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Mortality Rates of Snappers and Groupers

Stephen Ralston
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

ABSTRACT

Mortality concepts are briefly reviewed and general methods of estimating mortality rates discussed. Special attention is devoted to techniques used successfully in the study of snappers and groupers. In particular, catch curves, Z/K ratio estimates, and the Pauly equation are shown to account for the majority of mortality estimates reported from these two taxa. A review of the snapper and grouper literature indicates that instantaneous rates of natural mortality (M) can simply be predicted with knowledge of the von Bertalanffy growth coefficient (K)--the former being roughly twice the latter. Reported agents responsible for natural deaths in these groups include predation, parasitism, cold water shock, and red tide poisoning. Examining levels of exploitation suggests that snappers have been more intensively harvested than groupers, although stocks characterized by high ratios of fishing to natural mortality are known from both families. Based on the evidence reviewed it is concluded that these species have a relatively limited productive capacity and are vulnerable to overfishing.

INTRODUCTION

In the tropical and subtropical waters of the world, few demersal fishery resources are more important than the snappers (Lutjanidae) and groupers (subfamily Epinephelinae of the Serranidae) (Bullis and Jones 1976; Pauly 1979;

Munro 1983). Yet in spite of their significance, yield assessments of these species have until recently been few (e.g., Ralston and Polovina 1982; Huntsman et al. 1983; Kunzel et al. 1983; Munro 1983; Powers 1983). Now, however, regional studies of snapper and grouper biology have proliferated to the extent that a review and synthesis of the information recently gained could considerably aid their management.

Estimation of mortality rates is central to demographic analyses and most types of stock assessment (Gulland 1955). This is because losses from exploited populations largely control the yields that can be obtained from them (Beverton and Holt 1957; Gulland 1971; Ricker 1975). Yet, biologists frequently regard the topic with apprehension because of preconceived ideas about its complexity. In truth, mortality concepts are quite simple, although statistical problems often do occur.

The organization of this chapter is, therefore, designed to first introduce several basic concepts which define what mortality is and in general terms how it is expressed mathematically. This leads to a discussion of specific methods and techniques for estimating mortality rates, especially those that have been successfully applied to snappers and groupers in tropical systems. Because natural mortality is of special significance when analyzing potential yield, and is usually difficult to determine, I present a brief discussion of factors correlating with it. From these ideas I develop a predictor of natural mortality and test it on data obtained from the snapper/grouper literature. This is followed by a review of factors known to be responsible for natural deaths in these two taxa. Finally, I briefly discuss the relationship between natural mortality and optimum rates of fishing mortality.

MORTALITY AND ITS ESTIMATION

When considered from the classical perspective of the Beverton and Holt (1957) dynamic pool model, there are three factors that uniquely determine the yield from a stock of fish. These factors are recruitment, growth, and mortality. The first two are renewal processes, which add biomass to the exploitable phase of the life history. Conversely, mortality represents the loss of individuals, and thus biomass, from the population. This loss process is usually subdivided into two separate categories:

deaths attributable to fishing, and deaths due to all other sources. Collectively the latter are termed natural mortality.

Jensen (1939) was among the first to argue that the force of mortality factors acts in a multiplicative fashion. He showed for a variety of stocks (including cod, haddock, plaice, and herring) that the number of individuals in a cohort or year class is diminished by a fixed percentage from year to year. Similarly, Beverton and Holt (1959) presented evidence for long-lived species demonstrating that a constant fraction of a cohort is removed each year by the various agents of natural mortality. Moreover, we know that when basic operational and statistical assumptions have been met, a fixed amount of fishing effort removes a fixed fraction of the fully vulnerable portion of a stock (Ricker 1975). Thus, at least in theory, fishing mortality operates in a multiplicative manner as well. In practice this may not be true.

The multiplicative nature of mortality factors lends itself to expression by the exponential function, especially in its differential form. Then the instantaneous total mortality rate from all causes (Z) can simply be defined as the proportionality constant that relates the rate of change (dN/dt) of a cohort to its absolute abundance (N). That is,

$$dN/dt = -ZN$$

It is a great convenience that, when mortality is expressed in this manner, fishing (F) and natural (M) mortality rates are additive; that is, $Z = F + M$. A necessary corollary is that total mortality equals natural mortality in the absence of fishing. When acting in concert, M and F compete for the individuals remaining in a year class, each responsible for a certain percentage reduction over time. Instantaneous mortality rates, as shown above, are by definition measured in units of inverse time, most frequently per year.

Given that mortality factors are related and expressed in this fashion, what methods are available to estimate these rates? Although a wide variety of techniques have been employed, most can be classified according to three fundamental types of estimation: (1) age-specific procedures for true cohorts; (2) time-specific methods for synthetic cohorts; and (3) mark-recapture methods. A very brief description of each follows.

Ideally, the total mortality rate of a cohort is estimated by determining the number of individuals of age x that are alive at time t, that is, ($N_{x,t}$), and also the number of individuals of age x+1 at time t+1 ($N_{x+1,t+1}$). If time is measured in years, the ratio of the latter to the former provides an estimate of the annual survivorship fraction (S_x) for fish aged x. Furthermore, the age-specific total instantaneous mortality rate (Z_x) is equal to $-\ln(S_x)$. Note that in this calculation an actual cohort is tracked in time and successively sampled. Thus, the measured mortality rate is the actual rate experienced by the cohort (Gulland 1955). An important practical adjustment often employed is to substitute properly subscripted catch per unit effort indices of abundance for the actual numbers of fish (Gray 1979; Paloheimo 1980; but see Butler and McDonald 1979). Age-specific mortality estimates are typically used in cohort and virtual population analysis (Ricker 1975) and result in the most compelling mortality assessments.

A second approach to the problem is through the use of synthetic cohorts. Rather than repetitively sampling a population through time, a single sample is taken and the numbers of fish aged x, x+1, x+2, ..., x+i determined. Often this entails developing an age-length key (Fridriksson 1934; Gulland 1955), a nontrivial problem in its own right, especially if the key is used on samples taken at different times or places (Kimura 1977; Westrheim and Ricker 1978; Clark 1981). If the sampled population is assumed to be age-stationary (i.e., the age distribution remains the same from year to year), one can estimate mortality rates by forming the ratios of successive age classes exactly in the manner outlined previously. Note that computing mortality rates from "synthetic" cohorts actually produces estimates that are time-specific, as opposed to age-specific.

To analyze these kinds of data, Chapman and Robson (1960) and Robson and Chapman (1961) derived a minimum-variance, unbiased estimator of S for single age-frequency distributions in the situation where mortality rate is uniform across all age groups. Alternatively, the analysis of catch or survivorship curves (Ricker 1975) permits visual inspection of the data to look for possible violations of assumptions, especially that of constant mortality rate. These are simply semi-logarithmic plots of abundance against age, where the slope of the descending right-hand limb provides an estimate of total mortality rate. An important variation on this theme is the analysis of single length-frequency distributions to estimate the ratio of total mortality rate to von Bertalanffy growth coefficient (Z/K) (Beverton and Holt 1956; Ssentongo and Larkin 1973; Powell 1979; Wetherall et al. In press). With an independent estimate of K from the study of tag returns, otoliths, modal size progression, etc., it is possible to estimate Z by separating the ratio. Similarly, there are techniques that assume an underlying growth structure, which is then used to analyze length-frequency distributions. These methods produce mortality estimates after analytically reconstructing the unknown age-distribution (Olsen and LaPlace 1979; Pauly 1982; see also Schnute and Fournier 1980). Although all these various techniques are commonly used, each relies essentially on a single sample, be it age- or length-frequency, and each therefore suffers from the constraint of age stationarity, an assumption that frequently is not met.

A third class of mortality estimation techniques involves mark-recapture methods (Ricker 1975; Seber 1982). For example, it is generally possible to estimate exploitation fraction ($u = 1-\exp^{-F}$) in a marked population as the ratio of total marks in the catch to total marks in the population. From this, an estimate of fishing mortality is obtained directly. Similarly, total mortality rate can be estimated by determining the extinction rate of marks in the population at large. Other fairly detailed methods exist to estimate M. Mark-recapture methods have not been used, however, to estimate mortality rates of snappers and groupers.

While these three general categories account for the majority of mortality estimations, several other techniques have been developed that differ from them sufficiently to warrant specific mention. Green (1970), and later Ebert (1973), presented a method for estimating growth and total mortality rates by graphical and numerical means, respectively. Their method is restrictive in assuming age stationarity and full recruitment to the population over less than 1 month, but is appealing because it only requires estimates of average individual size at two times in the year. Saila and Lough (1981) derived an analytical solution to the same problem for an estimate of K, using this result in conjunction with the Z/K ratio method to separate the parameters. In yet another approach, Marten (1978) developed a procedure for determining total mortality rate from a length sample under conditions where fish growth can be considered linear over the size range of interest. Also, regression analysis has been used effectively to separate Z into its constituent components (Beverton and Holt 1957; Cushing 1968). Here total mortality can be regressed against nominal fishing effort, in which case the y-intercept provides an estimate of M (see also Marten 1978). Similarly, Csirke and Caddy (1983) have suggested that a parabolic nonlinear regression of yield on total mortality rate (Z) allows estimation of M as the point of the left hand or ascending x-intercept.

Another means of estimating mortality, particularly natural mortality, is by comparative life history studies of ecologically or taxonomically similar species (Adams 1980; Gunderson 1980). For example, Pauly (1980) suggests predicting instantaneous natural mortality rate from a multiple regression equation he derived from the study of 175 fish stocks. This equation incorporates three independent variables: (1) mean annual water temperature; (2) the von Bertalanffy growth coefficient K; and (3) either the asymptotic weight or length parameter from the von Bertalanffy growth model. Although the standard error of the estimate (0.247) is too large to permit precise estimation of natural mortality (estimated values of M have sometimes exceeded measured values of Z), this equation is still very useful when no historical information exists concerning the condition of a population in its unexploited state. Similarly, Hoenig (1983) presented an empirically derived equation which predicts total mortality rate from maximum age data.

MORTALITY ESTIMATION IN TROPICAL SNAPPERS AND GROUPERS

The only study of a snapper species in which age-specific mortality rates were determined for use in a cohort or virtual population analysis was that of Mahmoudi et al. (1984). The total catch of Rhomboplites aurorubens by age class, determined over a 10-year period, was estimated from size composition and total catch data from three distinct segments of the fishery (recreational, commercial hook-and-line, and commercial trawl). The data were aggregated and then recursively analyzed to obtain least squares estimates of age-specific fishing mortality rates from 1973 to 1982. Natural mortality was estimated from the Pauly (1980) equation. Given estimates of age-specific fishing mortality and catch it was possible to estimate the annual standing stock by age class and recruit year-class strength. A graph relating the number of spawning females and recruitment was also presented. Thus a full history of the fishery was derived and a detailed assessment of the stock's response to exploitation was gained. They concluded that an increase in yield per recruit could be achieved by reducing fishing mortality on fish aged 1-3 years.

Without question catch curve analysis has been used more frequently on lutjanids and serranids than any other method of mortality estimation (Moe 1969; Manooch and Haimovici 1978; Nagelkerken 1979; Low 1981; Ivo and Hanson 1982; Nelson and Manooch 1982; Brouard and Grandperrin 1984; Matheson and Huntsman 1984; Moore and Labisky 1984; Ralston 1984; Witzig and Huntsman 1984). Studies have involved the following species: *Epinephelus morio*, *E. cruentatus*, *E. niveatus*, *E. drummondhayi*, *Mycteroperca microlepis*, *Centropristis striata*, *Lutjanus purpureus*, *L. malabaricus*, *L. campechanus*, *Etelis carbunculus*, *E. coruscans*, *Pristipomoides flavipinnis*, *P. filamentosus*, and *P. multidens*. Typically, investigators have used hard parts, sometimes scales but more often otoliths, to develop a von Bertalanffy growth curve (see Manooch 1986).

Age-length data have usually been used to construct age-length keys, although some investigators have developed an age sample which is sufficiently large to permit analysis of population age structure directly (Moe 1969; Nagelkerken 1979; Low 1981). Otherwise, the use of age-length keys has been widespread, a practice that can result in seriously biased mortality estimates. Kimura (1977) and Westrheim and Ricker (1978) have both shown that a key derived from one population that is applied to another, or even if applied to the same stock sampled at different times, can produce substantial errors. This is because a single key used on divergent length-frequency data sets results in projected age distributions that tend to mimic the age distribution from which the key was derived. Misapplication of this method is therefore likely if the same key is used repeatedly. Consequently, when mortality estimates appear to remain uniform through time (e.g., Nelson and Manooch 1982; Witzig and Huntsman 1984), it is difficult to conclude that no change has occurred if only one age-length key was used. Clark (1981), however, has proposed a method to circumvent this problem, employing least squares to determine the overall age distribution of the population given the distribution of lengths within each age class (see also Bartoo and Parker 1983).

Another popular technique that can lead to error in mortality estimates is that of directly transforming lengths to ages using the inverse form of the von Bertalanffy growth equation (e.g., Mahmoudi et al. 1984). Age-frequency distributions developed in this fashion need not represent the actual age structure of the population (Ricker 1975; Bartoo and Parker 1983). When the data resulting from this procedure are analyzed by catch curve methods or otherwise, mortality estimates are likely to be biased.

At least two studies have used a modified catch curve approach. Pauly and Ingles (1982) estimated the total mortality rate of Epinephelus sexfasciatus using ELEFAN I (Pauly 1982), a computer program that generates length-converted catch curves from length-frequency data. Olsen and LaPlace (1979) also estimated total mortality rate in E. striatus by first restructuring length samples using probit analysis, and then deriving a probability function to estimate age class abundance by size class.

A method used extensively to estimate mortality rates, and apparently with great success, is the Z/K ratio technique and its subsequent modifications (Beverton and Holt 1956; Powell 1979; Wetherall et al. In press). In its simplest form, this method calculates the ratio of mortality to growth parameters from a length-frequency distribution adjusted to provide: (1) the size at which fish become fully vulnerable to the gear (l_c), and (2) the mean size of fish in the catch larger than l_c. It is attractive for its simplicity of data requirements and robustness of estimates (Powell 1979; Wetherall et al. In press; but see Majkowski 1982).

Several researchers have estimated mortality with this technique. Thompson and Munro (1978) computed Z for five species of Jamaican grouper: E. guttatus, E. striatus, M. venenosa, Cephalopholis fulva, and Petrometopon cruentatum. Because some length-frequency samples were obtained from unfished areas, they were also able to estimate natural mortality (i.e., Z = M). Brouard and Grandperrin (1984) used the Z/K ratio approach to estimate total mortality rates (= natural mortality) for six lutjanids in Vanuatu: Etelis carbunculus, E. coruscans, L. malabaricus, Pristipomoides flavipinnis, P. filamentosus, and P. multidens. By comparison, estimates calculated from this approach averaged 24% higher than synoptic catch curve estimates for the same species. Ralston and Williams (Unpub.) also performed Z/K analyses for the same species (excluding L. malabaricus), as well as *P. auricilla* and *P. zonatus* sampled in the Mariana Archipelago. Because their samples typically came from virgin populations, estimates of M were derived.

Age-specific mortality estimates for *L. purpureus* and *Plectropomus maculatus* were derived by Ivo and Gesteira (1974) and Goeden (1977), respectively, although the mortality rate was effectively constant among age classes in the latter study. Similarly, Nagelkerken (1979) and Manooch and Haimovici (1978) reported nonlinear descending limbs in catch curve analyses of *Epinephelus cruentatus* and *M. microlepis*. As a result, neither study attempted to estimate mortality. In the three studies where grouper mortality rates have demonstrated clear age-specific variation, all showed an increase in age specific mortality rate with increasing age (i.e., an upwardly convex catch curve). This finding is in agreement with the suggestion of Cushing (1968) that the collective force of natural mortality among the smaller fishes is largely due to predation but is more the result of physiological events (e.g., senility) for the larger, predatory species like snappers and groupers.

Another important means of estimating natural mortality rate (M) in the snappers and groupers has been the Pauly (1980) equation, used by Pauly and Ingles (1982) on *E. sexfasciatus*, Nelson and Manooch (1982) on *L. campechanus*, Brouard and Grandperrin (1984) on the six species mentioned previously (Pauly equation estimates were 46% greater than comparable catch curve estimates), Matheson and Huntsman (1984) on *E. niveatus* and *E. drummondhayi*, and Ralston (1984) on *Pristipomoides filamentosus* (equation estimate was 45% greater than a catch curve estimate from an unfished stock).

The only other two methods that have been employed to estimate mortality in these two groups are the Robson and Chapman (1961) maximum likelihood estimator, used by Nelson and Manooch (1982) on *L. campechanus*, and a regression of total mortality rate (Z) on nominal fishing effort, used to estimate natural mortality in *L. purpureus* by Ivo and Gesteira (1974). In the former study, the Robson-Chapman estimator produced estimates approximately 8% greater than catch curve estimates from the same data.

From this brief review, it is evident that three methods have accounted for the great majority of snapper/grouper mortality estimations: catch curves, Z/K ratios, and Pauly equation estimates. In situations where more than one of these has been used (Brouard and Grandperrin 1984; Ralston 1984), the Pauly (1980) equation produced estimates of M that were distinctly higher than catch curve estimates derived from virgin stocks, while Z/K ratio estimates lay midway between the two.

PREDICTING NATURAL MORTALITY

Estimating instantaneous natural mortality rate (M) is of special significance in fisheries research (Ricker 1975). Although it is one of the most difficult parameters in fisheries to estimate, virtually all age-structured yield models require it. Once obtained, however, its uses are multiple.

One particular application of natural mortality estimates is to estimate maximum sustained yield (MSY). Alverson and Pereyra (1969), based on the unpublished ideas of Gulland (1971) and an earlier Soviet study (Tiurin 1962), first proposed that at MSY the optimum level of fishing mortality (F_{opt}) could be directly estimated with the natural mortality rate. This particular conclusion applied not only to surplus-production models like the Graham-Schaefer formulation, but more loosely to the Beverton and Holt (1957) constant recruitment model as well (Gulland 1971). Saetersdal (1973) also advocated using M as a direct estimate of F_{opt} when assessing unexploited resources and catch statistics are unavailable. From these ideas a number of studies have estimated MSY by the following relationship:

$$MSY = 0.5 \; M \; B_o$$

where B_o represents exploitable virgin biomass. Kunzel et al. (1983), for example, estimated MSY for the lutjanids of the Mahe Plateau, Seychelles using this relationship.

Francis (1974), Deriso (1982), and Beddington and Cooke (1983) examined the theoretical basis for this approximation and concluded that it should hold only in situations where recruitment is constant over stock sizes ranging from B_o to $0.5 \; B_o$. They showed on a purely analytical basis that if an asymptotic form of spawner-recruit curve were applicable, then $F_{opt} < M$, whereas if a dome-shaped relationship were in effect, then $F_{opt} > M$. Furthermore, optimum fishing mortality relative to MSY was generally shown to be less than F_{opt} for yield/recruit analyses.

Because of the biological importance of natural mortality and its utility in yield assessment, a number of studies have tried to determine factors that might correlate with M, allowing its prediction from some other more easily estimated statistic. Beverton and Holt (1959) tabulated values of asymptotic size, K, maximum age, and M, and showed that the von Bertalanffy growth rate parameter K correlates well with M. Cushing (1968) summarized these findings in the statement "a fish with a high growth rate dies young" and presented plots of M versus K for the clupeoidei, gadiformes, salmonoidei, and pleuronectoidei.

More recently, Adams (1980) and Gunderson (1980) used r-K selection theory (MacArthur and Wilson 1967) as a basis for developing predictors of natural mortality. They concluded that the von Bertalanffy growth coefficient and the gonadosomatic index, respectively, were best correlated with M, although in all cases their trial predictors (size at maturity, asymptotic size, maximum age, and age at maturity) agreed well with r-K selection theory. Myers and Doyle (1983), under the assumption that fish life histories are evolutionary stable strategies, also estimated M from growth rate, fecundity, energy expenditure per egg, age and size at maturity, and a value of surplus energy available. Indeed, the Pauly (1980) equation itself relies on values of K, asymptotic size, and mean annual water temperature to predict M.

Based on the presumption that K is a good predictor of M, a survey of the snapper/grouper literature was undertaken that was designed to locate populations in which the von Bertalanffy growth coefficient (K) and the natural mortality rate were jointly estimated. An added appeal of K as a predictor of M is that both are measured in identical units (per year). Moreover, asymptotic size and mean annual water temperature are typically correlated with K and provide little independent information regarding M (but see Pauly 1980).

To determine if a more taxon-specific compilation of K and M statistics would increase the precision of natural mortality rate predictions, studies that used the Pauly (1980) equation to estimate snapper/grouper M were excluded unless an independent estimate was also given. Nineteen snapper/grouper stocks were identified in which the two parameters were both estimated. Table 8.1 summarizes the findings, including recent studies of 15 populations not incorporated in Pauly's original work. Some discussion of these is warranted.

Brouard and Grandperrin (1984) reported on six lutjanid species from Vanuatu, estimating Z by two independent means: catch curve and Z/K ratio. Growth was

TABLE 8.1
Summary information on growth and natural mortality determinations in the snapper and grouper families

Species	K	M	Source
Lutjanidae			
Etelis carbunculus	0.07	0.08	Brouard and Grandperrin 1984
E. coruscans	0.13	0.12	Brouard and Grandperrin 1984
	0.16	0.36	Ralston and Williams Unpub.
L. malabaricus	0.31	0.42	Brouard and Grandperrin 1984
L. purpureus	0.09	0.35	Menezes and Gesteira 1974 Ivo and Gesteira 1974
Ocyurus chrysurus	0.16	0.20	Piedra 1965
Pristipomoides auricilla	0.27	0.66	Ralston and Williams Unpub.
P. filamentosus	0.15	0.25	Ralston 1984 Ralston and Miyamoto 1983
	0.22	0.55	Ralston and Williams Unpub.
	0.29	0.53	Brouard and Grandperrin 1984
P. flavipinnis	0.36	0.83	Brouard and Grandperrin 1984
P. multidens	0.24	0.42	Brouard and Grandperrin 1984
	0.19	0.63	Ralston and Williams Unpub.
P. zonatus	0.20	0.53	Ralston and Williams Unpub.
Serranidae			
Epinephelus guttatus	0.24	0.68	Thompson and Munro 1978
E. niveatus	0.09	0.18	Moore and Labisky 1984
E. striatus	0.09	0.23	Thompson and Munro 1978
Mycteroperca venenosa	0.13	0.29	Thompson and Munro 1978
Plectropomus maculatus	0.13	0.30	Goeden 1977

estimated by total counts of daily otolith increments. Because exploitation was negligible, each calculation can be considered an independent estimate of M. The value given in the table is the average of these two estimates (see discussion above). Ralston and Williams (Unpub.) studied six lutjanids from the Marianas as well as P. multidens from Papua New Guinea. With the single exception of P. flavipinnis, all their estimates of total mortality could be considered equivalent to natural mortality because of low or nonexistent levels of fishing. However, one of the remaining species (Etelis carbunculus) was excluded due to an aberrant population structure. Growth rates were determined by numerical integration of daily otolith increments. Of the five serranid species studied by Thompson and Munro (1978), reasonably reliable growth curves were developed from modal progressions and hard parts for the three species listed in the table. They estimated the ratio of total mortality to growth from a number of areas, one of which could be considered virgin fishing grounds, and separated the ratio using their growth estimates. Where parameter estimates were specified as a range, the interval midpoint was used here. Although age-specific mortality rates were given by Goeden (1977, see above) for Plectropomus maculatus, survivorship from age 2 to 3 is used here because the remaining estimates are unaccountably low.

Natural mortality rate is then plotted against the von Bertalanffy growth rate parameter in Figure 8.1, where, not surprisingly, it is seen that M is positively correlated with K (r = 0.82). Closed symbols in the figure represent the 14 lutjanid stocks while the 5 open circles depict the serranids. Among the former, the circles are from the study of Brouard and Grandperrin (1984) in Vanuatu, the squares from Ralston and Williams' (Unpub.) work on Marianas stocks, and the triangles represent the remaining four investigations of snappers (Piedra 1965; Menezes and Gesteira 1974; Ivo and Gesteira 1974; Ralston 1984; Ralston and Miyamoto 1983).

Analysis of covariance was used to determine whether the data from snappers and groupers could be pooled. The results showed that no differences were evident in either slope (P = 0.29) or adjusted means (P = 0.42), although clearly the size of the grouper sample was small. The data were then pooled and analyzed by linear regression (solid line in figure), with the following result:

$$M = 0.0189 + 2.06\ K$$

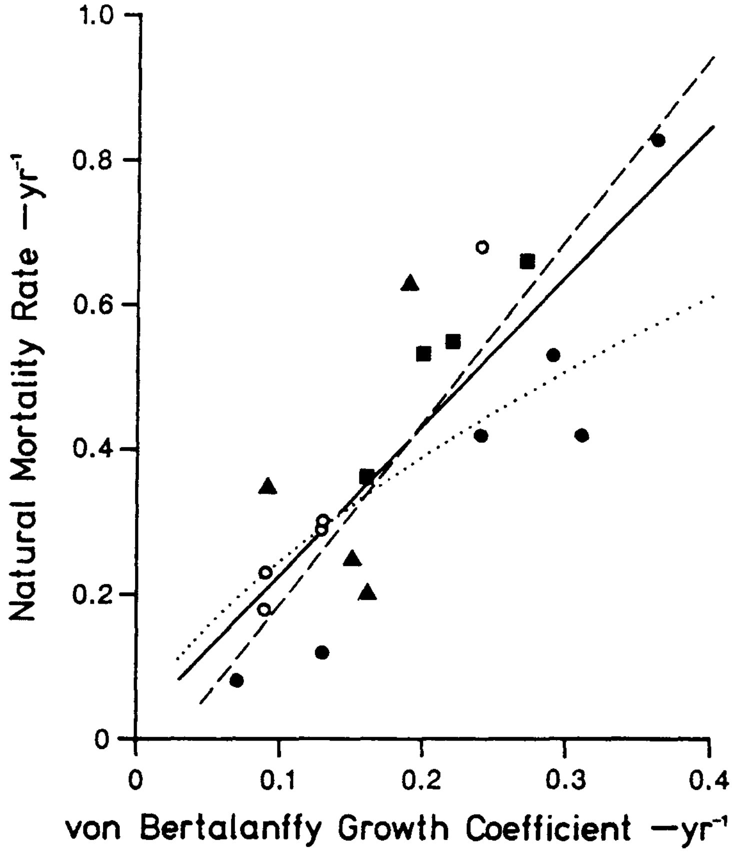

Figure 8.1 The relationship between natural mortality rate (M) and von Bertalanffy growth coefficient (K) for 19 stocks of snappers and groupers. See text for a detailed explanation of symbols

with standard errors for the intercept and slope equal to 0.0713 and 0.3528, respectively. The regression's slope was highly significant ($P < 0.0001$), although the estimate of intercept did not differ significantly from zero ($P = 0.79$). Thus, the ratio of natural mortality to growth rate within these two taxa is estimated to approximately 2, a simple rule of thumb that agrees with the data presented in Sylvester (1974). He presented length-frequency distributions for populations of *L. vivanus*, *L. buccanella*, and *Pristipomoides macrophthalmus* with negligible levels of exploitation, all of which had near linear descending (i.e., right-hand) limbs to the curves, a characteristic of populations with mortality to growth ratios (Z/K) equal to 2 (Powell 1979). Similarly, highly skewed length-frequency distributions of *L. campechanus* (Bradley and Bryan 1975; Fable 1980) and *Rhomboplites aurorubens* (Fable 1980) are known from heavily exploited populations in which Z/K greatly exceeds 2.0.

The estimate of mean squared error for the regression in Figure 8.1 is 0.015, and thus the standard deviation of residuals is s = 0.12 per year. Although predictions of individual and population M values depend on specifying the level of K (Snedecor and Cochran 1967), one would expect the 95% confidence interval for a prediction to lie very roughly ±0.24 per year above and below the regression line (i.e., two standard deviations). Similarly, approximately two-thirds of all observations are expected to lie within ±0.12 per year of the regression.

Presented in the figure as a dashed line is the functional regression (Ricker 1973) of M on K, where:

$$M = -0.0666 + 2.52\ K$$

Due to the nature of functional regressions, no statistical inference can be drawn from this result, except to say that it provides the best estimates of natural mortality rate if K is measured with a level of error comparable to that of M, a likely situation. If necessary, Ricker (1973) suggests using the symmetrical regression error limits obtained from the predictive analysis.

The dotted line in Figure 8.1 is the fit of a modified form of the Pauly (1980) equation to the data presented in Table 8.1. A simple $\log_{10}$ power function was made to pass through the means of log(K) and log(M), with the coefficient on the $\log_{10}$ K independent variable (0.665) obtained from the Pauly multiple regression equation. The result is to fit the data to his model, but using only one of the three variables he used. The graph shows that over the available range of K values the Pauly equation performs reasonably well, but tends toward overestimation of M for slow-growing species and underestimation of M for the faster growing ones.

The results presented here demonstrate that one can predict the natural mortality rate of snapper and grouper stocks with some accuracy, possessing nothing more than an estimate of the von Bertalanffy growth coefficient. These predictions are appreciably better than those calculated from the Pauly (1980) equation, both in terms of the distribution of residuals and the precision of estimates.

Comparable correlation coefficients were derived in the two studies (0.82 here versus 0.84 for Pauly's overall multiple correlation coefficient, and 0.58 for the second order partial correlation coefficient between M and K after the effects of temperature and asymptotic size were removed), although the range of available K values was 17 times greater in Pauly's study (0.04-4.92 per year). By necessity, residual variation must have correspondingly been reduced in Figure 8.1. Moreover, the standard deviation of $\log_{10}$ M values about the regression line (0.247) given in Pauly (1980) is indicative of a level of variation substantially greater than that in Figure 8.1 (s = 0.12 per year on untransformed M values). The improve ment in predictive capability of the K variable is likely due to restricting the analysis to more narrowly defined taxa and habitats.

AGENTS OF NATURAL MORTALITY

A number of studies have reported incidental observations on factors actually or potentially responsible for the natural deaths of snappers and groupers. There have been four agents identified to date, including predation, parasitism, cold water shock, and red tides.

Starck and Schroeder (1970) were among the first to document predation on either of these groups, observing a great barracuda, Sphyraena barracuda, strike a gray snapper, L. griseus, and also finding the remains of another in the stomach of a cubera snapper, L. cyanopterus. Additionally, they also believed green morays, Gymnothorax funebris, were important predators of L. griseus. Bradley and Bryan (1975) found juvenile red snapper, L. campechanus, in the gut contents of a lizard fish, Synodontidae, and a dolphin, Coryphaena hippurus, and speculated that "sharks probably also prey on snappers." Likewise, Olsen and LaPlace (1979) observed sharks attacking Epinephelus striatus that had formed a breeding aggregation, and Fable (1980) saw amberjack, Seriola dumerili, and S. barracuda consume L. campechanus and R. aurorubens that had recently been tagged and released. From the available evidence it seems likely that predation related mortality on snappers and groupers is strongly size dependent, being most severe on the young.

Parasitism of lutjanids has been documented in several investigations (Starck and Schroeder 1970; Skinner 1982; Brusca and Gilligan 1983), but was apparently only a serious problem where pollutants (ammonia, pesticides, etc.) so severely irritated and stressed a population of L. griseus that physical and physiological changes were induced, including epithelial hyperplasia, fusion of gill lamellae, and aneurisms. These changes resulted in reduced resistance to parasite infestations, which on occasion were debilitating (Skinner 1982).

Cold water shock has been cited repeatedly as a source of natural mortality in Florida's snappers and groupers. Starck and Schroeder (1970) reported that reduced water temperatures (11-14° C) resulting from cold snaps were known to kill L. griseus. Gilmore et al. (1978) observed mortality of E. itajara, E. morio, Mycteroperca microlepis, L. griseus, L. analis, and L. synagris from 13° C seawater. They also cite cold water intolerance by E. striatus, M. bonaci, Diplectrum formosum, L. apodus, L. jocu, and Ocyurus chrysurus. Likewise, Bohnsack (1983) observed E. striatus, L. apodus, and M. bonaci either dead or stunned from the effects of cold water (11-14° C) and concluded that "larger fish species and larger individuals within a species were the most sensitive to cold stress." Although in each of these studies thermal stress was cited as a major mortality factor, it is unlikely that most snappers and groupers, coming from more tropical climes, are similarly exposed to the threat of cold water shock.

The same is probably true of mass mortalities attributable to red tides, which typically are associated more with continental waters than insular areas. Smith (1976), however, documented extensive mortality in Gulf of Mexico populations of E. morio, E. itajara, M. microlepis, M. phenax, and L. griseus due to the effects of the red tide dinoflagellate Gymnodinium breve.

THE RELATIONSHIP OF FISHING MORTALITY TO NATURAL MORTALITY

As discussed previously, empirical and some theoretical justification exists to suppose that the optimum level of fishing mortality (F_{opt}) that can be applied to a stock to maximize biological yield is reasonably estimated by the natural mortality rate of the unfished population (Alverson and Pereyra 1969; Gulland 1971). Without detailed knowledge of the shape of the spawner-recruit relationship, however, it would seem more prudent to employ the range $0.8\ M < F_{opt} < 1.5\ M$ as reasonable bounds on an estimate of optimum fishing mortality (Francis 1974;

Deriso 1982; Beddington and Cooke 1983; Polovina 1986). Given this range for a target level of exploitation, what does the literature tell us about the intensity with which snapper/grouper stocks have been harvested?

A convenient means of expressing exploitation intensity is to scale fishing mortality by natural mortality, i.e., to form the ratio F/M. The ratio goes to zero in the absence of fishing and increases without bound as fishing mortality increases. An F/M ratio of 1.0 would correspond to the suggestion of Gulland (1971) that fishing mortality was at an optimal level. When properly scaled, comparisons become possible between stocks with differing mortality schedules and/or yield potentials.

The results presented in Table 8.2 provide a representative sampling of studies that have estimated snapper/grouper natural and fishing mortalities. The F/M ratio is presented for each, but some additional information is useful in interpreting the results.

The value for natural mortality used by Nelson and Manooch (1982) was obtained from the Pauly (1980) equation and equaled 0.20 per year. This estimate may be low since they estimated K = 0.17 per year. The relationship derived earlier would suggest that M = 0.36 per year may be a better estimate. If true, the F/M ratios listed for their study may be too high. The same is true of Matheson and Huntsman (1984), who used a Pauly estimate of M = 0.20 per year for E. drummondhayi when the von Bertalanffy growth rate parameter was determined to be K = 0.13 per year. For P. flavipinnis (Ralston and Williams Unpub.), the total mortality rate was determined by the Z/K regression method of Wetherall et al. (In press) and natural mortality from the relationship between K (0.20 per year) and M derived earlier. Although McErlean (1963) did not calculate the von Bertalanffy growth rate parameter or the mortality rate of M. microlepis, he presented information concerning both age at length and abundance in the catch by age class. These data were reanalyzed using a Walford plot and catch curve, respectively, yielding K = 0.14 per year and Z = 1.20 per year. Natural mortality was also estimated from the K of this species (M = 0.30 per year). One study that is not included is that of Moe (1969), because he estimated total mortality rate to be 0.32 per year with a K of 0.18 per year. These findings would suggest that the stock was lightly fished, even though it was believed to be heavily exploited for years.

The data from Table 8.2 were tabulated into a frequency distribution of F/M values, which is presented

TABLE 8.2
Summary information on the ratio of natural and fishing mortality estimates (F/M) for the snapper and grouper families

Species	F/M	Source
Lutjanidae		
Lutjanus campechanus	1.25	Nelson and Manooch 1982
	1.63	Nelson and Manooch 1982
	1.26	Nelson and Manooch 1982
	3.30	Nelson and Manooch 1982
L. purpureus	1.66	Ivo and Gesteira 1974
	1.94	Ivo and Hanson 1982
	2.23	Ivo and Hanson 1982
	1.73	Ivo and Hanson 1982
Pristipomoides filamentosus	1.92	Ralston 1984
P. flavipinnis	1.33	Ralston and Williams Unpub.
Serranidae		
Centropristis striata	1.77	Low 1981
	1.00	Low 1981
Epinephelus drummondhayi	0.85	Matheson and Huntsman 1984
	0.35	Matheson and Huntsman 1984
E. guttatus	0.28	Thompson and Munro 1978
	0.32	Thompson and Munro 1978
E. niveatus	0.27	Matheson 1981
	1.80	Matheson 1981
	1.93	Matheson and Huntsman 1984
	0.67	Matheson and Huntsman 1984
E. sexfasciatus	0.71	Pauly and Ingles 1982
E. striatus	2.52	Olson and LaPlace 1979
Mycteroperca microlepis	3.00	McErlean 1963 (recalculated)
M. phenax	2.00	Matheson et al. 1984
	1.24	Matheson et al. 1984

in Figure 8.2. Snapper stocks are shown in crosshatch and grouper populations are stippled. The solid line represents the frequency polygon for the combined snapper/grouper data.

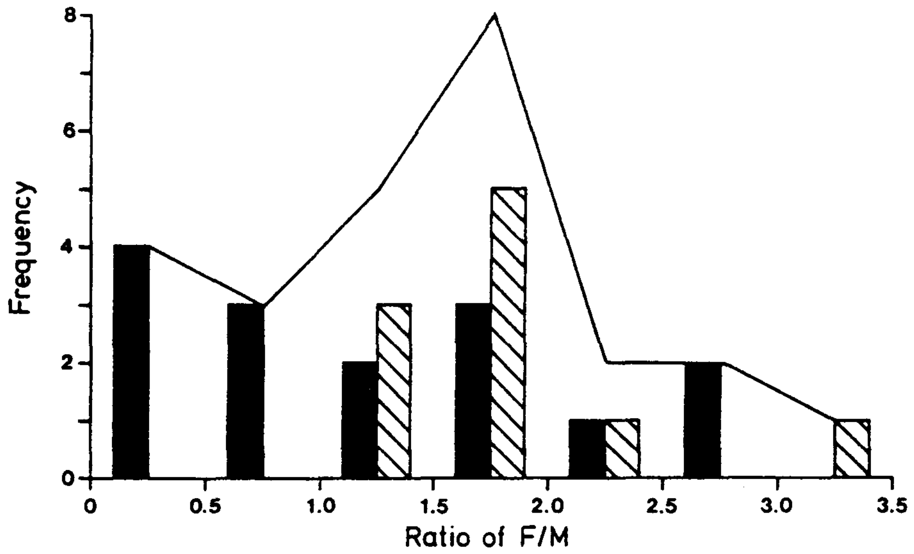

Figure 8.2 Exploitation intensity on snappers (crosshatch) and groupers (stiple). The figure presents the ratio of published values of fishing and natural mortality rates for 25 exploited stocks. The solid line represents the combined frequency polygon

At least two major trends are evident in the figure. It is clear that on a relative basis the lutjanid stocks reviewed here have been more intensely harvested than the groupers. Whether this conclusion is more generally warranted or whether it simply reflects a sampling or research bias is unknown. If, however, the pattern is real, it may reflect conservative fishing practices towards the epinephelines. This group is believed to be especially vulnerable to overexploitation, both because of their protogynous reproductive system and their tendency to aggregate during spawning (Johannes 1981; Shapiro 1986; but see Bannerot et al. 1986).

It is also apparent from the figure that many studies have determined fishing to natural mortality ratios far in excess of the 0.8 to 1.5 range suggested earlier. That some of these stocks are heavily exploited and have been so for years, is well documented (Camber 1955; Carpenter 1965; Ramirez 1970; Bradley and Bryan 1975; Tashiro and Coleman 1977). Nonetheless, the extreme levels of exploitation that seem to characterize some snapper and grouper stocks (e.g., the Louisiana stock of L. campechanus cited by Nelson and Manooch (1982), where $\bar{F} = 0.86$ per year and $F/M > 3.0$) are reason to assess the situation and develop alternative explanations for these data, including the following: (1) The theoretical basis for of the $F_{opt} = M$ approximation is in error; (2) the approximation is not applicable to snapper and grouper stocks; (3) the amount of replenishment or exchange between "stocks" is often so poorly understood that analyses of population dynamics tell us very little; and (4) some stocks are simply overfished due to lack of management action.

With regard to relative levels of exploitation, one observation by Adams (1980) is particularly relevant. So-called "K" selected species are those with late maturity, slow growth rate, large asymptotic size, low rates of natural mortality, and extended maximum age. Note that K here refers to carrying capacity, which should not be confused with the von Bertalanffy growth coefficient. Members of the Lutjanidae and Epinephelinae, when placed on an r-K continuum defined by the community of tropical species with which they are found, tend to fit this description well (Beverton and Holt 1959; Pauly 1980). Simulation studies (Adams 1980) and actual fisheries experience (Huntsman et al. 1983; Mahmoudi et al. 1984) have shown that for these kinds of species, maximum yield per recruit (sensu Beverton and Holt 1957) is obtained at lower levels of fishing mortality and higher ages of recruitment (i.e., entry to the fishery) than their ecological counterparts. Furthermore, the relatively low levels of natural mortality that characterize snappers and groupers indicate a low natural turnover ratio (Allen 1971) and thus a reduced productive capacity (Alverson and Pereyra 1969; Gulland 1971). Fisheries for these kinds of species are also likely to develop excessive harvesting capacity during the fishing-up process (Francis 1984; Leaman and Beamish 1984). Based upon these considerations and on the high economic value of snappers and groupers, it is important that future efforts to manage these resources show caution and appropriate restraint.

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