

# Implications of compensatory and additive mortality to the management of selected sportfish populations

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## Abstract

The compensatory mortality hypothesis postulates that a population's total mortality remains unchanged at low to intermediate exploitation rates because natural mortality decreases to compensate for reduced density, whereas the additive mortality hypothesis postulates that any increase in exploitation mortality results in an increase in total mortality. Fishing and natural mortality rates have generally been assumed to be additive rather than compensatory. We reviewed mortality estimates for some prominent sportfish populations to identify evidence for compensatory or additive mortality. For largemouth bass *Micropterus salmoides*, total annual mortality increased with annual exploitation suggesting additive mortality. For crappies *Pomoxis nigromaculatus* and *P. annularis*, annual exploitation did not seem to affect annual mortality at low to moderate annual exploitation, but annual mortality increased with annual exploitation as it increased beyond 40%, conforming to the compensatory mortality hypothesis. Northern pike *Esox lucius* mortality estimates revealed no relation between annual mortality and annual exploitation, and highly variable annual mortality for a given annual exploitation. Evidence from the literature suggests that mortality of northern pike may be compensatory for fish smaller than 40 cm total length, but additive for larger fish. Because compensatory natural mortality reduces the managers' ability to control annual mortality, we suggest that further consideration of the compensatory mortality hypothesis be given to species that have shown variable mortality responses to reductions in annual exploitation.

## Key words

effects of fishing, fish mortality, fish populations, sportfish populations.

## INTRODUCTION

Two hypotheses about the effect of harvest on populations have been proposed (Anderson & Burnham 1976; see review by Nichols *et al.* 1984): (i) harvest and natural mortalities operate additively (additive hypothesis), and (ii) populations compensate for harvest mortality by reducing rates of natural mortality (compensatory hypothesis). Additive mortality results in an increase in total mortality with increasing harvest mortality (Figure 1). The compensatory mortality hypothesis suggests that total mortality remains unchanged at low to intermediate levels of harvest, but increases as

harvest mortality surpasses a compensation point (Anderson & Burnham 1976, Figure 1). Likewise, compensatory mortality may result in higher rates of natural mortality if harvest is reduced so that total mortality remains unchanged; thus, the mechanism for compensatory mortality is some form, or forms, of density-dependent population regulation. Populations near carrying capacity are more likely to be regulated by density-dependent (compensatory) processes, and populations at low density by density-independent processes (Bartmann *et al.* 1992). Hence, a population may exhibit additive mortality at low density and compensatory mortality at high density, but a continuum of escalating partial compensation between completely additive and completely compensatory mortality may also occur (Nichols *et al.* 1984; Conroy & Kremenetz 1990).

The compensatory mortality hypothesis of Anderson & Burnham (1976) considers compensation through reduced natural mortality of adults, not through reduced recruitment to adulthood. However, previous work with fishes has

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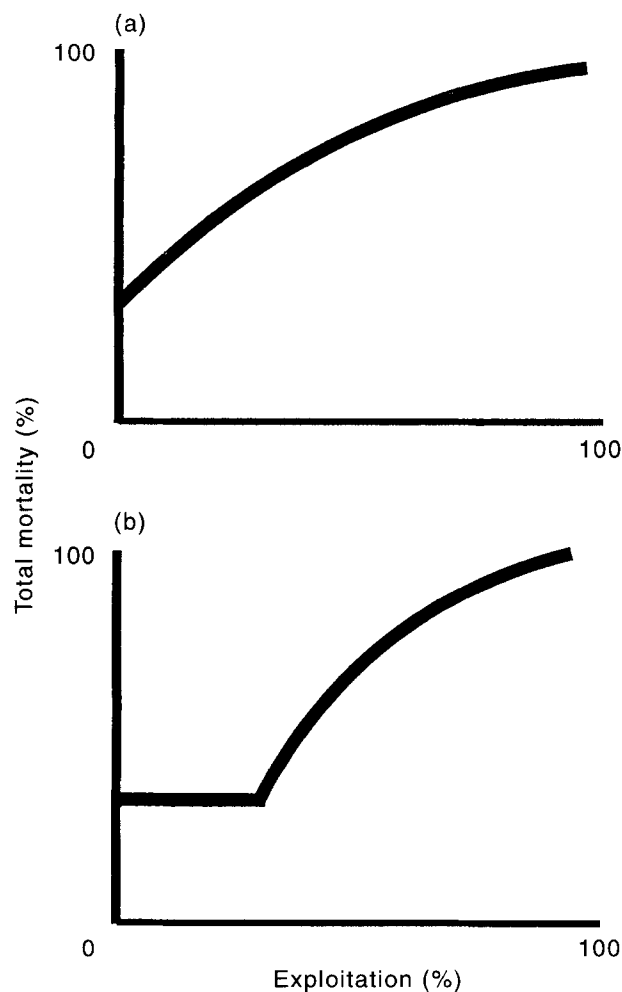
Accepted for publication 18 November 1997.

documented compensation through reduced recruitment (Lorda & Crecco 1987; Beverton & Iles 1992; Van Winkle *et al.* 1993; Rijnsdorp 1994). Goodyear (1980) and Shuter (1990) identified mechanisms for compensatory mortality in fishes, including high biotic potential, predation and starvation. They noted that these processes have the largest effect on fish populations during early-life stages because overall mortality is highest at that time.

However, exploitation and natural mortality rates for adult fishes have been assumed to be additive, and few studies have considered compensatory mortality for adult fishes (Youngs 1972 and Snow 1978 are exceptions). Thus, harvest restrictions for sport fishes are usually assumed to reduce total

mortality. However, if mortality is compensatory, little or no reduction in total mortality may occur. Therefore, harvest restrictions may be ineffective or their effect unpredictable.

The purpose of this paper is to encourage further consideration of compensatory mortality processes. Our approach was to examine the evidence for additive and compensatory mortality for black crappie *Pomoxis nigromaculatus*, white crappie *P. annularis*, largemouth bass *Micropterus salmoides*, and northern pike *Esox lucius* populations, and to discuss the additive and compensatory mortality hypotheses given case histories and the observed mortality trends across populations. We selected these species because they are important fisheries in North America, and because their mortality estimates have been reported often.



**Fig. 1.** Conceptual models of the relation between percentage total mortality and percentage exploitation under (a) the additive and (b) compensatory mortality hypotheses. The decelerating curve illustrates the reduced increase in annual mortality rate expected as annual exploitation rate captures a progressively larger proportion of the fish that would have otherwise been lost to conditional natural mortality rate.

### COMPENSATORY AND ADDITIVE MORTALITY MODELS

We used equations from Ricker (1975) for a type-2 fishery, in which fishing and natural mortality operate concurrently:

$$Z = F + M \quad (1)$$

$$A = 1 - e^{-Z} = u + v = m + n - mn \quad (2)$$

$$n = 1 - e^{-M} \quad (3)$$

$$m = 1 - e^{-F} \quad (4)$$

where:

$Z$  = instantaneous total mortality rate

$F$  = instantaneous fishing mortality rate

$M$  = instantaneous natural mortality rate

$A$  = actual annual total mortality rate (%)

$u$  = actual annual exploitation rate (mortality from fishing, %)

$v$  = actual annual natural mortality rate (%)

$n$  = conditional natural mortality rate, expected annual natural mortality rate in absence of fishing mortality (%)

$m$  = conditional fishing mortality rate, expected annual fishing mortality in absence of natural mortality (%)

We obtained estimates of annual exploitation and annual mortality from published reports identified through a computerized library search from the Fish and Wildlife Reference Service (1994) and from Wildlife and Fisheries Review (1995). We plotted annual mortality against annual exploitation and looked for trends like those identified in Figure 1. Theoretically, we expected the plot of annual mortality against annual exploitation to be direct and nonlinear (decelerating) if mortalities were additive (i.e.,  $n$  remained constant), because at high annual mortality further increases in annual exploitation could be achieved only through killing fish that were already going to die from natural causes.

Conversely, the plot was expected to be slopeless or nearly so if mortalities were compensatory. Our examination was qualitative and did not attempt to fit statistical models to the data. We did not test hypotheses concerning relations between annual exploitation and annual mortality because (i) regression analyses with these data may be biased because both annual exploitation and annual mortality were

measured with error (the result would be a flattening of the relationship between annual exploitation and annual mortality; (ii) mortality estimates across different populations may not represent a causal relationship between annual exploitation and annual mortality (Anderson & Burnham 1976); and (iii) for some species a sufficient number of exploitation estimates were not available over the range

**Table 1.** Annual mortality and annual exploitation rate estimates for largemouth bass populations. Estimates over successive years are means

Lake and location	Age interval	Year(s)	Annual mortality rate (%)	Annual exploitation rate (%)	Source
Whitmore, Minnesota	—	—	42	22	Cooper & Schafer (1954) <sup>a</sup>
Clear, California	—	1953	56	20	Kimsey (1957)
Browns, Wisconsin	—	—	24	12	Mraz & Threinen (1957) <sup>a</sup>
Sugarloaf, Minnesota	—	—	70	35	Cooper & Latta (1962) <sup>a</sup>
Sutherland, California	1–5	1956	68	20	La Faunce (1964) <sup>a</sup>
Sutherland, California	1–5	1957	78	40	La Faunce (1964) <sup>a</sup>
Sutherland, California	1–5	1958	73	47	La Faunce (1964) <sup>a</sup>
Sutherland, California	1–5	1959	55	35	La Faunce (1964) <sup>a</sup>
Merle Collins, California	—	1965	92	36	Rawstron & Hashagen (1972) <sup>a</sup>
Merle Collins, California	—	1966	71	45	Rawstron & Hashagen (1972) <sup>a</sup>
Merle Collins, California	—	1967	86	62	Rawstron & Hashagen (1972) <sup>a</sup>
Merle Collins, California	—	1968	76	65	Rawstron & Hashagen (1972) <sup>a</sup>
Merle Collins, California	—	1969	86	65	Rawstron & Hashagen (1972) <sup>a</sup>
Center Hill, Tennessee	—	1975–1976	58	37	Yeager & Van Den Avyle (1978) <sup>a</sup>
Mid Lake, Wisconsin	—	1976		53	Goedde & Coble (1981) <sup>b</sup>
Tobesofkee, Georgia	—	1977	91	56	Ager (1978) <sup>a</sup>
Chambers, Alabama	—	1979	79	58	Reed & Davies (1980) <sup>a</sup>
Shasta, California	2–4	1980	68	45	Van Woert (1980)
Ocmulgee, Georgia	—	—	32	11	Coomer & Holder (1981)
Thompson, Idaho	—	1981	62	48	Rieman (1982) <sup>a</sup>
Medicine, Idaho	—	1981	65	49	Rieman (1982) <sup>a</sup>
Fernan, Idaho	—	1981	82	72	Rieman (1982) <sup>a</sup>
Rum Creek, Georgia	—	1982–1983	88	10	Ager (1984)
Bartlett's Ferry, Georgia	—	1983–1986	79	14	Keefer (1982) <sup>a</sup>
Walter F. George, Georgia	—	1983–1986	56	25	Keefer (1982) <sup>a</sup>
Seminole, Georgia	—	1983–1986	58	14	Keefer (1982) <sup>a</sup>
Blackshear, Georgia	—	1983–1986	48	9	Keefer (1982) <sup>a</sup>
Lanier, Georgia	—	1986	43	16	Weaver (1989) <sup>a</sup>
Brown, Iowa	—	1988	68	32	Pitlo & Bonneau (1992) <sup>a</sup>
Brown, Iowa	—	1989	63	38	Pitlo & Bonneau (1992) <sup>a</sup>
Sunfish, Iowa	—	1988	53	53	Pitlo & Bonneau (1992) <sup>a</sup>
Sunfish, Iowa	—	1989	53	41	Pitlo & Bonneau (1992) <sup>a</sup>
Methodist, Iowa	—	1989	55	15	Pitlo & Bonneau (1992) <sup>a</sup>
Norwegian, Iowa	—	1989	46	41	Pitlo & Bonneau (1992) <sup>a</sup>
Minnesota Slough, Iowa	—	1989	58	22	Pitlo & Bonneau (1992) <sup>a</sup>

<sup>a</sup>Estimate was used in Figure 2; <sup>b</sup>represents exploitation in May 1976 on a previously unfished population.

necessary to test for additive *vs* compensatory mortality. Therefore, we examined overall trends across mortality estimates for each species to draw general conclusions about additive *vs* compensatory mortality. Additionally, we referred to case histories for each species to document mortality responses within specific populations.

### MORTALITY IN LARGEMOUTH BASS POPULATIONS

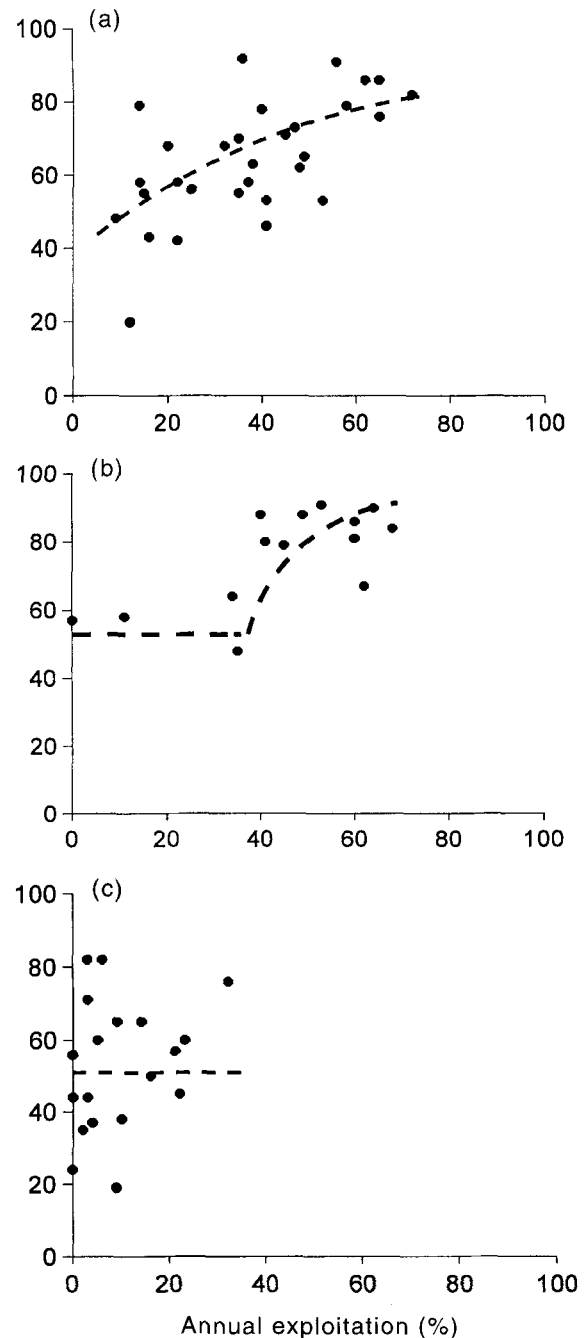
We compiled statistically independent estimates of annual mortality and annual exploitation for 34 largemouth bass populations (Table 1). Another estimate was obtained from Goedde & Coble (1981) who estimated annual exploitation but not annual mortality on a previously unfished population. Thirty estimates of annual exploitation for largemouth bass were made from returns of tagged fish harvested by anglers, and five from harvest estimates expressed as percentages of population estimates. Estimates of annual mortality were made from catch curves (Ricker 1975) reported from each study. Estimates of annual mortality averaged 64% (range 24–92), and estimates of annual exploitation averaged 36% (range 9–72).

We used only 30 of the 34 pairs of estimates to examine the relation between annual mortality and annual exploitation. The estimates made by Coomer and Holder (1981) were excluded because unlike the other studies, they represented mortality in a lotic environment, perhaps involving mortality mechanisms unlike those associated with lentic systems. Estimates made by Kimsey (1957), Van Woert (1980), and Ager (1984) were excluded because they made no correction for non-reporting of tags, tagging mortality, or tag loss. Although Ager (1978) did not correct for non-reporting rate, we used his estimates because he indicated non-reporting rate was probably negligible because tags were rewarded and could be redeemed at the boat ramp. The remaining studies estimated annual exploitation based on harvest estimates expressed as percentages of population estimates ( $n = 4$ ) or from tag returns from anglers ( $n = 26$ ), corrected for non-reporting rate, tag loss, and tagging mortality and some that considered these biases to be negligible.

Total mortality appeared to increase with exploitation across largemouth bass populations, as would be expected if annual mortality and annual exploitation were additive or only partially compensatory (Fig. 2). We are unable to conclude whether annual mortality and annual exploitation are strictly additive or partially compensatory. However, the apparent increase in annual mortality with annual exploitation suggested that completely compensatory mortality is not common across largemouth bass populations.

These results suggest that total mortality may be reduced through harvest restrictions. Accordingly, many field investi-

gations have documented the ability of fishery managers to control total mortality through size restrictions that have increased the density of many largemouth bass populations (e.g., Ming & McDannold 1975; Van Horn *et al.* 1981; Gabelhouse 1984; Summers 1988). Novinger (1984) cautioned that decreased growth may occur if size restrictions are implemented on largemouth bass populations, but



**Fig. 2.** Total annual mortality (%) plotted on annual exploitation (%) pike. The dashed lines represent our interpretation of the data. (a) Largemouth bass; (b) crappies; (c) northern pike.

noted that catch rates of highly exploited largemouth bass populations generally increase when size restrictions are imposed. Therefore, our results and the success of size restrictions suggest that harvest and total mortality for largemouth bass populations are either additive or only partially compensatory, rather than completely compensatory.

### MORTALITY IN WHITE CRAPPIE AND BLACK CRAPPIE POPULATIONS

We obtained 33 estimates of annual mortality and 18 estimates of annual exploitation (Table 2). All estimates of annual mortality were derived with catch curves (Ricker 1975). Estimates of annual exploitation were derived from returns of tagged fish harvested by anglers with the exception of Miller (1991), who used harvest estimates expressed as percentages of population estimates. Total annual mortality averaged 75% (range 39–94, mean was 75 for white crappie and 74 for black crappie), and annual exploitation averaged 48% (range 0–84, mean was 46 for white crappie and 50 for black crappie).

We combined white crappie and black crappie mortalities to assess the relation between annual mortality and annual exploitation because (i) their mortality rates were similar; (ii) the number of mortality estimates for each crappie species was low; (iii) it is difficult to manage each species independently because many anglers, and perhaps biologists (Smith *et al.* 1995) are unable to distinguish between the two species; and (iv) the species hybridize in some natural populations (Hooe & Buck 1991; Smith *et al.* 1994).

We excluded some crappie mortality estimates based on the same criteria used to exclude estimates for largemouth bass. Angyal *et al.* (1987) reported the highest estimates of annual mortality and lowest estimates of annual exploitation; however, their estimates were excluded because they confused actual annual natural mortality rate with conditional natural mortality rate. Snyder *et al.* (1990) indicated their estimates of annual exploitation were biased because fish had high emigration rates; thus, their exploitation rates were ignored. Although Colvin (1991a) did not correct for non-reporting rate, he speculated on what annual exploitation would have been had non-reporting rate been considered; thus, we included his estimates in our analysis, but we examined how an incorrect annual exploitation would have affected our conclusions. Larson *et al.* (1991) used a computer model to estimate annual mortality and annual exploitation from tag returns, resulting in estimates of annual mortality and annual exploitation that were not statistically independent. However, Larson *et al.* (1991) provided independent estimates of annual mortality using catch curves for Lake Allatoona in 1987 and 1988, and we obtained another independent estimate of annual mortality for Lake Sinclair

(S. Schleiger, Georgia Department of Natural Resources, pers. comm., 1993). We ignored the two non-independent estimates from Larson *et al.* (1991).

Also, we obtained one estimate of total mortality in absence of fishing from Lake Kathryn, Mississippi, which is a 25 ha oxbow adjacent to the Tennessee-Tombigbee Waterway in east-central Mississippi. Lake Kathryn is isolated from the Tennessee-Tombigbee Waterway, privately owned, and the harvest of white crappies was nil. We collected 454 white crappies using floating trap nets (Miranda *et al.* 1996), determined the age of five fish per centimetre group using whole sagittal otoliths as described by Maceina & Betsill (1987), and extrapolated to the entire sample with an age-length key (Ricker 1975). A catch curve revealed annual mortality was 57% (Table 2).

A total of 14 estimates was used to examine the relation between annual mortality and annual exploitation (Figure 2). The trend for crappie species was similar to the compensatory mortality model (Figure 1), with no apparent increase in annual mortality over low ranges of annual exploitation, then an increasing trend in annual mortality as annual exploitation increased past about 40%. Colvin's (1991a) estimates of annual exploitation were modified by  $\pm 10$  to account for possible inaccuracies of adjustments for non-reporting, but the trend across estimates was unaffected. Our interpretation should be considered tentative because the number of annual exploitation estimates below 40% were few, it was largely influenced by two data points below 20%, and at higher annual exploitation values annual mortality varied greatly. Nevertheless, evidence from crappies does not suggest as strong an increase in annual mortality with annual exploitation as seen in largemouth bass populations.

Results of field investigations about the effect of harvest on white crappie and black crappie populations are not as definitive as those for largemouth bass. Observations supportive of additive mortality have been made by Colvin (1991a,b) and Webb & Ott (1991). Colvin (1991a,b) concluded that annual exploitation was high in several white crappie fisheries in Missouri, and suggested that high annual exploitation resulted in white crappie fisheries composed mainly of fish ages 1 and 2. Additionally, he contended that if growth was satisfactory, regulations that reduced harvest of crappies ages 1 and 2 would increase the size of fish harvested by anglers. Webb and Ott (1991) also suggested that protecting younger year classes of white crappies might prevent growth overfishing (i.e., harvest that reduces the size of fish below the maximum yield-per-recruit) and improve the size structure and possibly the abundance of white crappie populations.

Conversely, Larson *et al.* (1991) suggested compensatory mortality for three black crappie populations. Larson *et al.*

(1991) found that annual exploitation varied from 40 to 68% but annual mortality remained almost constant, and they suggested that natural and harvest mortality operated in a compensatory manner.

The two studies on Lake Okeechobee (Table 2) present an interesting case. Schramm *et al.* (1985) documented high exploitation of black crappie under recreational and commercial harvest. Following the suspension of commercial

**Table 2.** Annual mortality and annual exploitation rate estimates for black crappies and white crappies. Estimates over successive years are means

Lake and location	Species	Age interval	Year(s)	Annual mortality rate (%)	Annual exploitation rate (%)	Source
Weiss, Alabama	Both	2–4	1988	64	34	Reed & Davies (1991) <sup>a</sup>
Columbus, Mississippi	Both	4–7	1993	79	45	Brock (1994) <sup>a</sup>
Beulah, Mississippi	Both	4–6	1993–1994	58	11	Brock (1994) <sup>a</sup>
Lee County, Alabama	Black	—	1978	90	—	Hornsby (1979)
Goat Rock, Georgia	Black	3–6	1980	76	—	Keefer (1982)
Hayes Center, Nebraska	Black	2–4	1979–1981	81	low	Ellison (1984)
Okeechobee, Florida	Black	—	1977–1980	—	65	Schramm <i>et al.</i> (1985)
Jamesport, Missouri	Black	3–4	1983–1986	—	84	Eder (1990)
Okeechobee, Florida	Black	2–7	1980–1984	39	—	Miller <i>et al.</i> (1990)
George, Florida	Black	1–6	1988–1990	52	—	Snyder <i>et al.</i> (1990)
Monroe, Florida	Black	1–6	1988–1990	54	—	Snyder <i>et al.</i> (1990)
Allatoona, Georgia	Black	2–7	1987	88	40	Larson <i>et al.</i> (1991) <sup>a</sup>
Allatoona, Georgia	Black	2–7	1988	90	64	Larson <i>et al.</i> (1991) <sup>a</sup>
Allatoona, Georgia	Black	2–4	1989	85	46	Larson <i>et al.</i> (1991)
Oconee, Georgia	Black	2–6	1987–1988	88	40	Larson <i>et al.</i> (1991)
Sinclair, Georgia	Black	2–5	1987–1989	84	68	Larson <i>et al.</i> (1991) <sup>a</sup>
Wylie, North Carolina and South Carolina	Black	1–2	1983–1986	81	—	McInerny & Degan (1991)
Wylie, North Carolina and South Carolina	Black	2–3	1982–1985	80	—	McInerny & Degan (1991)
Delaware, Ohio	Black	3–7	1987–1990	81	—	Miller (1991)
Pymatuning, Ohio	Black	3–6	1990	63	—	Miller (1991)
Hayers Center, Nebraska	White	2–4	1979–1981	74	low	Ellison (1984)
Chase, Kansas	White	3–8	1976–1985	64	—	Mosher (1985)
Lyon, Kansas	White	2–5	1977–1983	76	—	Mosher (1985)
Sooner Lake, Oklahoma	White	2–4	1977–1980	94	8	Angyal <i>et al.</i> (1987)
Stockton, Missouri	White	2–7	1981	86	60 <sup>b</sup>	Colvin (1991a) <sup>a</sup>
Pomme de Terre, Missouri	White	2–6	1981–1982	81	60 <sup>b</sup>	Colvin (1991a) <sup>a</sup>
Columbus, Mississippi	White	1–5	1988	77	—	Hammers & Miranda (1991)
Delaware, Ohio	White	2–6	1988–1990	72	—	Miller (1991)
Deer Creek, Ohio	White	2–8	1990	67	62	Miller (1991) <sup>a</sup>
Buckeye, Ohio	White	3–8	1990	56	—	Miller (1991)
Piedmont, Ohio	White	3–8	1990	71	—	Miller (1991)
Cowan, Ohio	White	2–5	1989–1990	48	35	Miller (1991) <sup>a</sup>
Skiatook, Oklahoma	White	1–4	1987	88	49	Zale & Stubbs (1991) <sup>a</sup>
Skiatook, Oklahoma	White	1–3	1988	80	41	Zale & Stubbs (1991) <sup>a</sup>
Skiatook, Oklahoma	White	1–4	1989	91	53	Zale & Stubbs (1991) <sup>a</sup>
Kathryn, Mississippi	White	4–9	1994	57	0	Miranda & Allen (unpubl. data, 1994) <sup>a</sup>

<sup>a</sup>Estimate was used in Figure 2; <sup>b</sup>Colvin estimated annual exploitation to be 48 at Stockton and 49 at Pomme de Terre, but predicted there could have been about 60 in both lakes had the estimates been adjusted for non-reporting of tags.

harvest, Miller *et al.* (1990) found annual mortality had declined, suggesting that annual exploitation acted additively with annual mortality during the commercial harvest period. However, growth rates of black crappies declined and density increased following the suspension of commercial harvest, and Miller *et al.* (1990) suggested that reinstating limited commercial fishing would improve growth rates and prevent the fishery from becoming dominated by subharvestable-sized fish. Thus, following suspension of commercial harvest on Lake Okeechobee, annual mortality decreased suggesting that annual exploitation and annual natural mortality rate had acted additively.

### MORTALITY IN NORTHERN PIKE POPULATIONS

We obtained 23 estimates of annual mortality and 22 estimates of annual exploitation for northern pike (Table 3).

Estimates of annual mortality were derived with catch curves. Fourteen estimates of annual exploitation were estimated with harvest estimates expressed as percentages of population estimates and eight with returns of tagged fish harvested by anglers. Estimates of annual mortality averaged 52% (range 19–82) and annual exploitation averaged 11% (range 0–46). We excluded Phillips and Bender (1984) because their estimates of annual exploitation were not corrected for non-reporting or tag loss. Snow and Beard (1972) did not estimate exploitation during 1968 and 1969, but a creel survey indicated that fishing effort during these years was lower than during 1966 and 1967. We used 3% as annual exploitation for 1968 and 1969, representing the highest estimate from previous years.

The remaining 19 estimates were used to examine relations between annual mortality and annual exploitation. The plot revealed variable annual mortality for a given annual

**Table 3.** Annual mortality and annual exploitation rate estimates for northern pike. Rates are expressed as percentages. Estimates over successive years are means

Lake and location	Age interval	Year(s)	Annual mortality rate (%)	Annual exploitation rate (%)	Source
Ball Club, Minnesota	—	1955	60	23	Johnson & Peterson (1955) <sup>a</sup>
Murphy Flowage, Wisconsin	—	1958	76	32	Snow (1958) <sup>a</sup>
Lake George, Minnesota	—	1964	65	14	Groeber (1964) <sup>a</sup>
Windermere, England	5–10	1954–1964	48	—	Kipling & Frost (1970)
Mill Lake, Michigan	—	1971	56	0	Schneider (1971) <sup>a</sup>
Bucks, Wisconsin	—	1965	57	21	Snow & Beard (1972) <sup>a</sup>
Bucks, Wisconsin	—	1966	44	3	Snow & Beard (1972) <sup>a</sup>
Bucks, Wisconsin	—	1967	35	2	Snow & Beard (1972) <sup>a</sup>
Bucks, Wisconsin	—	1968	71	3 <sup>b</sup>	Snow & Beard (1972) <sup>a</sup>
Bucks, Wisconsin	—	1969	82	3 <sup>b</sup>	Snow & Beard (1972) <sup>a</sup>
Escanaba, Wisconsin	4–7	1964–1972	82	6	Kempinger & Carline (1978) <sup>a</sup>
River Frome, England	1–11	1972–1977	44	0	Mann (1980) <sup>a</sup>
Mid Lake, Wisconsin	—	1976	—	46	Goedde & Coble (1981) <sup>c</sup>
Savanne Lake, Ontario	4–12	1977	19	9	Mosindy <i>et al.</i> (1987) <sup>a</sup>
Murray Lake, Michigan	—	1980	24	0	Diana (1983) <sup>a</sup>
Houghton, Michigan	—	1980	57	—	Diana (1983) <sup>a</sup>
Lac Vieux, Michigan	—	1980	36	—	Diana (1983) <sup>a</sup>
Connecticut River, Connecticut	3–6	1981–1983	52	12	Phillips & Bender (1984)
Julia, Minnesota	2–7	1988	45	22	Pierce <i>et al.</i> (1995) <sup>a</sup>
Medicine, Minnesota	2–7	1988	50	16	Pierce <i>et al.</i> (1995) <sup>a</sup>
North Twin, Minnesota	3–8	1988	37	4	Pierce <i>et al.</i> (1995) <sup>a</sup>
Coon, Minnesota	2–7	1990	38	10	Pierce <i>et al.</i> (1995) <sup>a</sup>
French, Minnesota	—	1989	—	7	Pierce <i>et al.</i> (1995) <sup>a</sup>
Sissabagamah, Minnesota	3–6	1989	65	9	Pierce <i>et al.</i> (1995) <sup>a</sup>
Wilkins, Minnesota	3–5	1989	60	5	Pierce <i>et al.</i> (1995) <sup>a</sup>

<sup>a</sup>Estimate was used in Figure 2. <sup>b</sup>Exploitation during 1968 and 1969 was not estimated directly, but a creel survey indicated that exploitation during these years was lower than during 1966–1967. We used an exploitation of 3% for these years. <sup>c</sup>Represents exploitation during May 1976 on a previously unfished population.

exploitation and no evident trend. Within the limited range of annual exploitation estimates available for northern pike (0–32%), no increase in annual mortality with increases in annual exploitation was evident. The large variability in annual mortality within a small range of annual exploitation suggests natural mortality varies widely. Also, given the variability in annual mortality, additional data for larger annual exploitation are unlikely to provide new insight.

Previous researchers have indicated that total mortality for northern pike was not affected by harvest. Snow and Beard (1972), Snow (1978) and Kimpinger and Carline (1978) documented that total mortality did not decline following reductions in fishing mortality. Kimpinger and Carline (1978) found that northern pike density almost doubled following the implementation of a 56 cm length limit in 1964, and annual natural mortality rate increased from 14% before the length limit to 76% in the post-regulation period (1964–1972). Snow and Beard (1972) documented no change in density or annual mortality for northern pike 25–45 cm long following implementation of a 45 cm length limit, and they suggested that annual natural mortality rate had compensated for reduced annual exploitation. Conversely, Diana (1983) found annual mortality was 24% in an unexploited population, whereas annual mortality was 57% in a nearby lake receiving fishing effort, and he attributed the difference in annual mortality to increased annual exploitation, suggesting additive mortality.

### POSSIBLE MECHANISMS

Although compensatory mortality of adults has seldom been considered in the fisheries management literature, it has been emphasized in the wildlife literature. In early work with bobwhite quail *Colinus virginianus*, Errington and Hamerstrom (1935) found that winter total mortality averaged 10% in hunted areas and 28% in non-hunted areas, and they suggested that a surplus existed in autumn that would disappear during winter, mostly from predation, if hunting was excluded. Similarly, reduced natural mortality of adult mallard ducks *Anas platyrhynchos* (Anderson & Burnham 1976; Rogers *et al.* 1979; Burnham & Anderson 1984; Burnham *et al.* 1984) and other duck species (reviewed by Nichols *et al.* 1984) has likely occurred following harvest, with strong evidence for male mallards. However, the mechanism for reduced natural mortality among ducks is not known.

Adult fishes are probably less susceptible to compensatory mortality than terrestrial vertebrates because fish are better able to adjust their growth rate to food availability, thus lengthening the period they can survive with limited food (Weatherley & Gill 1987; Shuter 1990). Thus, adult fishes exhibit density-dependent growth that typically prevents star-

vation and may serve as a mechanism of population control (Weatherley & Gill 1987).

Nevertheless, compensatory mortality in adult fishes may result from cumulative effects. During periods of reduced growth through intra- or interspecific competition for food, other stressors (e.g., disease, parasitism, predation) may act synergistically to cause density-dependent mortality. Cushing (1981) suggested that predation acts in a density-dependent manner in some pelagic marine fish stocks. We found examples of variable mortality responses of crappies and northern pike due to exploitation. However, compensatory mortality probably exerts the strongest effect on most fish populations during prejuvenile life stages (Goodyear 1980; Weatherley & Gill 1987; Shuter 1990).

Mortality responses appeared to differ between largemouth bass and crappie species. Mortality estimates revealed a roughly additive increase in annual mortality with increasing annual exploitation for largemouth bass. We also found no study that suggested compensatory mortality in adult largemouth bass. Mortality of crappie species revealed no increase in annual mortality over low ranges of annual exploitation, and Larson *et al.* (1991) suggested that compensatory mortality occurred in three black crappie populations.

We hypothesize that compensatory mortality may occur in some white crappie and black crappie populations. Dynamics of crappie populations reportedly differ from those of largemouth bass populations. Swingle and Swingle (1967) noted that crappie populations tend to be cyclic, with dominant year classes occurring every 3–5 years. Conversely, severe population cycles have not been documented for largemouth bass populations. A review by Ricklefs (1990) noted that density-dependent mortality most likely occurs during peak abundance of cyclic populations of insects, small mammals, and zooplankton. Similar processes may occur in crappie populations. Following periods of high recruitment, perhaps triggered by a favourable combination of environmental conditions and stock abundance, crappie populations may 'overshoot' their carrying capacity, resulting in density-dependent mortality of adult crappies that compensates for low to moderate annual exploitation. The lack of cyclic phenomena for largemouth bass populations suggests that largemouth bass recruitment seldom increase their density past carrying capacity, or that largemouth bass do not exhibit density-dependent mortality at high densities.

However, Webb & Ott (1991) suggested that white crappie population cycles may result from angler exploitation. They hypothesized that anglers may overharvest adult crappies and reduce their numbers to the extent where many anglers abandon the fishery, only to return and renew the cycle



when numbers of adult fish increase again. This phenomenon would indicate additive mortality and warrant further investigation.

We found no relation between annual mortality and annual exploitation for northern pike. Evidence from the literature suggests that cannibalism may result in compensatory mortality for northern pike less than about 40 cm total length, whereas mortality for larger northern pike is more likely to be additive. Mann (1982) found that cannibalism constituted the major source of natural mortality for northern pike less than 2 years old. Pierce *et al.* (1995) noted that northern pike were second numerically only to yellow perch *Perca flavescens* in the stomachs of 129 northern pike from two lakes. Grimm (1983) suggested that biomass of small northern pike could be regulated through cannibalism by larger fish. However, Kipling and Frost (1970) noted that northern pike longer than 40 cm were seldom eaten by other northern pike. Thus reducing annual exploitation of northern pike smaller than about 40 cm could result in higher annual natural mortality rate for those fish through cannibalism. Snow and Beard (1972) found that northern pike smaller than 46 cm contributed a substantial proportion of the harvest from Bucks Lake, Wisconsin, and they suggested that a 46 cm length limit would merely protect fish that would ultimately die from natural mortality. Furthermore, Kempinger and Carline (1978) suggested that length limits would increase natural mortality rates of protected fish, but their length limit protected mostly small northern pike (< 56 cm). Although reductions in annual exploitation would lead to slight increases in annual natural mortality rate under the additive hypothesis, more substantial increases in annual natural mortality rate would be expected under compensatory mortality.

Conversely, northern pike longer than about 40 cm may be less likely to exhibit compensatory mortality because they are not subjected to cannibalism. Pierce *et al.* (1995) found that exploitation was the major source of mortality for large northern pike and suggested that protecting large northern pike may reduce the density of small fish, possibly improving their growth rates and recruitment to larger sizes. Goedde and Coble (1981) found that the number of pike larger than 45 cm was reduced after angling was initiated in a previously unfished population. Thus, evidence suggests mortality for large northern pike is more likely additive than completely compensatory. No additive trend between annual mortality and annual exploitation was observed for northern pike, perhaps due to confounding differences in mortality response between northern pike larger than 40 cm and fish smaller than 40 cm, and because the range of annual exploitation estimates was small. If mortality estimates were available separately for fish smaller than and larger than 40 cm, some

of the variability in annual mortality may be removed, at least for the larger fish. Nevertheless, this additional information was not available. Further evaluation of the mechanisms for northern pike mortality is needed because of the apparent high variation in natural mortality rates.

### THE NEED FOR FURTHER CONSIDERATION

The likelihood for compensatory mortality should be further examined in recreational fisheries, inasmuch as the interpretation of ecological relations within and among fish populations, and the success of some managerial policies, depend on the populations' mortality response. Fishery managers may wish to implement or increase harvest restrictions on fisheries where exploitation is high, but if mortality is compensatory, reducing exploitation may not decrease annual mortality, which would reduce the benefits of the regulation.

Traditional yield models (Beverton & Holt 1957; Ricker 1975) as well as most recent models (e.g., Taylor 1981; Clark 1985; Beamesderfer 1991) assume additive mortality. These models may overestimate the true attainable yield if mortality is compensatory, because natural mortality would increase if exploitation was lowered through a simulated harvest regulation. Thus, under a compensatory model, fewer fish would be available for harvest than would be predicted using the additive mortality model. Conversely, if exploitation were increased and the additive model was assumed, attainable yield would be underestimated because natural mortality would decrease if mortality were compensatory. However, compensatory mortality has seldom been considered in fisheries models.

Managers have reduced annual mortality in many fish populations through harvest regulations, but some species such as northern pike and crappies have shown unpredictable responses to harvest regulations. Accurate estimates of annual exploitation and annual mortality, as well as documentation of mortality both before and after a regulation is implemented should provide more evidence for or against compensatory mortality in fish populations. We encourage researchers to test hypotheses of additive *vs* compensatory mortality, and suggest that for species that have shown unpredictable mortality responses to reductions in annual exploitation, managers should consider the possibility of compensatory mortality and its potential effects on annual mortality before the implementation of a harvest restriction.

### ACKNOWLEDGEMENTS

This research was funded by the Mississippi Department of Wildlife, Fisheries and Parks through Federal Aid in Sport Fish Restoration Act, Project F-105, and by the Mississippi Agriculture and Forestry Experiment Station. We especially thank K. Burnham for his technical insights. W. Burger,

M. Conroy, D. Jackson, R. Kaminski, D. Orth, H. Schramm, and three anonymous referees provided helpful comments on previous drafts of this manuscript. The Wildlife Research Unit is jointly sponsored by the Mississippi Department of Wildlife, Fisheries and Parks, Mississippi State University, and the US Geological Service.

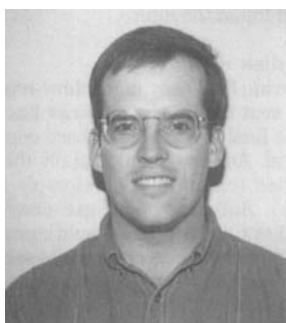
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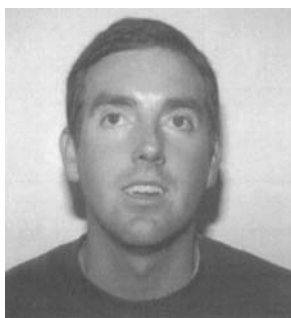
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