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Analysis

Economics of biodiversity and sustainable fisheries management

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ABSTRACT

Marine ecosystems are complex, and many marine species are ecologically interdependent. As a result, losing a species could produce a cascading effect on other species. Fishery scientists advocate an ecosystem-based approach to fishery management to meet long-term sustainable goals. This paper models the complex interrelationships among species and the relationship between biomass growth and phenotypic diversity. We found that the equilibrium stock and catch/yield levels are overestimated when the diversity is not accounted for. Consequently, if species are diverse, fishery policy based on a single fishery management could overestimate catch potentials and potentially results in biological overfishing and stock collapse.

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1. Introduction

Since the 1980s, global fish catches have been declining despite the continuation of global high fishing pressure and the seemingly efficient fisheries management policies in certain parts of the world (Watson and Pauly, 2001). Some stocks, e.g. North Sea cod, have completely collapsed, while others (e.g. Atlantic and Mediterranean bluefin tuna) sit at the threshold of collapse. Moreover, all commercially important fisheries in the world are critically over-exploited (Myers and Worm, 2003). In a bid to provide a possible scientific explanation for stock overfishing and collapse, Sterner (2007) used a model that disaggregated cod stock into subpopulations with divisible environmental carrying capacity, finding that management practices that do not account for subpopulations that are genetically different and have limited interbreeding may overestimate catch potentials. This could potentially lead to stock collapse. Thus, although species diversity may generally improve the stability and resilience of a marine ecological system, it may result in a lower equilibrium catch of targeted species.

Two major motives drive the intrinsic value of biodiversity conservation. First, when a species becomes extinct, the social value associated with its possible future use is lost (Solow et al., 1993; Bezabih, 2007). Second, natural ecosystems are complex and inter-

dependent; the loss of some species could lead to cascading changes, and small perturbations may lead to far-reaching changes with unexpected repercussions (Fromm, 2000; Heal, 2004; Bezabih, 2007). It is therefore important that fishery scientists advocate an ecosystem-based approach to fishery management to meet long-term management goals (Gaston, 1996; Jennings and Kaiser, 1998; Sanchirico et al., 2007).

Like Sterner (2007), this paper focuses on the relationship between biodiversity (measured by phenotypic variance and average phenotype of a functional group of species) and fish production potentials of a fishery. However, we draw on the ecological model of Norberg et al. (2001) and Norberg (2004) that do not disaggregate species into subpopulations to analyze the impact of phenotypic diversity on yield and stock. Like Norberg et al. (2001), Norberg (2004) and Bezabih (2007), our model aggregates the behaviour of species that belong to the same functional group with respect to overall productivity and phenotypic diversity. In order to account for the dynamics of marine ecological systems, phenotypic variance and average phenotype are used as a proxy for phenotypic diversity or biodiversity in our analysis. We have therefore extended the conventional logistic growth model to include phenotypic diversity, following Norberg et al. (2001), and then derive and compare the expressions for equilibrium stock and yield levels with those of the conventional model. Our model supposes that the growth of fish stock depends on the existing stock, average phenotype and the phenotypic variance of the species. In addition, the average phenotype evolves over time as an increasing function of the phenotypic variance. Note that the term 'phenotype' refers to the physical expression of a fish *genotype* and *genotype* is the genetic make-up of a fish at the locus

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that produces a specific phenotype. A fish is either homozygous or heterozygous at each locus (Tave, 1995).² There are two types of phenotype: qualitative phenotype (e.g. color, sex, scale pattern or type) or quantitative phenotype (e.g. weight, length). Phenotypic variance is the measure of a quantitative phenotype in a population (Tave, 1995).

The results that we have obtained showed that by accounting for phenotypic diversity in a bioeconomic model, equilibrium catch and effort levels are lower than otherwise. Invariably, at very low levels of phenotypic variance, the maximum sustainable yield given by the conventional logistic growth function may lead to overharvesting, and potentially collapse the stock. Consequently, our findings support the view of fishery scientists that an ecosystem-based approach to fishery management could lead to setting lower catch quotas and meeting long-term management goals of fisheries.

The rest of the paper is organized as follows: Section 2 presents dynamic models of the fish stock and average phenotype. The solution for the equilibrium stock level in the absence of harvest is presented in Section 3. In Section 4, a Gordon–Schaefer yield function is employed and the corresponding equilibrium yield and stock levels are presented and empirically illustrated. Section 5 presents an intertemporal profit maximization version of the problem and the last section, i.e., Section 6, provides a conclusion.

2. The model

The theoretical framework for this paper draws heavily on an ecological model developed by Norberg et al. (2001) which defines species interrelationships. By using moment approximation methods, the model captures the dynamics of the macroscopic/aggregate characteristics of a functional group of species in terms of total biomass, average phenotype and phenotypic variance. The total biomass aggregates the productivity of all the different species that belong to the same functional group at a given point in time. Similarly, the average phenotype measures the average of phenotypic characteristics in a population. The phenotypic variance, which has been used as a measure of diversity, represents the spread of individual species' phenotypes around the mean. Beginning with the seminal paper by Weitzman (1992), which used a genetic distance concept to derive a diversity function, several studies have been done to measure biodiversity (see e.g. Solow et al., 1993; Brock and Xepapadeas, 2003). To account for biodiversity, following Norberg et al. (2001), suppose that the equation of motion defining the dynamics of a multi-species fish stock x in a generic fishery is:

$$\dot{x} = (f + v f_s) x, \tag{1}$$

where $f=f(x,s)$ defines the growth rate of the stock (i.e., x) and s is the average phenotype of the functional group under consideration, v is phenotypic variance, and f_s is the partial derivative of the per capita instantaneous growth rate with respect to s . If we assume that the growth function has a global maximum, then $f_s > 0$ and $f_{ss} < 0$. Thus, $v f_{ss} < 0$ implies that if there are different species of which some are smaller in size-at-maturity (i.e. if v is high), then the average growth rate of the total biomass will be low.

Furthermore, following Norberg et al. (2001), suppose that the average phenotype evolves over time and the rate of evolution

depends on the phenotypic variance of the species. Let the equation that defines this dynamics be:

$$\dot{s} = v f_s - \frac{\alpha s}{x}. \tag{2}$$

From Eq. (2), $v f_s > 0$ implying the evolution of the average phenotype is increasing in the phenotypic variance. As a result, having more diverse species has a direct negative impact on total biomass growth and indirect positive impact through the growth in the average phenotype.

3. Equilibrium stock without harvest

The conventional logistic growth function of the fish stock is $\dot{x} = \rho x(1 - xk^{-1})$, where k is the environmental carrying capacity and ρ is intrinsic growth rate of the stock. In steady state (i.e., the stock level at which $\dot{x} = 0$), the equilibrium stock level is $x_c = k$. Moreover, let the specific functional form of the instantaneous growth rate be $f = \rho(1 - xk^{-1}) - \alpha s^{-1}$ so that $f + v f_{ss} = \rho(1 - xk^{-1}) - \alpha s^{-3}(s^2 + 2v)$. In steady state, we have $\rho(1 - xk^{-1}) = \alpha s^{-3}(2v + s^2)$. In addition, from Eq. (2), in steady state we have $s = (vx)^{1/3}$. Combining the two steady state equations for the average phenotype and solving for the equilibrium stock level gives:

$$\rho \left(1 - \frac{x_c^*}{k}\right) = \alpha \left(\frac{2v + \left(\frac{vx_c^*}{k}\right)^{2/3}}{vx_c^*} \right) \tag{3}$$

It can easily be verified that the equilibrium stock is less than the corresponding value for the conventional growth function with $\alpha = 0$ and that of the conventional logistic growth model (i.e. $x_c^* < x_c$) $\forall \alpha, v > 0$ since $\frac{dx_c^*}{d\alpha} < 0$. As a result, the conventional bioeconomic model overestimates the equilibrium stock.

4. Optimal yield and effort with Gordon–Schaefer harvest function

Assume there is human predation and let Y denote catch in kilograms defined by a Gordon–Schaefer function of the form $Y = \sigma E x$, where σ is the catchability coefficient and E is the fishing effort. Using the logistic growth function, in steady state, $\rho x(1 - xk^{-1}) = \sigma x E$, $x_z = k(1 - \sigma E \rho^{-1})$ and $Y_z^* = \sigma k E(1 - \sigma E \rho^{-1})$. On the other hand, if the planner accounts for both the phenotypic variance and average phenotype, we have:

$$\rho x \left(1 - \frac{x}{k}\right) \left(1 - \alpha x \frac{2v + s^2}{s^3}\right) = \sigma x E. \tag{4}$$

Using $s = (vx)^{1/3}$ and solving for x gives the following:

$$\rho \left(1 - \frac{x_c^{**}}{k}\right) \left(1 - \alpha \left(\frac{2v + \left(\frac{vx_c^{**}}{k}\right)^{2/3}}{vx_c^{**}} \right)\right) = \sigma E. \tag{5}$$

From Eq. (5) $x_c^{**} = x_c^{**}(E)$. The corresponding equilibrium yield as a function of effort is:

$$Y_z^{**}(E) = \sigma x_c^{**}(E) E. \tag{6}$$

² Locus is the location of a gene on a chromosome and the terms "gene" and "locus" are often used interchangeably (Tave, 1995).

Comparing the equilibrium yield values it can easily be verified that $Y_z^* > Y_z^{**} \forall \alpha, v, E > 0$. Thus, a relatively low diverse ecosystem is associated with low equilibrium yield.

4.1. Numerical illustration

In this subsection, we present an empirical illustration of the relationship between the phenotypic variance and the equilibrium yields based on the conventional model (i.e., Y_z^*) and Eq. (6) using data on tuna fishing in Ghana. The marine fish resources in Ghana are classified as small pelagic (which cover a wide range of species), large pelagic, demersal, and mollusc and crustaceans. The large pelagics are mainly tuna. Tropical tunas are characterized by relatively small to medium size, rapid growth and early age at maturity, low spawning duration and short life span (Fromentin and Fonteneau, 2001). The three main species found in schools in the tropical and subtropical waters are skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*) tunas (Fonteneau et al., 2000). The three species are piscivores (i.e., they are carnivorous species preying on other fish) and therefore belong to the same functional group. Of the three species, skipjack is a gregarious species; from its first year of life, it spawns opportunistically throughout the year and in vast sectors of the ocean. This has kept the population viable. On the other hand, catches of yellowfin and bigeye tunas in the Atlantic oceans are presently close to or above the maximum sustainable yield (Hallier and Gaertner, 2008). Table A1 summarizes the life history of the three tuna species. From the table, skipjack spawns throughout the year but reaches a maximum weight of less than a half of the other two species, while the bigeye spawns only 3 months per year.

In Ghana, the fishing fleet exploits the three main tuna species managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) (Bannerman et al., 2005). The ICCAT carries out biophysical studies focusing on the effects of fishing on tuna stock abundance, and set minimum-size limits and fishing quotas (i.e., total allowable catch) for some species including the bluefin tuna. This does not include the three species under consideration here. Thus, although Ghana has a large proportion of the three species, the country is not obliged to set catch limits (Obeng, 2003). So far, the only regulation that exists is the PNDC Law 256 of 1991, which mandates that all tuna vessels to operate in joint-venture with Ghanaians, with the Ghanaian(s) owing at least 25% of the shares. As a result of the inadequate policy, the fishery has experienced three major changes, namely the dominance of the pole and line fishery over the past three decades, the use of fish aggregating devices (FADs) since the early 1990s and the re-introduction of the purse seine fleet (Fonteneau et al., 2000;

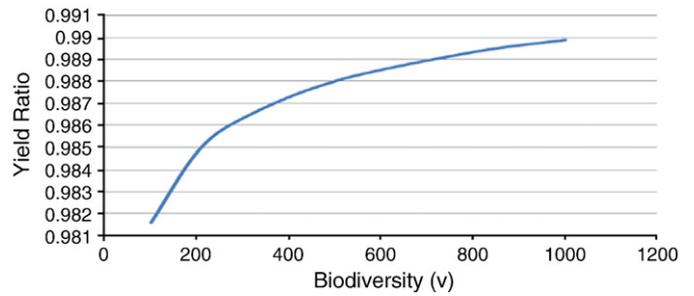


Fig. 2. The ratio of equilibrium yields (with and without diversity) and phenotypic diversity (v). The ratio approaches one as diversity increases.

Bannerman et al., 2005). With the increasing fishing efforts, total catch increased sharply in the late 1990s through 2001. However, the total catch has since generally declined. For example, catches of 88,000 t in 2002 dropped to 66,000 t and 63,000 t in 2002 and 2004 respectively. It is therefore important that the government enacts a policy to regulate catch.

For the purpose of the simulation, the parameter values, which are extracted from Bortier-Verstraaten (2002), are on the three species of tuna: bigeye, skipjack and yellowfin. Although these three species mix in schools, they are different in terms of quantitative phenotype. In addition, the species compete for food resources and have different growth potentials. Like Norberg et al. (2001), we have considered species that have different phenotypes, but belong to the same functional group for this analysis. Some additional parameter values have been chosen for convenience. Table A2 presents all the parameter values used for the simulation.

The plot of the equilibrium catch functions with and without diversity is presented in Fig. 1. The data for the plot has been generated by using Mathematica 6 software to solve the relevant equations. The equilibrium catch/yield function that accounts for diversity exhibits depensation, which indicates that an equilibrium level of effort based on the conventional model (i.e., effort level corresponding to the maximum of the conventional catch function), may lead to stock collapse.

5. Dynamic optimization and biodiversity

Suppose that the social planner maximizes the discounted value of the stream of profit from a fishery subject to the equations of motion of the stock and the average phenotype. If the social planner does not account for phenotypic diversity, the optimization problem is:

$$V(x, s, h) = \max_h \int_0^\infty (ph - c(x, h))e^{-rt} dt, \tag{7}$$

subject to:

$$\dot{x} = \rho x(1 - x/k) - h, \tag{8}$$

where p is the competitive price per kilogram of catch (h); the total benefit from fishing is ph ; $c(x, h) = c(x)h$; and $c(x)$ is the cost

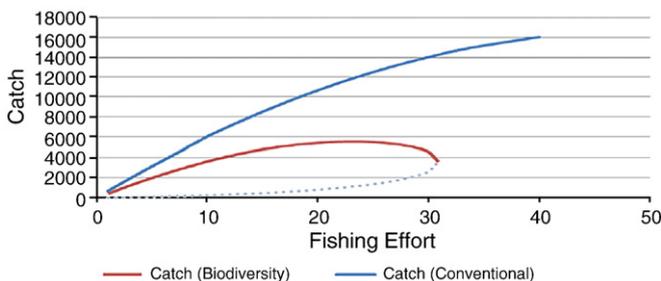


Fig. 1. Equilibrium catch functions if diversity has been accounted for (catch biodiversity) and if diversity has not been accounted for (catch conventional). The catch biodiversity function shows that effort levels beyond some threshold (i.e., where the curve turns) may lead to stock collapse.

per unit of harvest. The corresponding current value Hamiltonian is:

$$H(x, s, h) = (p - c(x))h + \lambda(\rho x(1 - x/k)x - h). \tag{9}$$

Where λ and μ are the shadow values of the fish stock and the stock of the average phenotype respectively. The maximum principle is:

$$\frac{\partial H}{\partial h} = p - c(x) - \lambda = 0 \Rightarrow p - c(x) = \lambda. \tag{10}$$

From Eq. (10) if an interior solution exists, in inter-temporal equilibrium, marginal profit from harvest (i.e $p - c(x)$) must equate the shadow value of the fish stock (i.e. λ).

5.1. Dynamic equilibrium

The co-state equation for the fish stock is Eq. (11).

$$\dot{\lambda} - r\lambda = -\frac{\partial H}{\partial x} = c_x h - \lambda \rho \left(1 - 2xk^{-1}\right), \tag{11}$$

$$r\lambda = \dot{\lambda} + \lambda \rho \left(1 - 2xk^{-1}\right) - c_x h.$$

Eq. (11) shows that in dynamic equilibrium, the marginal benefit from preserving a unit of fish (i.e $\dot{\lambda} + \lambda \rho(1 - 2xk^{-1}) - c_x h$) must reflect the opportunity cost of harvesting that unit and investing the proceeds in a bank at an interest rate of r (i.e., $r\lambda$). Note that the marginal benefit includes a capital gain (i.e $\dot{\lambda}$), the value of a marginal gain in the growth of the fish stock (i.e. $\lambda \rho(1 - 2xk^{-1})$), some stock effect on the cost of harvest (i.e. $-c_x h$). In steady state $\dot{\lambda} = \dot{x} = 0$ so that

$$p - c(x) = \frac{-c_x h}{r - \rho \left(1 - 2xk^{-1}\right)} = \frac{-c_x x \rho \left(1 - xk^{-1}\right)}{r - \rho \left(1 - 2xk^{-1}\right)}, \tag{12}$$

where $h = \rho x(1 - xk^{-1})$. Suppose that the social planner accounts for biodiversity, the optimization program will consist of maximizing Eq. (7) subject to Eqs. (2) and (13).

$$x = \rho x \left(1 - xk^{-1}\right) \left(\alpha x \frac{s^2 + 2v}{s^3} \right) \left(h. \tag{13}$$

The corresponding current value Hamiltonian is Eq. (14)

$$H(x, s, h) = (p - c(x))h + \lambda \rho x \left(1 - \frac{x}{k}\right) \left(\alpha x \frac{2v + s^2}{s^3} \right) \left(h \right) \left(14 \right) + \mu \alpha \left(\frac{v}{s^2} - \frac{s}{x} \right) \left($$

The maximum principle is the same as Eq. (10) but the co-state equations are Eqs. (15) and (16):

$$r\lambda = \dot{\lambda} + \lambda \left(\rho \left(1 - \frac{2x}{k}\right) \left(\alpha \left(\frac{2v + s^2}{s^3} \right) \right) + \mu \alpha \frac{s}{x^2} - c_x h, \tag{15} \left($$

$$r\mu = \dot{\mu} + \lambda \alpha \frac{6v + s^2}{s^4} \left(\alpha \left(\frac{2v + s^2}{s^3} \right) \right) \left(\mu \alpha \left(\frac{2v}{s^3} + \frac{1}{x} \right), \tag{16}$$

Eq. (15) shows that in a dynamic equilibrium, the marginal benefit from preserving a unit of fish (i.e $\dot{\lambda} + \lambda \left(\rho \left(1 - \frac{2x}{k}\right) \left(\alpha \left(\frac{2v + s^2}{s^3} \right) \right) + \mu \alpha \frac{s}{x^2} - c_x h \right)$ must reflect the opportunity cost of harvesting that unit and investing the proceeds in a bank at an interest rate of r (i.e., $r\lambda$). In the same light, Eq. (16) indicates that in a dynamic equilibrium the marginal gain from harvesting one unit of fish today (i.e., $r\mu$) should reflect the opportunity cost of some marginal capital gain on improved average phenotype (i.e. $\dot{\mu}$) plus some stock effects (i.e., $\lambda \alpha \left(\frac{6v + s^2}{s^4} \right) x - \mu \alpha \left(\frac{2v}{s^3} + \frac{1}{x} \right)$). In steady state $\dot{\lambda} = \dot{\mu} = \dot{x} = \dot{s} = 0$ and

$$p - c(x) = \frac{-c_x x \left(\rho \left(1 - xk^{-1}\right) - \alpha \left(2v + (vx)^{2/3} \right) (vx)^{-1} \right)}{\left(r - \rho \left(1 - \frac{2x}{k}\right) \left(\alpha \left(\frac{2v + (vx)^{2/3}}{vx} \right) \left(\alpha^2 \left(\frac{6v + (vx)^{2/3}}{vx(vx + 3\alpha)} \right) \right) \right) \right)} \tag{17}$$

where $c(x) = (\alpha x)^{-1} c$. Using the figures on Table A2, we have computed and compared the optimum levels of stock and catch based on Eqs. (12) and (17) for different values of the phenotypic variance. The results, which are presented on Table A3, show that the optimal stock and catch levels are overestimated if the conventional growth model is used and the phenotypic diversity (v) is relatively low. As the diversity increases, all other things being equal, the optimal catch and stock levels approach the corresponding values for the conventional model.

Furthermore, we have presented the plot of the ratio of equilibrium catch with phenotypic diversity and that of the conventional model for varying levels of v in Fig. 2. The most important is the fact that the ratio approaches 1 as v increases.

6. Conclusion

Although research in marine and ecological sciences have established a clear link between biologically diverse ecosystems and the resilience of such systems, bioeconomic models applied to fisheries management assume logistic growth functions that exhibit pure compensation. This paper presents a digression from this practice by extending the ecological model developed by Norberg et al. (2001) to analyse the impact of phenotypic variance and average phenotype (i.e., a proxy for biodiversity) on equilibrium catch and effort. The results obtained showed that by accounting for biodiversity, equilibrium levels of catch and effort are lower than otherwise. Indeed, with very low levels of diversity measured by phenotypic variance, the so-called maximum sustainable yield that is consistent with the standard logistic growth function may lead to overfishing.

Furthermore, we have also established that in a dynamic equilibrium if the social planner maximises profit and the cost per unit effort is lower than the fixed price of fish, the equilibrium catch levels are lower for all values of the phenotypic variance compared to what exists for the conventional model. As noted by Sanchirico et al. (2007), an ecosystem-based approach to fishery management should be encouraged to meet long-term management goals.

Appendix A

Table A1

Life history traits of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye tunas (*Thunnus obesus*).

Name	Spawning duration (month/yr)	Length at maturity (cm)	Weight at maturity (kg)	Age at maturity (yrs)	Maximum length (cm)	Maximum weight (kg)	Maximum age (yrs)	Juvenile growth (%Lyr ⁻¹)
Skipjack	12	45	1.7	1.5	75	23	4.5	40.0
Yellowfin	6	105	25.0	2.8	170	176	7.5	22.1
Bigeye	3	115	31.0	3.5	180	225	6.0	18.3

Note: The table is adapted from Fromentin and Fonteneau (2001).

Table A2

Parameter values used for three tuna species used for simulations.

Parameter	Description	Value
ρ	Intrinsic growth rate*	1.59
v	Phenotypic variance	0.001, 1, 1000
α	A scalar	0.4
k	Carrying capacity*	664.81 t
σ	Catchability coefficient*	0.01573
c	Cost per unit harvest*	0.56
p	Price per ton of fish	1

The figures associated with the starred parameters are taken/computed from Bortier-Verstraaten (2002). The tuna species considered here are skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*). Since the three species are aggregated for the purpose of our analysis, some of the figures are averages. In addition, different values of the phenotypic variance (i.e. v) have been assumed to determine the impact of diversity on equilibrium stock and yield levels.

Table A3

Equilibrium catch and effort for different levels of phenotypic variance.

Variable	Conventional model	Phenotypic diversity		
		$v = 0.001$	$v = 1.0$	$v = 1000$
h^*	263.907	86.2813	235.596	261.234
x_p^*	344.582	209.814	332.465	342.985

Note that h^* is equilibrium harvest and x_p^* is equilibrium stock. The equilibrium harvest and stock increase as phenotypic diversity increases.

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