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NATURAL MORTALITY OF GAG GROUPER FROM 1950 TO 2009 GENERATED BY AN ECOSIM MODEL

SEDAR 33 Working Paper

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Abstract

To move beyond the assumption of constant natural mortality in stock assessment models, we have begun to rely on multi-species and ecosystem model to provide estimates of time and age-specific rates of natural mortality. We used an Ecopath with Ecosim model of the West Florida Shelf to estimate natural mortality for 3 age class of gag grouper from 1950 to 2009. Variability in M decreased with age and compensatory improvements in survival caused mortality rates to decline during periods of low abundance. We also found the model to be sensitive to the parameters the strength of the compensatory response. These estimates could be used to apply time-varying, age-specific natural mortality in the current stock assessment for gag grouper.

Introduction

Traditionally, single species stock assessment models have assumed a constant rate of natural mortality over time and sometimes age. This has been the case not because it was believed that mortality was constant but because the ability to quantify changes in natural mortality did not exist until recently. Through the development of trophic dynamic models, we now have the capability to describe how natural mortality has changed with predator abundance and food availability. The purpose of this paper is to describe estimates of natural mortality derived by an Ecopath with Ecosim model and demonstrate the sensitivity of the model to assumptions about density-dependent effects and predator impacts. The intention is for these estimates to be considered for inclusion in the SEDAR 33 stock assessment for Gulf of Mexico gag grouper.

Modeling Approach

Ecopath with Ecosim (EwE) is a modeling package that facilitates management of basic biomass and trophic interaction data for whole ecosystems and has been widely used for analysis of exploited aquatic resources. The Ecopath component of EwE is a mass-balanced representation of the food web and the Ecosim component simulates ecosystem dynamics over time by changing fishing mortality, fishing effort, or environmental forcing functions. EwE allows for coarse age structure representation and it can be calibrated to fit time series of abundance and catch. The basic data requirements for Ecopath are biomass, total mortality or production rate, consumption rate, diet composition, landings, and discards. Details of EwE and examples of applications to fisheries ecology and management are provided elsewhere (Christensen and Walters 2004; Walters and Martell 2004). This paper will focus on the estimation of natural mortality.

In Ecopath, mortality is partitioned into components of fishing, predation, and other mortality such that $Z = F + M2 + M0$ where F is fishing mortality, $M2$ is predation mortality, and $M0$ is other (unexplained mortality). In Ecopath, Z is specified by the user, $M2$ is calculated from diet compositions and consumption rates of predators, F is determined based on total removals by the fishery, and $M0$ is simply the remainder of Z not accounted for by F or $M2$. Predation mortality is calculated as

$$M2_i = \sum_{j=1}^{n} Q_j \cdot DC_{ji}$$

where Q_j is the total consumption rate for group *j* and DC_{ji} is the contribution of prey *i* to the diet of predator *j*.

In Ecosim, biomass dynamics are modeled on a monthly time step as a series of differential equations where change in biomass is predicted as a function of consumption minus losses to predation, fishing, and other mortalities (ignoring migration) using the equation

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} - (M0_i + F_i) \times B_i$$

where the two summations estimate consumption rates, the first expressing total consumption by group *i* and the second the predation by all predators on the same group *i* (Christensen and Walters 2004). These two consumption equations combined with fishery and environmental change predicts time-varying gains and losses for the species involved.

Consumption is predicted based on foraging arena theory which assumes that prey are divided into states that make them vulnerable or invulnerable to predators and that predation is dependent upon the exchange rate between these two states (Ahrens *et al.* 2012; Walters *et al.* 1997). Partitioning of prey into these two states may arise out of spatial and temporal risk sensitive behavioral patterns of predators and prey (e.g. hiding when not feeding). Foraging arena theory predicts less variation in natural mortality than would be expected from changes in predator abundance and can help explain why natural mortality rates are not typically proportional to predator abundance.

The basic equation for predicting consumption is

$$Q_{ij} = \frac{a_{ij} v_{ij} B_i P_j}{2v_{ij} + a_{ij} P_j}$$

where a_{ij} is the effective search rate, B is the prey biomass, P is the predator biomass, and v_{ij} is the base vulnerability exchange rate. The v_{ij} represent the rate that prey move from invulnerable to vulnerable states and there is one parameter for each predator-prey interaction. The model for consumption has been elaborated to included components for feeding time, forcing functions, mediation effects of third party organisms, and handling time limits (Christensen and Walters 2004).

In Ecosim, vulnerability parameters are essentially multipliers on predation mortality rates. For example, a vulnerability of 2 implies that a predator could, at most, double the predation mortality exerted on its prey when predator biomass increases. Very low vulnerability exchange rates imply ‘bottom-up’ processes because changes in predator abundances do not result in drastic changes to prey biomass. Low v_{ij} cause stronger compensatory responses to increased mortality, and a reduced capacity to increase following reductions in mortality. High settings of v imply ‘top-down’ control where consumption increases dramatically with predator abundance and therefore produces more dynamic predator-prey interactions.

Methods

Development of the WFS Reef Fish EwE Model

We developed the model around managed (target) species in the eastern Gulf of Mexico including reef fishes (groupers and snappers), coastal migratory pelagics (mackerels), and highly migratory pelagics as defined by the GMFMC and NMFS. The area being modeled extends from the Florida panhandle south to a boundary that excludes the Florida Keys. Particular emphasis was given to select groupers and snappers that inhabit reefs and hardbottom on the west Florida shelf and support valuable commercial and recreational fisheries. These were represented in the model by 2 or 3 age classes to capture basic ontogenetic changes in diet, habitat, and fishery selectivity. Because several reef fishes were further divided into life-stages, coastal and inshore species were included because they interact with juveniles that have not yet migrated to offshore reefs. Aggregate groups of non-target fishes, invertebrates, zooplankton, and primary producers are necessary for a complete food web and were also included. The resulting model consisted of 70 biomass pools including one each for dolphins and seabirds, 43 fish groups (of which 11 are non-adult life stages), 18 invertebrate groups, 4 primary producers, and 3 detritus groups. The fishery included four recreational (shore based, private boat, charter boat, and headboat) and nine commercial fishing 'fleets' (vertical line, bottom longline, pelagic longling, pelagic troll, gill/trammel nets, cast nets, purse/haul seines, trawls, fish traps, and crab traps).

Gag grouper was included as a multistanza group with three age classes. The 0-1 year old age group represents the juveniles that generally reside in nearshore to estuarine habitats and are not usually caught in the fishery. The 1-3 year old group represents those individuals that have begun the migration to deeper waters and offshore reef areas and are often captured by the fishery but below the legal size limit. All of the fishing mortality on the youngest two groups is in the form of discards. The age 3+ group is the adult group which is considered to be fully recruited to the fishery. Basic input parameters for the multi-stanza model along with Ecopath base mortality rates are provided in Table 1.

To assimilate the diet matrix, we combined stomach content data from a literature search with those collected by the FWC FIM gut lab. A total of 43,170 stomachs from 235 species in 119 published studies and FIM data were included in the diet matrix. Of these, none observed gag as a prey item and only two studies, one for jack crevalle (Saloman and Naughton 1984) and the other on gag (Naughton and Saloman 1985) recorded *Mycteroperca spp.* as a prey item. Predators that were observed with small amounts of unidentified Serranidae in their stomachs included king mackerel (Saloman and Naughton 1983), sailfish (Jolley 1977; Rosas-Alayola *et al.* 2002), cobia (Franks *et al.* 1996), greater amberjack (Manooch and Haimovici 1983), scamp (Matheson *et al.* 1986), yellowfin grouper (Randall 1967), and red grouper (Weaver 1996), some of which were collected outside the West Florida Shelf. Therefore, the proportion of any predator's diet that is gag was determined by distributing the portion of the diet composition that was identified at coarser taxonomic levels to groups in the model based on the relative biomass of the prey groups and/or their known contribution to the diet. Predation mortalities resulting from this procedure are provided in Table 2.

The Ecosim model was run from 1950 to 2009. Time series for calibrating the model were obtained directly from stock assessments or taken from fisheries independent and other various survey data. We used nutrient loads from the Mississippi River to force phytoplankton production on the west Florida shelf and capture the major changes in productivity that have taken place over the last 60 years (Goolsby and Battaglin 2000; Aulenbach *et al*. 2007). In addition to nutrients from the Mississippi River, chlorophyll-a production along the west Florida shelf is also affected by upwelling and physical transport processes (Castillo *et al.* 2001; Gilbes *et al.* 2002; Gilbes *et al.* 1996) not captured in the Mississippi River nutrient load time series.

Model Calibration

In order to calibrate the model, biomass, catch, and total mortality parameters were rescaled to represent a historic (1950s) condition. This involved increasing biomass, reducing catch, and reducing total mortality to a level closer to natural mortality. In most cases, the stock assessment or time series data provided the information necessary to make such adjustments. The most important parameters when calibrating Ecosim models are the vulnerability exchange rates (v). Other parameters are available to modify how quickly organisms adjust the time they spend foraging, the sensitivity of other mortality to changes in feeding time, the effect that predators have on feeding time, handling time effects, and prey switching. Overall, the model is less sensitive to these parameters but they do provide the ability to stabilize consumption rates, model density dependent natural mortality, represent varying degrees of recruitment compensation, simulate risk sensitive foraging behavior, and adjust the responsiveness of predators to prey abundances.

To fit the model to time series, manual adjustments were made to the foraging arena parameters, especially the vulnerability exchange rates, to correct for any gross divergence from the data. For example, groups that were crashing out of the model usually required that v_{ij}'s be reduced or feeding time varied to allow for compensatory improvements in survival at low stock sizes. After correcting for any obvious errors, an automated search was executed that adjusts the v_{ij}'s to minimize the sum of squared deviation between predicted and observed data. This process was repeated iteratively, focusing on the group with the poorest fit, until all groups were able to at least reproduce the major patterns in biomass and catch over the entire time period. As a diagnostic, we compared the F_{msy} values from Ecosim to those estimated by the single species stock assessment models. F_{msy} was estimated by incrementing fishing mortality rates and running Ecosim to equilibrium while holding other groups stationary.

This was done to correct for any erroneous parameters estimated during the search routine and calibration process that were not consistent with largely agreed upon biological reference points. Model fit to time series of biomass and catch are shown in Figure 1 and Figure 2.

Generating Time Series of M for Gag

Each simulation of the Ecosim model provides monthly estimates of fishing mortality, predation mortality, and unexplained mortality. We generated estimates of *M* for each age stanza and each year using the baseline diet composition and resulting predation mortalities provided in Table 1. We also performed additional simulations to estimate natural mortality under alternative hypotheses about predation mortality and compensatory survival. To included compensatory changes in survival, there must be a non-zero feeding time adjustment rate combined with a high proportion of other mortality being sensitive to changes in feeding time. This represents density-dependent changes in juvenile mortality rates such that when biomass decreases feeding time, and thus time exposed to predation, also decreases causing a reduction in natural mortality rates. The compensatory effect can be increased by setting low values for the vulnerability exchange rates, increasing the foraging time adjustment rate, or increasing the proportion of *M0* sensitive to feeding time. When the feeding time adjustment rate is set to 0, compensatory responses in growth rate are created and mortality does not change with abundance. The baseline simulation and 4 sensitivity runs are described below.

Baseline Simulation. The baseline simulation includes moderate compensatory effects and risk-sensitive foraging in the juvenile groups. In this configuration, the vulnerability exchange rates of prey to gag 0-1 and gag 1-3 groups were 1.5 and 2 respectively. Feeding time adjustment was set to 0.5 and the proportion of other mortality sensitive to changes in feeding time was set to 1 for both juvenile groups and 0.15 and 0.5 for the adult group. The vulnerability settings for the adult group were determined during the calibration process.

Strong Compensation in Survival. As described above, compensatory survival can be made stronger by increasing the feeding time adjustment rate and/or proportion of *M0* sensitive to time spent feeding or by lowering the values of the vulnerability exchange rates. To increase the compensatory response from the baseline scenario, vulnerability of prey to the gag 0-1 and gag 1-3 groups were reduced to 1.25 and 2 respectively. The vulnerabilities for the adult group remained unchanged from the calibrated version, however the feeding time adjustment rate was increased to 0.5.

Weak Compensation in Survival. To reduce the strength of compensatory changes in mortality, feeding time adjustment rates for the two juvenile groups were set to 0.2 and the adult group was set to 0. Vulnerability exchange rates of prey to gag 0-1 and gag 1-3 were 5 and 10 respectively while the vulnerabilities for the adult group were determined during the calibration process.

Additional Predators. Because the predators on gag are poorly defined based on available stomach content data, we performed a sensitivity run using the baseline scenario in which additional predators were assigned to gag. For example, there is little quantitative information describing the diet of goliath grouper and that which does exist does not list gag as a prey item and suggests that their diet consists mainly of crustaceans (Koenig and Coleman 2009). However, while diving on the west Florida shelf a goliath grouper was observed eating a gag grouper (Dr. Daryl Parkyn, University of Florida, personal communication), an interaction not included in the baseline scenario. It is also a reasonable assumption that there is some predation by large coastal sharks on gag. To test for the impact of these predators on natural mortality rates over time, we back calculated the diet compensation necessary to account for 5% of the total mortality for each age group of gag and assigned a v_{ij} of 4 for each newly created interaction.

Results

Estimated natural mortality rates are provided in Figure 3 and Table 3. As expected, variability in natural mortality decreased with age in all simulations. *M* for gag age 0-1 varied between 1 and 3, while M for ages 1-3 varied between 0.6 and 0.9 and for ages 3+ the range for M was 0.10-0.17. For the age 0-1 group base simulation, natural mortality declined from 3.0 in the beginning of the simulation to about 1.9 during the early 1990’s then increased to nearly 2.4 from 1995-2000 and has since declined to a value near 1.75. This is due to density dependent effects on survival such that feeding time and time spent exposed to predation declines with abundance. Natural mortality for ages 1-3 declined from 0.9 in 1950 to about 0.65 in 1980 and it has since remained between 0.65 and 0.75. The adult group also showed a decline in *M* from 0.15 in 1950 to 0.13 in 1980 and has fluctuated between 0.12 and 0.13 ever since.

The effect of compensation in mortality is clear when comparing rates across scenarios and examining the emergent stock-recruit relationships. Strong compensation leads to more change in M and more stable biomass trajectories. Thus, the number of recruits is flat across a wide range of adult abundance with a steep slope at the origin and sometimes a dome shape with lower juveniles at high adult abundances (Figure 4). Weak compensation results in less change to mortality but more variability in biomass estimates. The emergent stock-recruit relationship then appears to be nearly a straight line out of the origin where juveniles are almost proportional to the number of adults. The base model falls between these two extreme scenarios and a typical Beverton-Holt shaped curve emerges with a moderately steep slope at the origin.

The effect of adding large coastal sharks and goliath grouper as predators on gag was minimal, especially in the juvenile groups. The impact of including additional predators is more pronounced for the adult group than the juveniles because the assumed predation mortality (5% of *Z*) by those two species on adult gag is higher than any predators already accounted for in the model. In the adult group, natural mortality in this scenario was lower than the base simulations after about 1970 when the biomass of sharks and goliath grouper began to rapidly decline. For the juvenile groups, the natural mortality rates in the base and additional predators simulations were indistinguishable from one another because the hypothesized predation mortality rates were small compared to the total predation mortality already accounted for in the model.

Discussion

We have demonstrated the ability of Ecosim to generate estimates of natural mortality rates over time and for specific age classes in response to changes in abundance of predators and prey. Several methods have been proposed for incorporating this type of information into a single species stock assessment model, each with advantages and disadvantages. Some methods include adding another mortality agent as a separate fleet in the model (Moustahfid *et al.* 2009a; Moustahfid *et al.* 2009b; Muller and Taylor 2012), estimating an additional parameter in the model (SEDAR 2009), or including these deviations as an error term in the model. The best method depends on the model being used and which is most appropriate for gag is beyond the scope of this paper and will be discussed elsewhere.

However, using models to estimate natural mortality has limitations which are not unique to Ecopath with Ecosim. One limitation, and probably the most difficult to overcome, is that predators are poorly defined for gag. Most diet studies focus on determining the importance of prey to a specific predator with little attention given to rare prey items, especially small fishes and juveniles that are difficult to identify. In cases where an abundant predator with a high consumption rate “incidentally” preys upon a juvenile gag, the predation mortality can be very large and impact the juvenile group greatly even when their contribution to the overall diet is trivially small. While it is safe to assume that large-bodied adults are not preyed upon as often as smaller fishes, isolated predation events do likely occur. Diet studies on large offshore predators are few and encounters with fish large enough to consume an adult gag are rare during most surveys and likely to miss any isolated predation events. We addressed this limitation by conducting sensitivity runs under alternative hypothesis about predation mortality rates. These runs indicated that there would need to be a rather large amount of predation mortality added to the model in order to have an effect (>10% of Z). Other modeling approaches such as Atlantis and OSMOSE do not utilize diet composition data but rather predict predator-prey interactions based on spatio-temporal overlap and gape limitations. These approaches could be helpful in improving diet matrices for use in Ecopath with Ecosim models.

Episodic mortality events, such as those caused by red tides, cold kills, or chemical spills were not included in this model and natural mortality could be underestimated for years when such events occurred. Some approaches to account for this source of mortality include specifying a fleet as a separate mortality agent (e.g. a ‘red tide’ fleet) or modifying production rates through mediation and forcing functions. These capabilities are currently under development and near completion and will likely be included in future development of this model (Dr. Cameron Ainsworth, University of South Florida, personal communication).

The abundance of recruits predicted by the EwE model differed from the single species stock assessment model and was generally more stable. This could be due to differences in model parameterizations and/or bad time series data especially in the earlier years. The single species models estimate recruits based on assumptions of constant survival and adult reproduction, and may or may not reflect actual abundances. Long-term fisheries independent time series of abundance for the juvenile groups is critical to obtaining more reliable and accurate mortality rates because the model could then be calibrated to observations that may actually reflect changes in abundance due to predation and/or episodic mortality events.

Despite these limitations, we should continue to confront the complex parameterization issues of ecosystem and multi-species fisheries models. Through hypothesis testing and alternative configurations of the models, we can at least identify which factors affect natural mortality and the magnitude required to create an impact. Furthermore, these models will surely lead to more productive discussions about hypotheses that drive natural mortality and allow for direct, quantitative comparisons between them.

Tables

Table 1. Basic input parameters and estimated mortality rates for gag grouper

Parameter	gag 0-1	gag 1-3	gag 3+
von Bertalanffy *K*	-	-	0.140
$W_{maturity}/W_{max}$	-	-	0.077
Age start (months)	0	12	36
biomass (t/km2)	0.0005	0.0050	0.1346
Q/B	28.237	9.248	3.036
Z	3.000	0.900	0.180
F	0.011	0.016	0.026
M2	1.137	0.077	3.685E-5
M0	1.852	0.806	0.154

Table 2. Predation mortality rates of gag grouper for base model.

Predator	gag 0-1	gag 1-3	gag 3+
billfish/tuna			3.64E-05
cobia	0.010	0.0011	
king mackerel adult	0.346	0.0377	
jacks/dolphinfish/other pelagics	0.001	0.0001	
yellowedge grouper 1-3	0.011		
yellowedge grouper 3+	0.162		
red grouper 1-3	0.262		
black grouper 0-1	0.023		
black grouper 3+	0.037	0.0076	
other shallow water grouper	0.205	0.0223	
amberjacks	0.079	0.0086	

Table 3. Natural mortality estimates from 1950 to 2009 for 3 age groups of gag, averaged across all months in each year.

	Gag 0-1				Gag 1-3				Gag 3+			
Year	Base	Strong Comp	Weak Comp	Base +predators	Base	Strong Comp	Weak Comp	Base +predators	Base	Strong Comp	Weak Comp	Base +predators
1950	3.00	2.99	2.99	2.99	0.88	0.88	0.88	0.88	0.15	0.15	0.15	0.15
1951	3.01	3.00	3.00	3.00	0.89	0.89	0.88	0.89	0.15	0.15	0.15	0.15
1952	3.00	3.00	3.00	2.99	0.89	0.89	0.89	0.89	0.15	0.15	0.15	0.15
1953	2.99	2.99	2.99	2.99	0.89	0.88	0.88	0.89	0.15	0.15	0.15	0.15
1954	2.98	2.99	2.98	2.98	0.88	0.88	0.88	0.88	0.15	0.15	0.15	0.15
1955	2.94	2.93	2.96	2.96	0.87	0.87	0.87	0.87	0.15	0.15	0.15	0.15
1956	3.02	2.95	3.01	3.02	0.85	0.85	0.85	0.85	0.15	0.15	0.15	0.15
1957	2.96	2.95	3.00	3.01	0.88	0.87	0.86	0.88	0.15	0.15	0.15	0.15
1958	2.98	2.91	3.00	2.99	0.84	0.83	0.85	0.83	0.15	0.15	0.15	0.15
1959	3.00	2.96	3.02	3.03	0.86	0.86	0.86	0.87	0.15	0.16	0.15	0.15
1960	2.96	2.96	2.98	2.99	0.88	0.88	0.88	0.89	0.16	0.16	0.15	0.16
1961	2.93	2.94	2.95	2.94	0.89	0.89	0.88	0.89	0.16	0.16	0.15	0.16
1962	2.91	2.93	2.92	2.92	0.90	0.90	0.89	0.90	0.16	0.16	0.15	0.16
1963	2.94	2.95	2.94	2.94	0.91	0.92	0.89	0.91	0.16	0.16	0.15	0.16
1964	2.94	2.99	2.94	2.94	0.95	0.95	0.91	0.95	0.16	0.16	0.15	0.16
1965	2.86	2.92	2.88	2.88	0.92	0.92	0.90	0.91	0.15	0.15	0.15	0.15
1966	2.95	2.89	2.94	2.95	0.87	0.87	0.86	0.86	0.15	0.14	0.15	0.14
1967	2.96	2.99	2.99	3.01	0.94	0.95	0.89	0.94	0.15	0.15	0.15	0.15
1968	2.87	2.92	2.92	2.92	0.91	0.90	0.89	0.91	0.15	0.15	0.15	0.15
1969	2.89	2.79	2.93	2.94	0.82	0.81	0.83	0.81	0.14	0.13	0.15	0.14
1970	2.97	2.82	3.04	3.07	0.81	0.81	0.80	0.81	0.14	0.13	0.15	0.13
1971	2.98	2.88	3.07	3.11	0.82	0.82	0.81	0.83	0.14	0.13	0.15	0.13
1972	2.87	2.84	3.00	3.02	0.81	0.80	0.82	0.82	0.14	0.13	0.15	0.14
1973	2.82	2.74	2.96	2.98	0.75	0.75	0.79	0.75	0.14	0.13	0.15	0.13
1974	2.80	2.73	2.96	3.00	0.74	0.74	0.77	0.74	0.14	0.13	0.15	0.13
1975	2.69	2.71	2.89	2.93	0.73	0.75	0.76	0.74	0.14	0.13	0.16	0.13
1976	2.52	2.66	2.77	2.80	0.73	0.75	0.77	0.74	0.14	0.13	0.16	0.13
1977	2.39	2.62	2.66	2.69	0.73	0.77	0.77	0.75	0.14	0.13	0.16	0.13
1978	2.19	2.49	2.51	2.54	0.72	0.77	0.75	0.73	0.14	0.13	0.15	0.13
1979	2.12	2.38	2.46	2.50	0.66	0.71	0.71	0.66	0.13	0.12	0.15	0.12
1980	2.15	2.40	2.49	2.58	0.65	0.72	0.69	0.66	0.13	0.12	0.15	0.12
1981	2.09	2.48	2.47	2.53	0.71	0.80	0.72	0.73	0.13	0.12	0.16	0.12
1982	1.96	2.40	2.37	2.39	0.71	0.79	0.74	0.72	0.13	0.12	0.16	0.12
1983	1.89	2.32	2.31	2.34	0.65	0.72	0.71	0.66	0.13	0.12	0.16	0.12
1984	1.84	2.29	2.28	2.34	0.63	0.72	0.69	0.64	0.12	0.10	0.15	0.11
1985	1.95	2.33	2.38	2.44	0.66	0.76	0.70	0.67	0.13	0.12	0.16	0.12
1986	1.75	2.32	2.25	2.29	0.66	0.74	0.70	0.67	0.12	0.11	0.16	0.11

1987	1.67	2.25	2.17	2.20	0.66	0.76	0.71	0.67	0.13	0.11	0.16	0.12
1988	1.63	2.26	2.12	2.15	0.69	0.81	0.73	0.70	0.13	0.12	0.16	0.12
1989	1.47	2.21	1.99	2.01	0.72	0.86	0.75	0.74	0.13	0.13	0.16	0.12
1990	1.38	2.11	1.89	1.90	0.69	0.82	0.73	0.70	0.13	0.12	0.15	0.12
1991	1.43	2.08	1.91	1.94	0.65	0.79	0.71	0.65	0.13	0.12	0.15	0.12
1992	1.44	2.12	1.94	1.98	0.64	0.79	0.69	0.65	0.13	0.12	0.16	0.12
1993	1.38	2.10	1.91	1.94	0.65	0.80	0.69	0.67	0.13	0.12	0.16	0.12
1994	1.37	2.08	1.88	1.91	0.63	0.76	0.69	0.64	0.12	0.11	0.15	0.11
1995	1.43	2.12	1.95	1.98	0.66	0.82	0.70	0.67	0.12	0.11	0.15	0.11
1996	1.49	2.17	1.99	2.01	0.67	0.83	0.71	0.69	0.12	0.11	0.15	0.11
1997	1.59	2.19	2.07	2.08	0.68	0.83	0.72	0.69	0.12	0.10	0.15	0.11
1998	1.73	2.24	2.17	2.19	0.67	0.80	0.71	0.67	0.12	0.11	0.15	0.11
1999	1.79	2.28	2.24	2.26	0.68	0.80	0.72	0.68	0.12	0.10	0.15	0.11
2000	1.95	2.39	2.34	2.37	0.71	0.83	0.74	0.72	0.12	0.11	0.16	0.12
2001	1.80	2.40	2.27	2.27	0.75	0.87	0.77	0.76	0.13	0.11	0.16	0.12
2002	1.66	2.32	2.12	2.12	0.69	0.79	0.76	0.69	0.13	0.11	0.16	0.11
2003	1.63	2.32	2.10	2.12	0.70	0.83	0.75	0.70	0.12	0.11	0.15	0.11
2004	1.56	2.32	2.04	2.07	0.70	0.84	0.75	0.71	0.13	0.11	0.16	0.12
2005	1.46	2.29	1.97	1.99	0.67	0.78	0.74	0.67	0.13	0.12	0.16	0.12
2006	1.39	2.32	1.93	1.95	0.68	0.81	0.75	0.69	0.12	0.11	0.16	0.11
2007	1.29	2.27	1.85	1.87	0.69	0.82	0.76	0.70	0.12	0.11	0.16	0.12
2008	1.19	2.17	1.76	1.77	0.62	0.72	0.72	0.62	0.13	0.12	0.17	0.12
2009	1.13	2.18	1.73	1.76	0.59	0.69	0.70	0.59	0.13	0.12	0.17	0.12

Figures

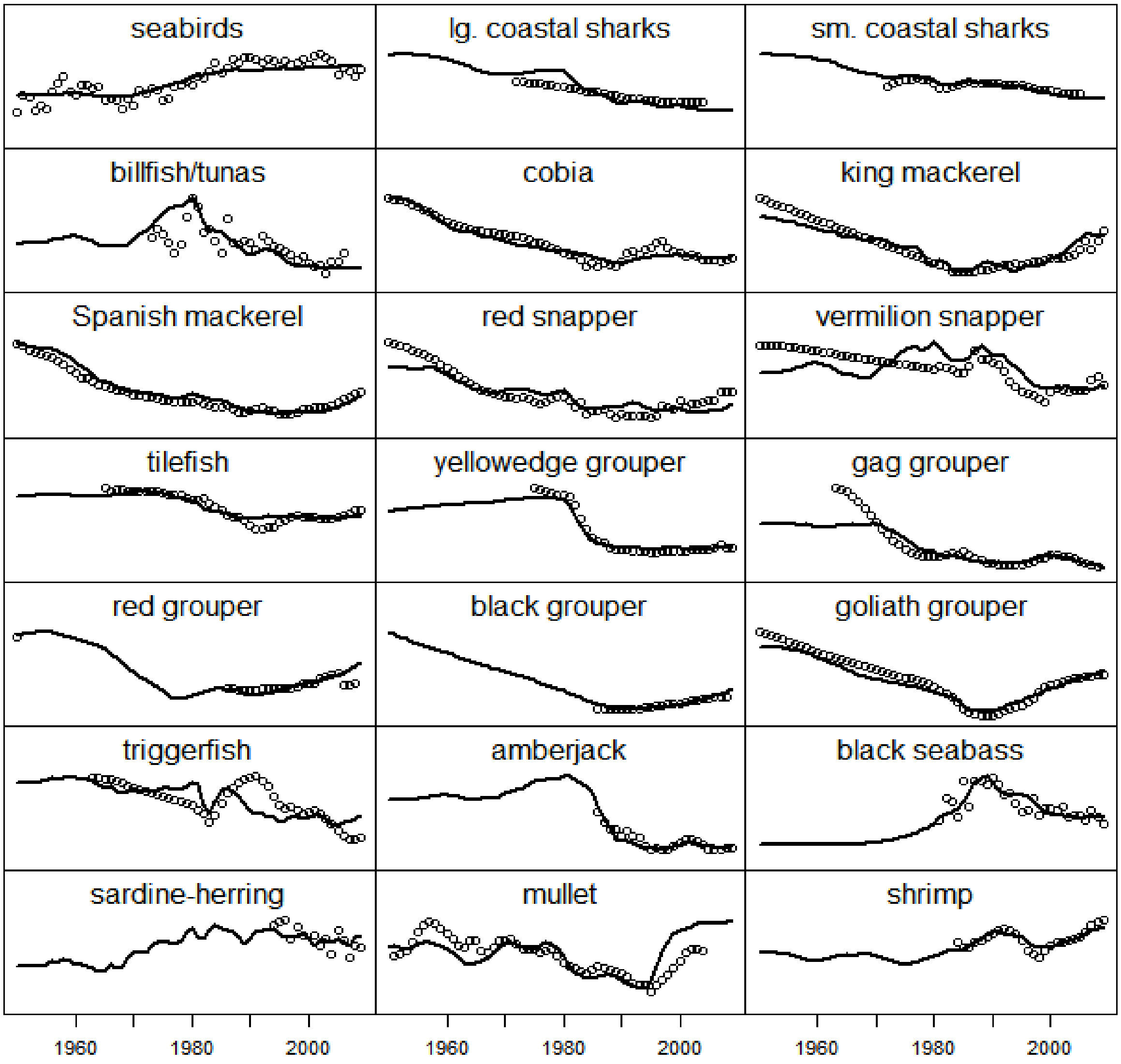

Figure 1. Fits to biomass of select groups. The solid line is the biomass predicted by Ecosim and the circles are the ‘observed’ abundances.

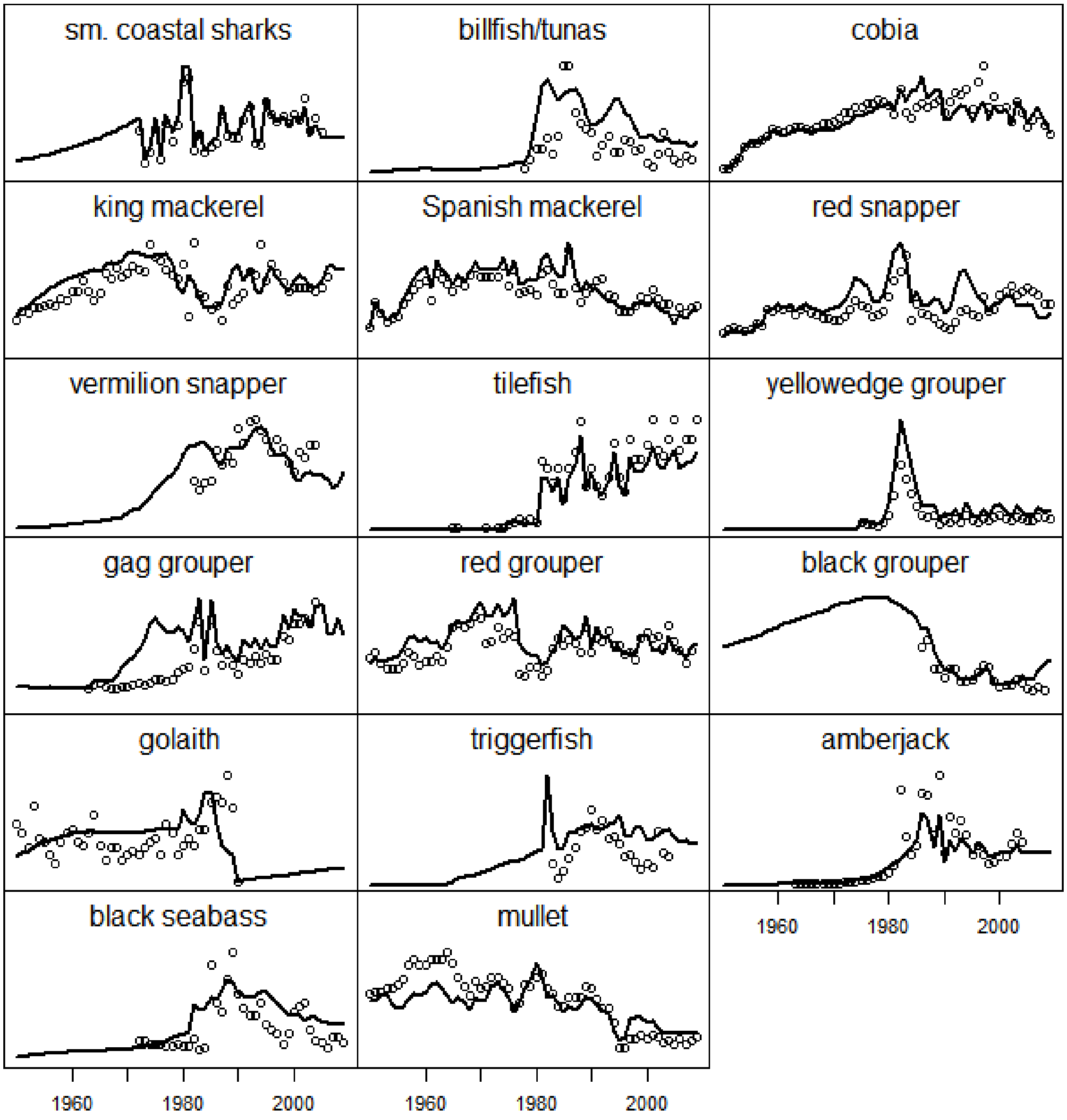

Figure 2. Fits to catch of select groups. The solid line is the catch predicted by Ecosim and the circles are actual observed catches.

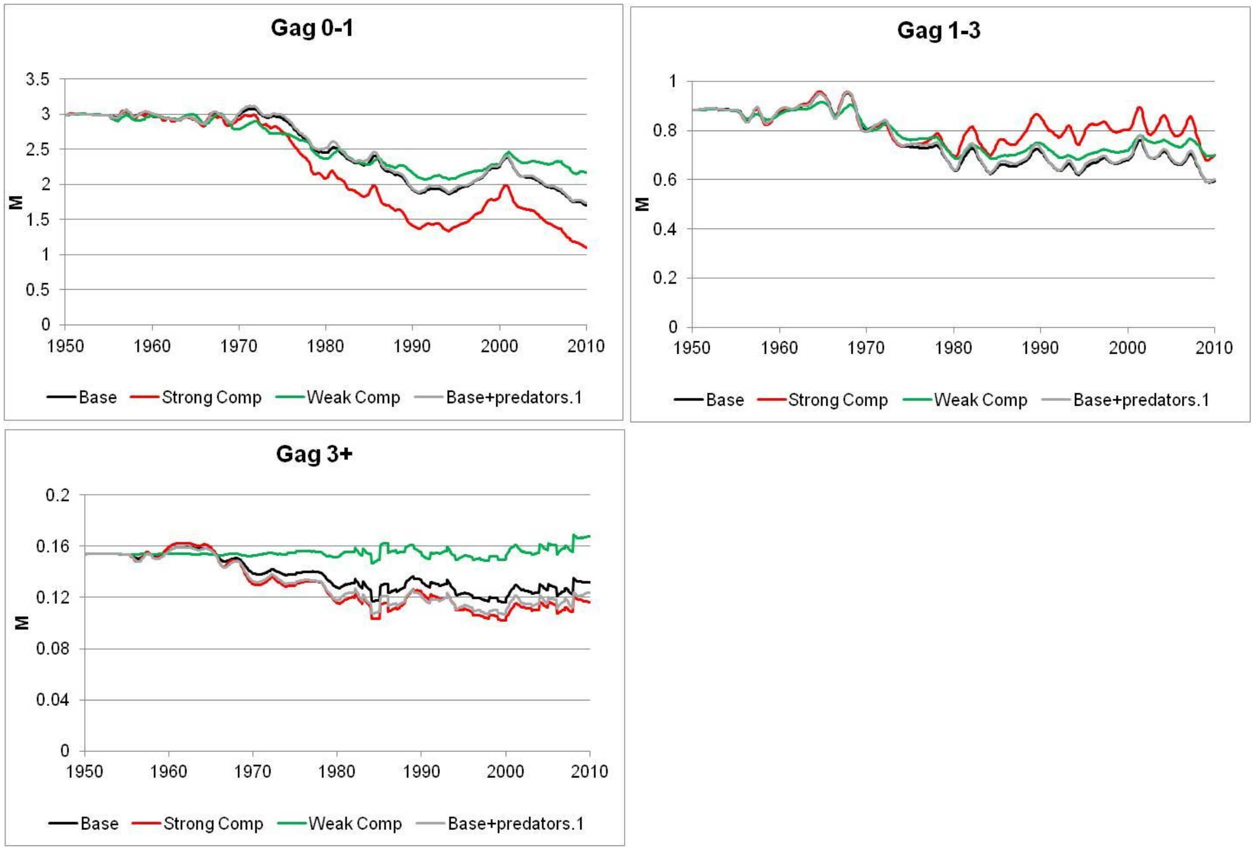

Figure 3. Natural mortality estimates from 1950 to 2009 for 3 age groups of gag.

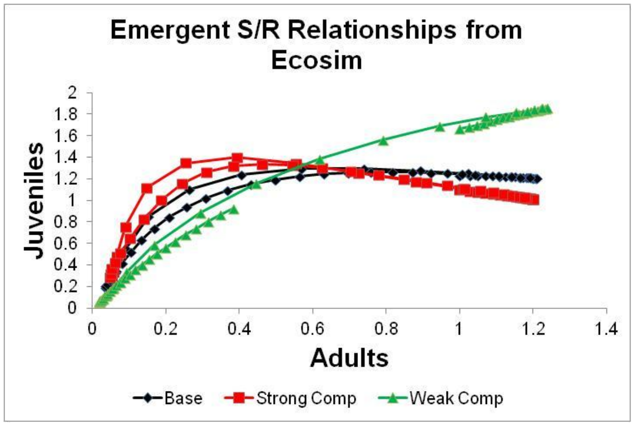

Figure 4. Emergent stock-recruit relationships for gag under three different levels of compensation effects.

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