Quasi-cycles in crappie populations are forced by interactions among population characteristics and environment

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Abstract: Crappie (Pomoxis spp.) populations have been characterized as cyclic, with strong year-classes recurring at 2- to 4-year intervals. We evaluated the potential for cyclic trends in crappie populations using a population model that included a density-dependent stock recruitment function and random environmental variation. Slow, medium, and fast growth were simulated over 100 years. The model predicted highly variable recruitment that was strongly influenced by environmental fluctuation at low and intermediate stock densities. At high stock density, recruitment was low, even if environmental conditions were favorable. Significant quasi-cycles occurred, but they were not sustained throughout the time series due to random environmental fluctuation. Quasi-cycles occurred because intermediate stock density and favorable environmental conditions occasionally combined to produce a very strong year-class that greatly increased stock density in the following 1–3 years and produced low recruitment, even if environmental conditions were favorable. Empirical data from 32 years of sampling age-0 crappies at Ross Barnett Reservoir showed trends similar to the simulated fluctuations. We conclude that crappie populations likely do not exhibit true cycles but may show quasi-cycles as a result of the interaction between random fluctuations in environment and density-dependent mechanisms. The frequency of such quasi-cycles may be enhanced by rapid growth and high exploitation.

Résumé : Les populations de mariganes, Pomoxis spp., ont été définies comme cycliques, avec des classes d’âge plus importantes réapparaissant à des intervalles de 2-4 ans. Un modèle de population qui inclut une fonction de recrutement du stock dépendante de la densité et une variation aléatoire de l'environnement a permis d’évaluer l’existence de tendances cycliques chez les mariganes. Des croissances lentes, moyennes et rapides ont été simulées sur des périodes de 100 ans. Le modèle prédit, aux densités basses et intermédiaires de stock, un recrutement très variable qui est influencé par les fluctuations environnementales. Aux fortes densités, le recrutement est faible, même lorsque les conditions environnementales sont favorables. Il y a des quasi-cycles significatifs, mais ils ne se maintiennent pas au cours de séries temporelles à cause de la fluctuation aléatoire de l’environnement. Ces quasi-cycles apparaissent parce que la combinaison occasionnelle d’une densité moyenne du stock et des conditions favorables du milieu génère une classe d’âge beaucoup plus importante qui augmente la densité du stock pendant les 1–3 années subséquentes et donne lieu à un faible recrutement, même en présence de conditions environnementales favorables. Des données empiriques prouvent de 32 années d’échantillonnage de mariganes d’âge 0 au réservoir Ross Barnett montrent des tendances semblables aux fluctuations simulées par le modèle. En conclusion, les populations de mariganes ne subissent vraisemblablement pas de vrais cycles, mais elles affichent des quasi-cycles qui résultent de l’interaction entre les fluctuations aléatoires de l’environnement et les mécanismes dépendants de la densité. La fréquence de tels quasi-cycles peut être accrue par une croissance rapide et une forte exploitation.

[Intaduit par la Rédaction]

Introduction

Some of the most intriguing examples of fluctuations in animal abundance are population cycles. Classic examples of cycles in abundance exist for mammals and bird populations (reviewed by Begon et al. 1996). Population cycles also occur in fish populations (Townsend 1989; Myers et al. 1998). Suggested mechanisms for cycles include delayed density-dependent interactions between recruits and stock fish (e.g., intraspecific competition for food, cannibalism) (Ricker 1997; Sanderson et al. 1999), chronic fluctuations in reproductive output based on age at first breeding by adults (Townsend 1989; Ricker 1997), and the interaction of stochastic processes with fishing mortality (Myers et al. 1998). Begon et al. (1996) noted that populations often do not show perfect cycles but may show a tendency toward cyclic population patterns.

Crappie (Pomoxis spp.) populations are often major components of fish assemblages in North American lakes and reservoirs. Population densities of crappies have been characterized as cyclic (Thompson 1941; Swingle and Swingle 1967), with strong year-classes recurring every 2–5 years.
Crappie recruitment dynamics may be erratic with irregular circular patterns that lead to fisheries often characterized as “boom and bust” due to fluctuations in yield. Fluctuations have been attributed to density-dependent and density-independent factors. Several authors have reported that high fish density can reduce population fecundity and age-0 fish survival due to intraspecific competition (e.g., Swingle and Swingle 1967; Guy and Willis 1995) or cannibalism (Thompson 1941). Other authors have ascribed population fluctuations to variability in environmental conditions such as water level and water retention time (e.g., Guy and Willis 1995; Maceina and Stimpert 1998) and to variable angler exploitation among years (Webb and Ott 1991). We suspect that fluctuations are driven by the interaction within and among density-dependent and density-independent factors and that the unpredictability of the fluctuations is a function of the strength of the interactions, which vary over time and space (Allen and Miranda 1998).

Simulation models have been useful for evaluating population cycles (Townsend et al. 1990; Myers et al. 1998). Because long-term data (i.e., >30–50 years) from fish populations are rare, models allow for the investigation of potential long-term trends in population abundance emerging from the interaction of density-dependent and density-independent effects. We used a population model to simulate fluctuations in crappie populations. Our objective was to identify the mechanisms that might drive fluctuations in crappie population abundance.

**Methods**

We used an age-structured population model to simulate a white crappie (*Pomoxis annularis*) population. The age-structured model increased biomass of the population by age-specific somatic growth, reduced population abundance by age-specific natural, fishing, and hooking mortalities, and increased abundance by recruitment to age 1. The model simulated density-dependent responses of growth, natural mortality, and recruitment. Additionally, recruitment was modified by a random function that simulated environmental fluctuations. The model divided each year into three 4-month periods (February–May (period 1), June–September (period 2), October–January (period 3)) to simulate seasonal variations in population parameters. Below, we briefly describe the model (details are given in Allen and Miranda 1998) and the data used.

**Growth**

We modeled slow, medium, and fast growth representing 1 SD below the mean, the mean, and 1 SD above the mean growth of crappie in a data set of 65 lake-years compiled by Allen and Miranda (1995). Because seasonal growth increments for crappies were not available, we used estimates published for bluegill (*Lepomis macrochirus*) (Moyle and Cech 1988) and assigned 0.2 of annual growth to seasonal period 1, 0.5 to period 2, and 0.3 to period 3. Density-dependent growth was modeled as a decaying exponential function of stock density fit to empirical data from Ross Barnett Reservoir, Mississippi, described by Allen and Miranda (1998). The model assumed that all fish of a given age were of the same length and that there was no gender-specific growth rate, as none was reported in an extensive review conducted by Carlander (1977).

**Initial population density and age structure**

The population density and age structure used to initiate simulation experiments were derived by applying annual mortality to the average numerical density (34 ha⁻¹) of adult white crappies longer than 20 cm in Ross Barnett Reservoir (1963–1994). In this reservoir, white crappies usually reach 20 cm and enter the fishery by age 3 (T. Holman, Mississippi Department of Wildlife, Fisheries and Parks, P.O. Box 451, Jackson, MS 39205, U.S.A., unpublished data). Given 0.3 annual natural mortality and density of fish age 3 and older, we adjusted density to include age-2 fish ([34/(1 - 0.3)] = 49) and age-1 fish (49/(1 - 0.3) = 70) in the population density estimate. We distributed the 70 fish across ages 1–7 according to existing annual mortality rates.

A 10-year period of instability in population density and structure occurred when simulations began. This instability resulted from the stable age distribution’s adjustment to the applied rate of recruitment and mortality. After this period of instability, the populations formed a new, stationary age distribution. Results exclude the 10-year instability period.

**Recruitment function**

Recruitment to age 1 was modeled with a dome-shaped curve identified by empirical data to best describe the relationship between density of crappie stocks and recruitment (Allen and Miranda 1998). The curve was characterized by (Ricker 1975)

\[
R = \frac{Se^{a(l-S/5R)(1-vd)}}{1-vd}
\]

where \( R \) is recruits (number of age-1 fish), \( S \) is stock (number of fish older than age 1), \( a \) is the coefficient of density dependence determining the shape of the curve (\( a = 2.901 \)), \( SR \) is the number of stock fish (older than age 1) when \( S = R (SR = 70) \), \( v \) is mortality between samples taken at a fixed time period in the first year of life and the same period in the second year (\( v = 0.68 \), as per Allen and Miranda 1998), and \( d \) is a random deviate.

The effect that random environmental fluctuations may have on recruitment was evaluated by varying \( v \) through \( d \). A random number generator produced normally distributed values of \( d \) with mean = 1 and SD = 0.6. We used 0.6 as the standard deviation because it emulated, both in magnitude of variation and in periodicity, recruitment dynamics of crappies in four reservoirs examined by Allen and Miranda (1998). Effects of environmental variation alone were evaluated by setting \( a = 0 \) in eq. 1 and effects of density-dependent recruitment alone by setting \( d = 1 \). Simulated populations that fluctuated due to random environmental conditions and those that fluctuated due to density-dependent recruitment were compared with those that fluctuated due to both.

**Exploitation**

We used the average exploitation rate (\( \mu = 0.42 \)) for white crappies from Allen and Miranda (1995). Distribution of \( \mu \) among periods within each year was estimated from year-long harvest surveys made at Ross Barnett Reservoir (Allen and Miranda 1998). The surveys indicated that 58, 19, and 23% of the annual crappie harvest occurred during periods 1, 2, and 3, respectively. Given that 58% of the harvest occurred in period 1, an annual exploitation of 0.42 would result in \( \mu_{period 1} = 1 - e^{-0.385} \). Correspondingly, \( \mu_{period 2} \) was estimated at 0.10 and \( \mu_{period 3} \) at 0.12 for the mean \( \mu \) of 0.42. Exploitation was applied only to fish 20 cm and longer.

**Natural mortality**

Annual natural mortality estimates averaged about 0.3 for white crappie populations (Allen and Miranda 1995). No data were available concerning seasonal fluctuations in natural mortality. Therefore, natural mortality rates were assumed to be 0.11 in each of the three periods (i.e., \( 1 - e^{-0.33} \)). Density-dependent natural mortality was modeled as a rising exponential function of stock density fit to empirical data from Ross Barnett Reservoir and illustrated by Allen and Miranda (1998). The model described the proportion of average natural mortality achieved as a function of stock density. Random fluctuations in natural mortality of stock fish were
incorporated by varying mortality with a normally distributed random deviate with 0.6 SD.

Hooking mortality

Hooking mortality of fish that had to be released because they were smaller than the length limit was estimated from the literature. Hubbard and Miranda (1989) found 3% hooking mortality when white crappies were caught from shallow water (1.2 m), but mortality rates as high as 67% occurred when fish were raised from 16 m to the surface. Muneneke (1992) reported 9% hooking mortality of white crappies caught out of a reservoir. We arbitrarily used 10% hooking mortality of released fish during each period for all simulations.

Analyses

We conducted 100-year simulations for each level of growth. The number of recruits to age 1 and adult abundance (number of age 2 and older fish in the population) were recorded for each year. To assess whether modeled recruitment dynamics were completely random or contained serial autocorrelations (e.g., cycles or patterns), we used the Ljung–Box test (Ljung and Box 1978) using procedure ARIMA (SAS Institute, Inc. 1996). If the Ljung–Box test was significant, we conducted simple time series analyses described by Potts et al. (1984) to identify patterns. Cyclic patterns should contain positive autocorrelations among peaks (e.g., years 4, 8, 12, etc.) and negative autocorrelations for troughs (i.e., years 2, 6, 10, etc.) (Potts et al. 1984). We constructed correlograms to assess patterns in recruitment (Potts et al. 1984). Autocorrelations at each lagged year were tested for significance (P < 0.05) using procedure ARIMA (SAS Institute, Inc. 1996).

We also tested whether selected environmental conditions tended to be cyclic and potentially impart cyclicity on fish populations. For this, we used temperature and precipitation data recorded annually during February–May of 1930–1992 at a weather station operated by the Mississippi Agricultural Experiment Station, Starkville, Miss. Temperature represented the mean of minimum values recorded daily during the February–May period and precipitation the total for each period. We chose temperature because it can influence factors such as time of spawning, length of growing season, and food availability and precipitation because it can influence discharge and lake levels and thereby the entire aquatic ecosystem. The Ljung–Box test was used to examine whether temperature and precipitation time series were completely random or contained serial autocorrelations.

Recruitment data from 32 years of sampling at Ross Barnett Reservoir (described in Allen and Miranda 1998) were used as reference to assess if the simulated populations resembled empirical data. The Ljung–Box test was applied to examine whether density of white crappies in the reservoir exhibited serial autocorrelations over the 32-year period. If so, the time series analysis described earlier was used to characterize patterns that were compared qualitatively with those of the simulated populations. The purpose of this analysis was not to identify whether the simulated population closely tracked the Ross Barnett empirical data but to verify that the simulations were realistic.

Results

Intensity of simulated recruitment to age 1 was influenced by the interaction of density-dependent and density-independent factors (Fig. 1). When environmental effects were held constant and recruitment was allowed to vary in response to density dependence, recruitment averaged 83 fish-ha$^{-1}$ and ranged from 61 to 96 fish-ha$^{-1}$. Conversely, when environment was varied at random and the density-dependence function held constant, recruitment averaged 76 fish-ha$^{-1}$ and ranged from 19 to 184 fish-ha$^{-1}$. When environmental fluctuation and density dependence were allowed to interact, recruitment averaged 87 fish-ha$^{-1}$ and ranged from 0 to 257 fish-ha$^{-1}$. Recruitment was random when environment was varied at random (Ljung–Box tests, P = 0.33) and not random when density dependence but not environment (P < 0.001) or density dependence together with environment (P < 0.001) controlled fluctuation.

Stock density influenced the intensity of recruitment fluctuation (Fig. 2). Simulated recruitment was highly variable at low and intermediate stock densities (<100 adults-ha$^{-1}$) but was <50 recruits-ha$^{-1}$ at stock densities >150 adults-ha$^{-1}$ (Fig. 2). At low and intermediate stock densities, environmental variation caused highly variable recruitment, suggesting that although the potential for a strong year-class existed, environmental conditions determined the magnitude of recruitment. Conversely, at high stock densities, recruitment was low, even though environmental conditions were random (i.e., sometimes favorable).

Recruitment fluctuated greatly among years, with strong year-classes recurring every 2–10 years (Fig. 3). Moderate peaks in recruitment were usually followed by 1–2 years of reduced recruitment, whereas strong peaks in recruitment were usually followed by very low recruitment in the following 1–2 years (Fig. 3). This occurred because intermediate stock density and favorable environmental conditions coincided to produce a strong year-class, which greatly increased stock density in the following year and led to low recruitment through density-dependent processes, even if environmental conditions were favorable. Minor changes in recruitment did not greatly affect stock density in subsequent years, often resulting in less variable recruitment for 1–2 years.

Rate of growth also influenced dynamics of recruitment (Fig. 3). Recruitment was not random in models containing density-dependent recruitment for any level of growth (Ljung–Box tests, all P < 0.001) and contained autocorrelations. Correlograms for the slow-growth model exhibited a significant, negative autocorrelation with 1- and 2-year lagged values and then an irregular pattern of alternating positive and negative autocorrelations in 2- to 4-year intervals. Autocorrelations were not significant through the entire time series (Fig. 3) but were significant (P < 0.05) at lag years 1, 2, and 12 and marginally significant (P < 0.10) at lag years 4, 10, and 13. The medium growth showed a similar pattern of alternating irregular negative and positive autocorrelations at 2–4 years with significant correlations at lag years 1 and 12 and marginally significant correlations at lag years 8 and 11. Conversely, the fast-growth model showed regularly alternating negative and positive autocorrelations, suggesting significant 2-year cycles. However, the fast-growth correlogram was "damped," with autocorrelations becoming nonsignificant through time (Fig. 3).

Empirical recruitment data for 32 years at Ross Barnett Reservoir showed highly variable recruitment with apparent oscillations (Fig. 4). Recruitment was not random as evidenced by the significant (P = 0.005) Ljung–Box test. The correlogram exhibited a general trend of alternating positive and negative autocorrelations at 2- to 3-year intervals with significant positive autocorrelations at lag years 1, 5, and 6 (Fig. 4).

Environmental variation showed both random and nonrandom trends. Precipitation during February–May of 1930–
Fig. 1. Simulated crappie recruits to age 1 for models containing both density-dependent recruitment and environmental variation, only environmental variation, and only density-dependent recruitment. All simulations are run with the medium growth rate.

Fig. 2. Density of crappie recruits to age 1 plotted against density of adults (age 2 and older) for all simulations. Simulations with fast (circles), medium (squares), and slow (crosses) growth rates are shown.
Fig. 3. Simulated time series of crappie recruits to age 1 for (A) slow, (B) medium, and (C) fast growth rate models. Panels to the right are autocorrelations in recruitment plotted against lag year for each simulation. Bars reaching the horizontal lines are significant autocorrelations ($P < 0.05$). Statistical power decreased with increasing lag year due to changes in sample size, resulting in changes in the position of the horizontal lines.

Recruits to age 1 (N/ha$^{-1}$)

A

B

C

Year

Lag year

1992 did not differ from completely random (Ljung–Box test, $P = 0.92$). However, temperature patterns across the same time period were not random (Ljung–Box test, $P = 0.02$), but alternating positive and negative autocorrelations in temperature were not evident from a correlogram.

Discussion

Our model predictions at medium and slow growth appeared similar to recruitment dynamics at Ross Barnett Reservoir, with trends of 2–3 years of low recruitment usually followed by 2–3 years of strong recruitment. Growth rates at Ross Barnett Reservoir produced harvestable-size white crappies (20 cm total length) around age 3, similar to the medium growth rate that we modeled. Although our model exhibited recruitment dynamics that resembled those seen at Ross Barnett Reservoir, a perfect match was not expected because a number of factors not considered by our model also influence crappie dynamics. For example, environmental variation was assumed to be random. A test of this assumption showed that while rainfall appeared to be random during 1930–1992 at a station not far from Ross Barnett
Reservoir, temperature was not random and could have contributed to shape patterns in white crappie population dynamics. Moreover, the model assumed constant exploitation over years, yet exploitation may also be cyclic where anglers abandon the fishery when catch rates decline and return after a strong year-class grows to maturity (Webb and Ott 1991). Conceivably, $u$ has its own dynamics including lag periods where it exceeds average because interest in the fishery has not adjusted to the exhaustion of a strong year-class, or vice versa. Because no data were available to incorporate the dynamics of exploitation into our model, the model considered none of these potential interactions, yet it seemed to adequately sketch recruitment dynamics of white crappies in Ross Barnett Reservoir.

Truly cyclic populations have shown serial (i.e., repeated patterns) autocorrelations that are significant for up to 30 years (Begon et al. 1996). Data from our model and Ross Barnett Reservoir did not exhibit serial autocorrelations throughout the time series, suggesting that the actual and simulated crappie populations did not exhibit true cycles. Begon et al. (1996) termed such populations as "quasi-cyclic," where the time series exhibits a periodic tendency that does not persist, or tends to damp, due to disturbances caused by erratic environmental variation. Quasi-cycles resulted because years of very high recruitment increased stock density to produce low recruitment the following 1 year (fast growth) or 2–3 years (slow and medium growth), even if environmental conditions were favorable. The fast-growing white crappies showed significant 2-year quasi-cycles that became nonsignificant after a lag of 4 years, whereas the slow- and medium-growth populations exhibited quasi-cycles that, although they did not damp, were not serial (i.e., consistently significant throughout the time series). Damping was not evident because reduced growth protected a strong year-class from harvest and thereby helped stabilize stock abundance, yet fluctuations were not precisely serial because the next strong year-class had to await irregular periods for favorable environmental conditions. Two-year quasi-cycles under fast growth resulted because fish became harvestable at age 2 (20 cm total length), which quickly subjected a strong year-class to harvest, reduced stock abundance, and resulted in a high probability of strong year-classes at 2-year intervals. Thus, rapid growth could shorten the periods between peaks in recruitment and result in more frequent quasi-cycles.

Similar to our simulation of fast-growing white crappies, Cryer et al. (1986), Wyatt (1988), and Townsend and Perrow (1989) documented 2-year cycles in two roach (Rutilus rutilus) populations, but mechanisms for the cycles differed between populations (Townsend and Perrow 1989). In one lake, competition between age-0 and adult fish reduced growth and fecundity in years following good recruitment, resulting in high and low recruitment at 2-year intervals (Townsend and Perrow 1989). Age-0 and age-1 crappies are both zooplanktivorous (Mathur and Robbins 1971; O’Brien et al. 1984; Sạch et al. 1991), and thus, production of a strong year-class could potentially affect food availability for the succeeding year-class. Density-dependent growth of crappies has been documented frequently for young (Swingle and Swingle 1967; Allen and Miranda 1998) and adult fish (Schramm et al. 1985; Miller et al. 1990). Occurrence of a strong crappie year-class could potentially reduce growth and survival of a subsequent year-class if food availability were limited, which could lead to 2-year cycles due to competition between successive year-classes. Our model used a Ricker-type stock–recruitment curve but did not explicitly model competition between successive age-classes. Conversely, in a second lake, roach exhibited rapid growth and matured in 2 years, resulting in strong recruitment at 2-year intervals (Townsend and Perrow 1989). Similarly, our model exhibited 2-year quasi-cycles at the fast growth rate, but quasi-cycles were due to stock fish being exposed to harvest early, which reduced stock density to trigger another quasi-cycle.

Sanderson et al. (1999) found that combined density-dependent effects resulted in 5-year cycles for a yellow perch (Perca flavescens) population. Following production of a strong year-class, competition between age-0 and age-1 fish and cannibalism on age-0 fish prevented recruitment for about 5 years until the strong year-class became sexually
mature, when the cycle would repeat (Sanderson et al. 1999). Crappie population cycles due to cannibalism would likely result in cycles longer than 2 years because adults are not piscivorous until age 2 and older. However, cannibalism has seldom been documented as a regulatory factor in crappie populations (Thompson 1941), and our model did not consider cannibalism in determining recruitment.

Myers et al. (1998) found that high exploitation would intensify cycles in sockeye salmon (Oncorhynchus nerka) populations. Further simulations with our model also suggested that exploitation could influence cycles. Highly exploited crappie populations underwent rapid reductions in adult density, resulting in more frequent occurrence of quasi-cycles than simulations at low exploitation. However, periodicity of the cycles was not persistent throughout the time series, at high or low levels of exploitation. Random environmental fluctuations in our model apparently interacted with adult population density, and the influence of environment over density shifted periodically but randomly, forcing a damping in the autocorrelation.

Our model predicted that an interaction between stock density and environmental variation would combine to determine recruitment. Previous authors have attributed crappie recruitment fluctuations to independent effects of stock density (Swingle and Swingle 1967; Allen and Miranda 1998) and environment (e.g., McDonough and Buchanan 1991; Mitzner 1991; Maceina and Stimpert 1998). However, the lack of persistent cycles in simulated and empirical crappie populations underscores our contention that fluctuations are driven by both density-dependent and density-independent factors and that the unpredictability of the fluctuations is a function of the strength of the interactions, which vary over time. Density-dependent recruitment without environmental variation resulted in relatively minor recruitment fluctuations. Environmental variation greatly accentuated the occurrence and intensity of cycles, resulting in highly variable recruitment. We conclude that these cycles are likely not true cycles but instead are quasi-cycles resulting from the interaction between random fluctuations in environment and more predictable density-dependent mechanisms. The frequency of such quasi-cycles was influenced by growth rate and exploitation. Fishery managers should consider both environmental fluctuations and population density when addressing factors related to crappie recruitment dynamics.

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