in 1989. With the cooperation of army officials, grenade fishing was stopped, and we studied the recovery of the cichlid fish populations.

1 Materials and Methods

This study was conducted in Lake Xiloá, Nicaragua (12°13'N, 86°19'W). A detailed description of the lake is given elsewhere (Barlow et al., 1976; McKaye and Barlow, 1976; McKaye, 1984). Five study sites were established within Lake Xiloá (Sites A – E; see Vivas and McKaye, 2001). Four of these sites (A – D) contained permanently marked transects used to collect data on the depth distribution and density of breeding pairs. Site E, adjacent to C, was established to avoid removal and/or perturbation of fishes at the transect sites.

Sites A – D contained transects following the depth contours every 3 m of depth between 1.5 m and 28.5 m. The maximum transect depth differed among sites due to variation in suitable nesting structure. Fixed 30-m transect lines were placed at Sites A – C, while 20-m transect lines were used at Site D, a small rock outcropping bordered by sand. A diver using an 8-mm underwater video camera recorded the occurrence of all breeding pairs with fry within 2 m of either side of the transect line. Thus, the transects covered a total area of 120 m² for Sites A – C and 80 m² for Site D. Transects did not overlap due to the slope of the lake floor.

Data on behavior and reproductive success were collected at Site E. All data collections were made with the use of open-circuit SCUBA. All means reported below are given with *SE* unless otherwise stated.

1.1 Rainfall

Monthly rainfall data for Nicaragua were obtained from the Global Precipitation Climatology Centre (GPCC) project (www.dwd.de/research/gpcc/visu_gpcc.html). Surface maps were used from the rain gauge monitoring product program for September 1990 to December 1994 (Xie et al., 1996) and from the GPCC program for January 1995 to August 1996. The spatial resolution of these products is between 2.5° × 2.5° latitude and 1° × 1° longitude. The monthly rainfall from these programs was measured in mm and reported as a range. The average rainfall for each month was calculated as the average of the maximum and minimum values of the range.

1.2 Breeding seasonality

Videotaping began in September of 1990 at Sites A and B; in October 1991 at Site D; and in December 1992 at Site C. Video data were collected through September 1995. Sites A – D were videotaped on a bi-weekly basis. Since videotaping began in September, we designated this month as the beginning of each annual

season. When breeding pairs of *N. nematopus* with fry were encountered, the diver stopped and videotaped the parents with young for approximately 10 s. The depth distribution and breeding density of *N. nematopus* pairs with young were obtained from the video transects. For comparison with McKaye's (1977) depth distribution, only data from Site A are considered in this study, as this was the site where the previous research was conducted.

1.3 Size of reproductive individuals

We collected 20 non-territorial individuals from December 1995 to January 1996 (i.e., near the breeding peak) at Site E. We recorded standard length (SL) for each individual and inspected gonads to determine reproductive condition. Individuals were classified as either reproductive (i.e., sperm in testes or gravid gonads) or non-reproductive.

Data on the relationship between female body size and fecundity were collected during November and December of 1995. We separated 25 paired females from their mates during the territorial stage (i.e., prior to egg deposition) for gonadal inspection. For each female, SL was measured and the number of mature eggs (> 1.6 mm in diameter) in the gonads was counted.

1.4 Pair formation

Breeding pairs were collected at Site E from October 1995 through May 1996. The wet mass and SL were measured for each individual. The wet mass was measured with a 50 g Pesola spring scale accurate to ± 1.0 g. The SL of individuals was measured to the nearest mm. In cases where measurements were taken underwater, only the SL was measured. To compare the slopes and y-intercepts of pair formation data between McKaye (1986) and the current study, we performed regression analysis (Zar, 1996).

1.5 Reproductive success

We examined the reproductive success of *N. nematopus* from October 1995 through April 1996 and from August 1996 through May 1997 at Site E. Artificial ($n=50$) and natural nests ($n=64$) were used to examine fry survivorship. Natural nesting cavities in the rocks can be severely damaged or destroyed if disturbed. These nests also make it difficult to discern between early stages of offspring development. Artificial nests allowed us to standardize the size of nesting cavities and to differentiate among stages of the breeding cycle that occurred within the nesting cavity (i.e., egg and wriggler stages). Information gained from artificial nests on the length of the egg and wriggler stages was used to infer the time of egg deposition for natural nests. Artifi-

cial nests were made from aluminum soda cans (6.5 cm diameter \times 12 cm height), each containing one entrance hole. Four different entrance hole sizes were used (smallest: 10 mm wide \times 14 mm wide; largest: 20 mm wide \times 35 mm long) to accommodate a full size range of females. The size range of females was determined from data collected at Lake Xiloá during the 1970s (McKaye, 1986).

A diver partially buried a total of 160 artificial nests throughout the rocky outcropping forming Site E. Each nest (artificial and natural) was then marked with an individually numbered survey flag. The depths of all flagged nests were recorded. We checked each nest a minimum of every two days and a maximum of every four days throughout the study. During each visit to a nest, we recorded the nest number, the stage of the reproductive cycle (territorial, egg, wriggler, or fry stage), an estimate of the brood size (i.e., number of young), and the age of the brood. We also counted the number of eggs laid within the artificial nests ($n = 50$). Flaps were cut into the artificial nests were used to enable egg counts. Not all clutches could be counted on a single day due to underwater time constraints. Therefore, a sub-sample of nests at Site E was taken. Visual egg counts and brood size estimates were conducted from September 1995 through April 1996. Brood size estimates ($n = 114$) included broods emerging from both natural and artificial nests.

To check the accuracy of brood size estimations, divers visually estimated the size of broods away from the study area and then captured the young to determine the actual count. This procedure yielded observer accuracy of $\pm 10\%$ of the actual brood size. Brood age was determined from the time young became free-swimming; therefore, time spent in the egg and wriggler stages (approximately 8 – 10 days) was not included in the age of the young. Since nests were not visited daily, brood age was accurate to within ± 2 days.

Brood success was calculated for three categories: pre-fry stages (egg and wriggler), fry less than three weeks of age, and fry greater than three weeks of age (McKaye, 1977). We defined brood failure as a pair missing for two or more consecutive visits (4 – 8 days) or as replacement by another pair. We were able to discern brood failure from replacement by a new brood without marking the individuals because artificial nests were easily checked for the presence of eggs, wrigglers, and fry. Thus, any change within the breeding cycle was readily detected (e.g., wrigglers replaced by eggs). We calculated the ultimate brood success by multiplying the

probability of succeeding to the pre-fry stage with the probability of succeeding to the fry less than three weeks of age stage.

2 Results

2.1 Breeding seasonality and rainfall

We observed a consistent unimodal breeding season for *N. nematopus*. Peak breeding density occurred in December and ranged between an average of 48 and 82 pairs during the five-year study period. During the remainder of the year, the average breeding density was significantly lower, ranging from 1 to 15 pairs (Mann–Whitney U test, $P < 0.05$; Fig. 2). The bulk of rainfall occurred 2–4 months prior to the peak in breeding. Little rainfall occurred in December (Fig. 2).

The density of breeding pairs fluctuated from year to year during our study. We observed a 76% increase in the annual density of breeding *N. nematopus* pairs from the 1990–91 breeding season to the 1991–92 breeding season, with smaller incremental increases throughout the remainder of the study (Fig. 3). Over the five-year period, the breeding population of *N. nematopus* increased by a total of 136%, and the breeding period expanded (Fig. 2). Breeding *N. nematopus* pairs with fry

were distributed from a depth of 1.5 m to 28.5 m at Site A, with an average depth of 7.7 ± 0.2 m. Over 90% of breeding pairs were found above 10.5 m.

During the 1990–91 season, breeding was observed from November to March, with approximately 51% of the total estimated breeding taking place in December. In 1994–95, however, the breeding season expanded to cover the full year, with only 31% of the total estimated breeding taking place in December (Fig. 2). This expansion of breeding outside the peak occurred gradually over the five-year study period.

2.2 Sizes of reproductive individuals

A total of 76 non-territorial individuals were captured by gillnet to determine the potential size of reproductive males and females. Of these, 44 individuals (24 females and 20 males) were reproductive. The smallest reproductive female was 31 mm SL, which was the same size as the smallest paired female (see pair formation below). The smallest male (22 mm) with sperm-producing testes was, however, half the size of the smallest paired male (Fig. 4). The remaining 32 individuals sampled were non-reproductive and ranged in size from 18 mm to 65 mm SL.

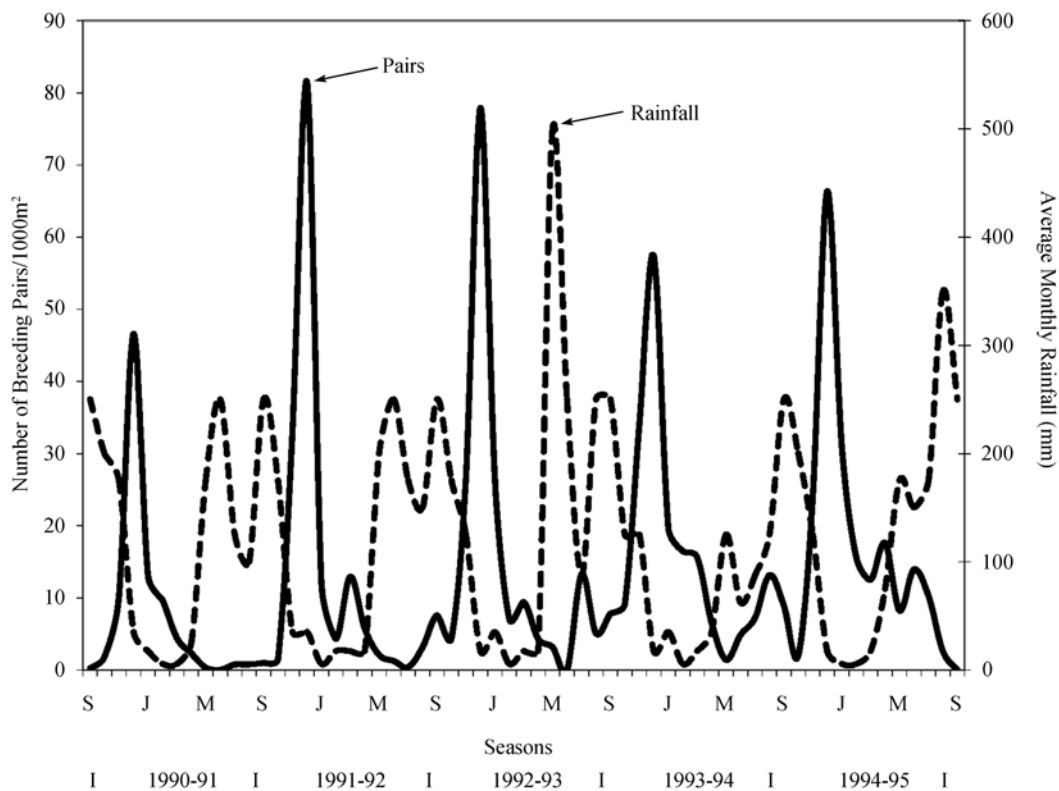


Fig. 2 The breeding seasonality of *N. nematopus* (solid line) from September 1990 to September 1995 with average monthly rainfall (dashed line).

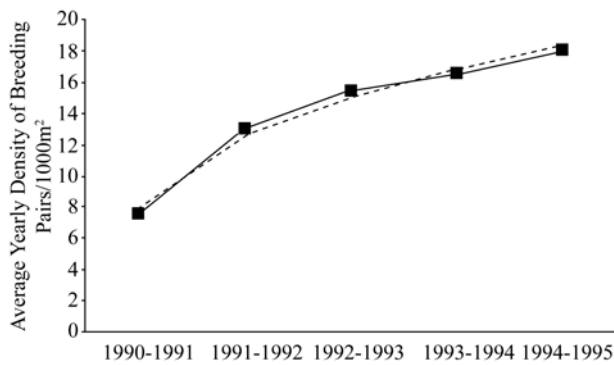


Fig. 3 The average yearly density of breeding *N. nematopus* pairs. Dashed line is logarithmic fit ($r^2 = 0.89$).

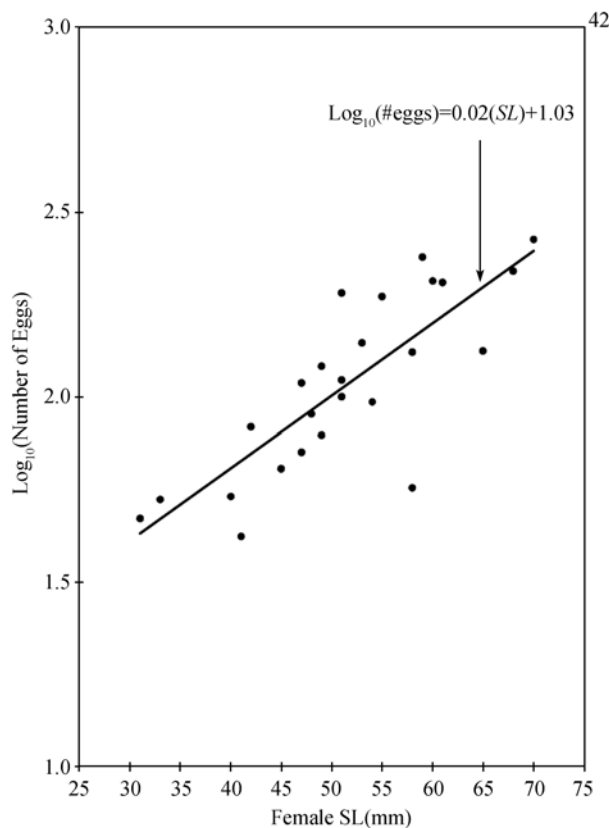


Fig. 4 Size distribution of reproductively mature males. Territory-holding males ($n = 261$) were paired with females, while non-territory holding males ($n = 20$) were unpaired and captured by gillnets.

Small mature males were observed on occasion near nests of breeding pairs in the territorial stage (i.e., prior to egg deposition). During four observations on breeding pairs, small individuals that remained near a territorial pair were captured and the gonads examined. In all four cases, the small individual contained mature testes.

The average female ($n = 25$) fecundity was 124 ± 13 eggs. The average SL of sampled females was 51.4 ± 2.0 mm. As few as 42 mature eggs were found in a 41

mm SL female weighing 2.5 g, while the maximum number of mature eggs was 267 for a 70 mm SL female weighing 10.5 g. Fecundity increased as maternal size increased ($\log_{10}(\text{number of eggs}) = 0.02(\text{SL}) + 1.03$, $f_{1,23} = 43.35$, $r^2 = 0.64$, $P < 0.01$).

2.3 Pair formation

Mean SLs for paired males and females were 70.2 ± 0.5 mm (44 – 95 mm) and 50.9 ± 0.6 mm (31 – 77 mm), respectively ($n = 261$ pairs). Breeding pairs of *N. nematopus* were sexually dimorphic in size, with males being the larger sex (two-tailed t -test: $t_{520} = 25.7$, $P < 0.01$). Paired females were, on average, 73% the length of their male counterparts. The average wet masses for territorial males and females were 12.2 ± 0.3 g (5.5 – 26.3 g) and 4.8 ± 0.2 g (1.0 – 10.5 g), respectively ($n = 138$ pairs). The average paired female was 39% the mass of her mate. We established a length–mass relationship for male and female *N. nematopus* of $\log(\text{mass}) = 0.02(\text{SL}) - 0.15$ ($F_{1,136} = 1319.7$, $r^2 = 0.91$, $P < 0.01$) and $\log(\text{mass}) = 0.02(\text{SL}) - 0.67$ ($F_{1,136} = 2226.9$, $r^2 = 0.94$, $P < 0.01$), respectively.

N. nematopus exhibited size–assortative mating. ($F_{1,259} = 195.2$, $r^2 = 0.66$, $P < 0.05$). The slopes between the 1972–74 study and our 1995–97 study did not differ significantly (Fig. 5). We did find, however, that the y -intercepts for the two regression lines were significantly different between the two studies (Fig. 5). Females in 1995–97 paired with smaller males as compared to similarly sized females in 1972–1974.

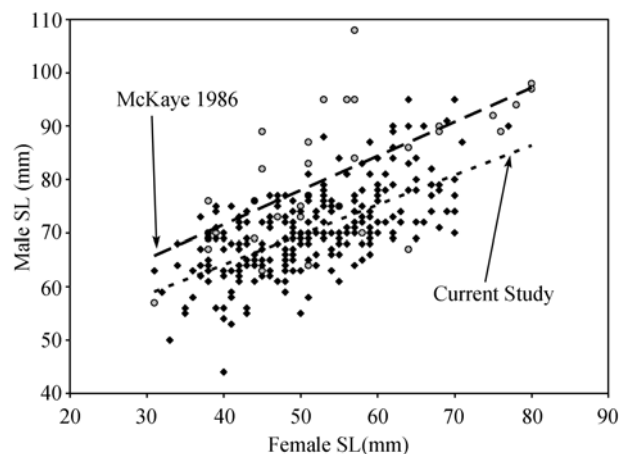


Fig. 5 The temporal variation in size–assortative mating relationships of *N. nematopus* from McKaye 1986 and the current study. The slopes of the two lines did not differ significantly (two-tailed t -test, $t_{295} = 0.27$, $P > 0.05$), but the y -intercepts did differ between the two lines (two-tailed t -test, $t_{296} = 7.68$, $P < 0.05$).

2.4 Reproductive success

We monitored a total of 503 breeding pairs for brood success during the 1995–97 sample periods. Approximately 85% of the pairs had fry that emerged from the nesting cavity (i.e., survive the egg and wriggler stages). Approximately three out of ten pairs that laid eggs had young that survived to three weeks of age (Table 1).

Table 1 Temporal variation in brood success. Total brood success was determined by integrating the pre-fry (egg and wriggler stages) with that of fry < 3 weeks of age.

Year	<i>n</i>	Pre-fry (%)	Fry < 3 weeks (%)	Brood success (%)
1995–97	503	85.3	34.7	29.6
1973 ^a	22	80.0	47.3	37.8

^adata modified from McKaye (1977). Total brood success was determined by integrating the pre-fry (egg and wriggler stages) with that of fry < 3 weeks of age.

Mean clutch size of pairs observed in artificial nests was 104 ± 9 eggs ($n = 50$). The mean number of emerging fry in all broods observed at age 1 – 3 days decreased by 44% to 57.8 ± 3.2 fry ($n = 114$ broods). The average number of fry in broods at 19 – 21 days of age was 32.0 ± 3.4 fry ($n = 31$ broods). The mean number of fry per surviving brood began to increase after 19 – 21 days due to the adoption of foreign fry. The average age at which fry dispersed from surviving broods was 27 ± 1 day ($n = 23$).

Fry and brood survivorship curves were constructed from the 114 broods followed throughout the fry stage. By age 7 – 9 days, approximately 50% of the fry were missing (Fig. 6A). Brood survivorship (when there was no adoption) decreased at a constant rate during the first three weeks, with an average brood loss of $12\% \pm 1\%$ ($n = 7$) between the age classes (Fig. 6B).

Finally, we examined the relationship between brood success and parental size. We determined that the mean SL of paired males and females with young less than three weeks of age was 67.7 ± 0.6 mm and 47.8 ± 0.8 mm, respectively ($n = 108$), while the mean SL of successful breeding pairs (fry \geq three weeks of age) was 69.8 ± 1.0 mm and 49.8 ± 1.4 mm, respectively ($n = 38$). Successful breeding pairs of *N. nematopus* did not differ significantly in size from unsuccessful breeding pairs (Mann–Whitney *U* test; males: $U = 1746.0$, $P > 0.05$; females: $U = 1739.5$, $P > 0.05$).

3 Discussion

Our data demonstrated a consistent unimodal breeding peak in December for *N. nematopus* over a five-year period. This breeding peak differed dramatically from the bimodal breeding season hypothesized previously (McKaye, 1977). This change in breeding peaks was also found in all other Lake Xiloá cichlids (Schweighofer, 1999; Murry et al., 2001; van den Berghe and McKaye, 2001; Vivas and McKaye, 2001; 2002; McKaye et al., 2002). McKaye et al. (2002) found that the peak breeding period of *A. citrinellus* complex, consisting of three sympatric species, *Amphilophus xiloensis* (Stauffer and McKaye, 2002), *Amphilophus sagitae* (Stauffer and McKaye, 2002), and *Amphilophus amarillo* (Stauffer and McKaye, 2002), also occurred during December, which differed from the previously reported peak of July and August (McKaye, 1977). These three species did, however, have a minor breeding peak during these latter two months (McKaye et al., 2002). Our data indicate that a dramatic change in the breeding seasonality of this cichlid community has occurred within the past two decades.

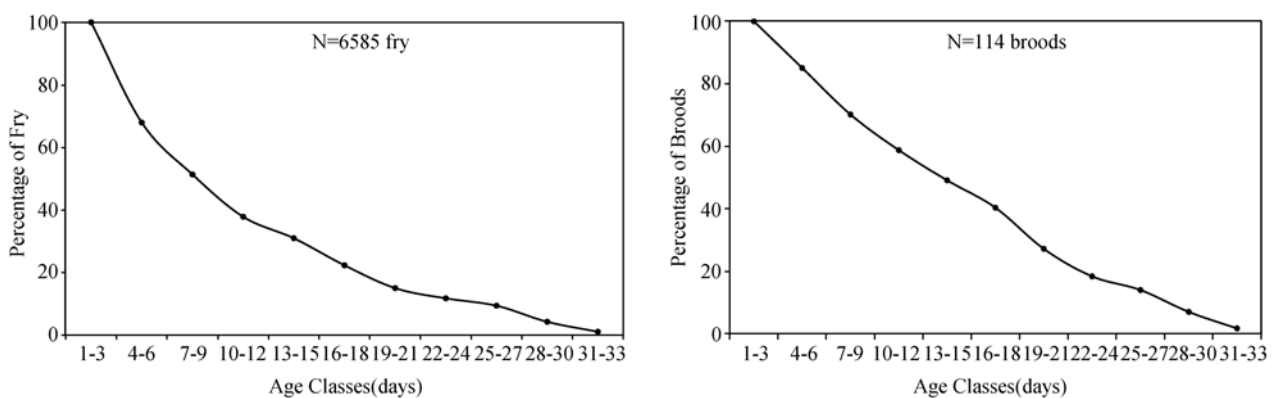


Fig. 6 The fry survivorship curve (A) and brood survivorship curve (B) of *N. nematopus*. The ages of the young are given in days as free-swimming fry.

A comparison of the peak breeding densities of *N. nematopus* between the two studies demonstrated a substantial decline in breeding. McKaye (1977) reported that approximately 55 pairs of *N. nematopus* per 1000 m² bred during both observed breeding peaks (July to August and February to March). These two peak densities differed substantially from the approximately 8 pairs per 1000 m² ± 1 pair ($n = 20$ months) observed during the same four months of the current study. If we examine, however, our average density of breeding fish during the peak in December (66 pairs/1000 m²) and the total of McKaye's two peak breeding periods (56 pairs/1000 m² and 54 pairs/1000 m²), then the current study demonstrates a 40% reduction in breeding. This is only true if the hypothesized lull during October through January is accurate. The potential exists, however, that McKaye (1977) observed the tail ends of a unimodal breeding season for *N. nematopus* that extended from August to February. If this were true, then the reduction in breeding would be substantially higher than 40%.

The expansion of the breeding season in the current study lends support to the extended unimodal breeding season, but why did the breeding season of *N. nematopus* lengthen? Our data demonstrated a rapid increase in the average annual density of breeding pairs between the 1990–91 and 1991–92 seasons, with smaller increases during subsequent seasons. The 176% increase in breeding between the first two seasons might be explained by the termination of grenade fishing practices within Lake Xiloá at the end of 1990. During the 1980s, individuals frequently threw grenades into shallow sections of the lake to collect fish more quickly than possible with traditional techniques (personal observation). This grenade fishing severely impacted all fishes that occur and/or breed above 10 m in depth, since the explosions killed both adult and young fishes. Since 90% of all breeding *N. nematopus* occur above 10.5 m, this species was extremely susceptible to grenade fishing practices, and the termination of such practices is the likely explanation for the sharp increase in breeding density. This dramatic increase might have played a role in the expansion of the breeding season.

The observed variation in the length of the breeding season could be the result of several abiotic factors. An influx of nutrients into the lake due to abnormally high rainfall could have stimulated the production of plankton, which is a main source of food for the fry and adults of many cichlids (Barlow, 1974; Lowe-McConnell, 1979; McKaye, 1984). Rainfall, however, was

fairly consistent throughout this study and does not seem to explain the increase in breeding season length (Fig. 2). Wind currents are also known to affect plankton production within deep tropical lacustrine systems (Lowe-McConnell, 1979). Unfortunately, wind speed data were not available for Lake Xiloá. Other abiotic factors such as photoperiod and water temperature are unlikely to produce such variation in the length of the breeding season, as year-to-year variation is small within tropical systems (Lowe-McConnell, 1979).

Within the breeding season, *N. nematopus* exhibited size-assortative mating (McKaye, 1986; this study). A significant change in the size of paired males was evident, however, between these studies. During the 1970s, for example, a 50 mm SL female paired with a 78 ± 2 mm SL male, while the same size female in the current study paired with a 70 ± 1 mm SL male. The shift in male size might be due to the different locations and/or substrates within the lake examined by the two studies. McKaye's (1986) study was conducted at Site A, while the current study collected the majority of breeding pairs at Site E. Site A is a fairly vertical rock face where nest sites are limited to natural holes or cracks in the solid rock. Site E, on the other hand, is a gently sloping outcropping of rocks strewn across a sandy bottom, where nest cavities can be excavated in the numerous crevices between the rocks. Paired males collected near Site A during the current study were noticeably larger (63 – 90 mm SL) than paired males at Site E (50 – 79 mm SL). The same trend holds true for females (Site A: 40 – 77 mm SL; Site E: 33 – 70 mm SL), but the difference is less pronounced. We believe that the difference in male and female size between areas of the lake could be due to either greater food availability and/or increased competition for breeding areas at Site A. These two hypotheses have yet to be examined quantitatively.

Often, larger pairs of cichlids gain a reproductive advantage because they provide more effective parental care (Perrone, 1978; McKaye, 1986; Alonzo et al., 2001). Our study, however, found no correlation between brood success and parental size in *N. nematopus*. Varying results on this relationship have been observed in the convict cichlid, *Archocentrus nigrofasciatus* (Keenleyside, 1985; Wisenden 1994; Alonzo et al., 2001). Such a correlation might be dependent on breeding heterospecifics within each individual ecosystem. Smaller species like *N. nematopus* and *A. nigrofasciatus* are likely to benefit from breeding synchronously in and around larger species via cooperative defense against predators (McKaye, 1984).

In summary, our data demonstrate a dramatic change in the breeding seasonality of *N. nematopus* over a 25-year period. The effects of extensive grenade fishing practices during the 1980s likely played a substantial role in the observed change. The balance between divergent selection due to competition for breeding sites and stabilizing predation pressure on offspring might determine the breeding seasons within this cichlid community (Schweighofer, 1999; Alonzo et al., 2001; Murry et al., 2001; van den Berghe and McKaye, 2001; Vivas and McKaye, 2001; 2002; McKaye et al., 2002). This hypothesis will require further testing in Lake Xiloá and other cichlid communities.

Acknowledgments We would like to thank the Universidad Centroamericana, Ave Maria University, the Nicaraguan Ministry of Natural Resources, and the Nicaraguan armed forces for their support. Several people aided in the fieldwork and improvement of this manuscript: B. Murry, R. Vivas, J. Hoogland, R. Raesly, D. Shumway, M. Sweighofer, R. Chang, N. Checker, G. Bachman, and A. Aspbury. Most importantly this work was stimulated by K.R. McKaye's experience as an undergraduate in caring for *N. nematopus* in Dr. George W. Barlow's laboratory and Dr. Barlow's curiosity to know more about the natural history of this species. This research was funded in part by the National Science Foundation, the United States Agency for International Development, and the Fulbright program to KRM and EvdB.

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