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Multiple species fisheries with no ecological interaction: two-species Schaefer model applied to lake trout and lake whitefish

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The two-species Schaefer model for species that are captured with the same fishing gear, but which do not interact ecologically, was applied to examine the relation between the maximum sustainable yields for lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) fished together and separately. Lake trout and lake whitefish are two important species in the Laurentian Great Lakes that historically have been fished with the same gear. Naturally reproducing lake trout populations have disappeared from most of the Great Lakes, but the lake whitefish supports a large fishery. Application of the logistic surplus production model to lake trout alone does not indicate serious over-exploitation, but applied to lake trout and lake whitefish together indicates that at the total maximum sustainable yield of the two species together, the lake trout is seriously over-exploited and abundance is low. A fishery can be optimized for only one species at a time, and, if several non-interacting species are exploited, some will be over-exploited and some will be under-utilized. One species among several in a multiple species fishery can, in theory, be fished to extinction at the total maximum sustainable yield of the combined species.

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Introduction

Lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) were two important commercial species in the Laurentian Great Lakes of North America, and historically both were exploited mainly with 4.5 inch (diagonal mesh) gillnets. When assessed separately, neither lake trout nor lake whitefish appear to have been severely over-exploited, yet today naturally reproducing lake trout populations are extinct in much of the Great Lakes and they are protected from commercial exploitation. The lake whitefish continues to support a thriving commercial fishery. Sea lamprey predation was identified as a contributing factor in the demise of the lake trout (e.g. Jensen, 1978), but sea lamprey also prey on lake whitefish (Jensen, 1976). In this study the two fisheries are assessed together.

Interactive fisheries are complex, but a workable theory is slowly developing (e.g. Beverton and Holt, 1954; Larkin, 1963, 1966; Paulik *et al.*, 1967; Hilborn, 1976; Horwood, 1976; Hobson and Lenarz, 1977; May *et al.*, 1979; Murawski *et al.*, 1983; Shepherd, 1988). The Schaefer (1954) model provides the simplest approach for the assessment of interaction fisheries (Larkin, 1963, 1966; Horwood, 1976; May *et al.*, 1979); it has been applied to mixed fisheries both by modelling the populations separately (Larkin, 1963, 1966; Horwood, 1976) and by modelling total biomass (Pinhorn, 1976). Horwood (1976) has shown that these two approaches can result in different models. In this study, the populations are modelled separately, as in Horwood (1976), but no restriction is placed on fishing effort; yield is optimized[1] using the relation between yield and effort, which is simple, rather than the relation between yield and biomass, as in Horwood (1976), which is complex.

The model

The logistic surplus production model has been widely applied to individual species; it assumes that the capacity of a population to increase is a function of population size, and that the maximum capacity to increase occurs at an intermediate population size where the maximum sustainable yield also occurs. The equations for two species caught together with the same fishing gear, but otherwise independent, are:

$$dy/dt = dy_1/dt + dy_2/dt \tag{1}$$

[1] The term "optimize" is used in this paper to mean ... adjustment of the appropriate input variable to bring the yield, whether of one species or two combined, to the maximum sustainable level which can be achieved within the constraints of the particular circumstances.

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$$dy_1/dt = q_1EB_1 \quad (2)$$

$$dy_2/dt = q_2EB_2 \quad (3)$$

$$dB_1/dt = k_1B_1 - k_1B_1^2/K_1 - q_1EB_1 \quad (4)$$

$$dB_2/dt = k_2B_2 - k_2B_2^2/K_2 - q_2EB_2 \quad (5)$$

where: y = total yield; y_1 = yield of lake whitefish; y_2 = yield of lake trout; B_1 = biomass of lake whitefish; B_2 = biomass of lake trout; k_1 = population growth coefficient of lake whitefish; k_2 = population growth coefficient of lake trout; K_1 = environmental carrying capacity of lake whitefish; K_2 = environmental carrying capacity of lake trout; q_1 = catchability coefficient of lake whitefish; q_2 = catchability coefficient of lake trout; E = fishing effort, one unit is 1000 linear feet of 4.5 inch diagonal mesh gillnet.

At equilibrium, where $dB_1/dt = dB_2/dt = 0$, annual equilibrium yields Y_1 and Y_2 for each species separately are given by the equations

$$Y_1 = k_1B_1 - k_1B_1^2/K_1 \quad (6)$$

$$Y_2 = k_2B_2 - k_2B_2^2/K_2 \quad (7)$$

These equations can be applied for each species to obtain the maximum sustainable yield (MSY), fishing effort at the MSY, and biomass at the MSY (e.g. Schaefer, 1954). For each species separately, the biomass values at the MSY are $B_1 = K_1/2$ and $B_2 = K_2/2$. The maximum sustainable yields are $MSY_1 = k_1K_1/4$ and $MSY_2 = k_2K_2/4$. The fishing efforts at the maximum sustainable yields are $E_1 = k_1/2q_1$ and $E_2 = k_2/2q_2$. The equilibrium relations between annual yield and effort for the two species separately are:

$$Y_1 = q_1K_1E - K_1q_1^2E^2/k_1 \quad (8)$$

$$Y_2 = q_2K_2E - K_2q_2^2E^2/k_2 \quad (9)$$

The above results are well known.

To obtain the MSY of the two species optimized together it is essential to use the equation for equilibrium annual yield as a function of fishing effort

$$Y = Y_1 + Y_2 = q_1K_1E - K_1q_1^2E^2/k_1 + q_2K_2E - K_2q_2^2E^2/k_2 \quad (10)$$

rather than as a funciton of biomass. In the biomass equation, applied by Horwood (1976), the biomass of each species must be considered when the fishery is optimized, but in the above equation fishing effort is the same variable for both species, and this enables effort at the MSY to be easily determined. Thus, fishing effort at the MSY for the two species together is

$$E_{OPT} = \frac{q_1K_1 + q_2K_2}{2(K_1q_1^2/k_1 + K_2q_2^2/k_2)}. \quad (11)$$

Substitution of Equation (11) for the yield equation (Equation 10) gives the total MSY.

Maximum sustainable yield as a function of population growth rate and catchability coefficient

Equations (1) and (11) give the MSY of multiple species fisheries with different population growth rates and catchability coefficients. Fishing effort at the MSY for two species together is a combination of the efforts at the MSYs for the two species exploited separately; in most circumstances two or more species exploited together cannot all be exploited at their maximum sustainable levels; some species will be exploited at higher levels, others at lower levels.

To study exploitation of two species whose growth and catchability coefficients were different, two species were first considered with $k = 0.75$ per year, $q = 1.0 \times 10^{-6}$ per unit of effort, and $B_{inf} = 1000$ Mt for both species. Then the population growth coefficient and catchability coefficient of species 2 were varied, and the MSY, biomass at the MSY, and effort at the MSY were calculated as functions of k or q with all other parameters constant.

If their catchability coefficients were different, the total MSY of two species optimized together was either equal to or less than the total MSY of two species optimized separately (Fig. 1a). When two species were optimized together, yield for the species with the lower catchability coefficient was either the same or lower (Fig. 1b). Fishing efforts at the MSY for two species optimized together were the same, but fishing efforts at the MSY for the two species optimized separately were different (Fig. 1c). The biomass of each species for fisheries optimized separately was $B_{inf}/2$ (Fig. 1d). If the two species were optimized together, the biomass of the two species was different (Fig. 1d).

If the catchability coefficients for two species were the same, but the population growth coefficients were different, optimization of yield for the two species together resulted in a total MYS that was the same or less than the total MSY of the two species optimized separately (Fig. 2a). When optimized together, yield for each species was the same or below its MSY for separate optimization (Fig. 2b). Fishing effort at the MSY for the two species optimized together was between that for the two species optimized separately (Fig. 2c). The optimum effort for species 2 increased as its population growth coefficient increased (Fig. 2c). If the fisheries for two species were optimized together, the biomass of the species with the smaller growth coefficient was below $B_{inf}/2$, and the biomass of the species with the higher growth coefficient was above $B_{inf}/2$ (Fig. 2d). Thus, the species with a high growth coefficient was under-exploited while the species with a low growth coefficient was over-exploited.

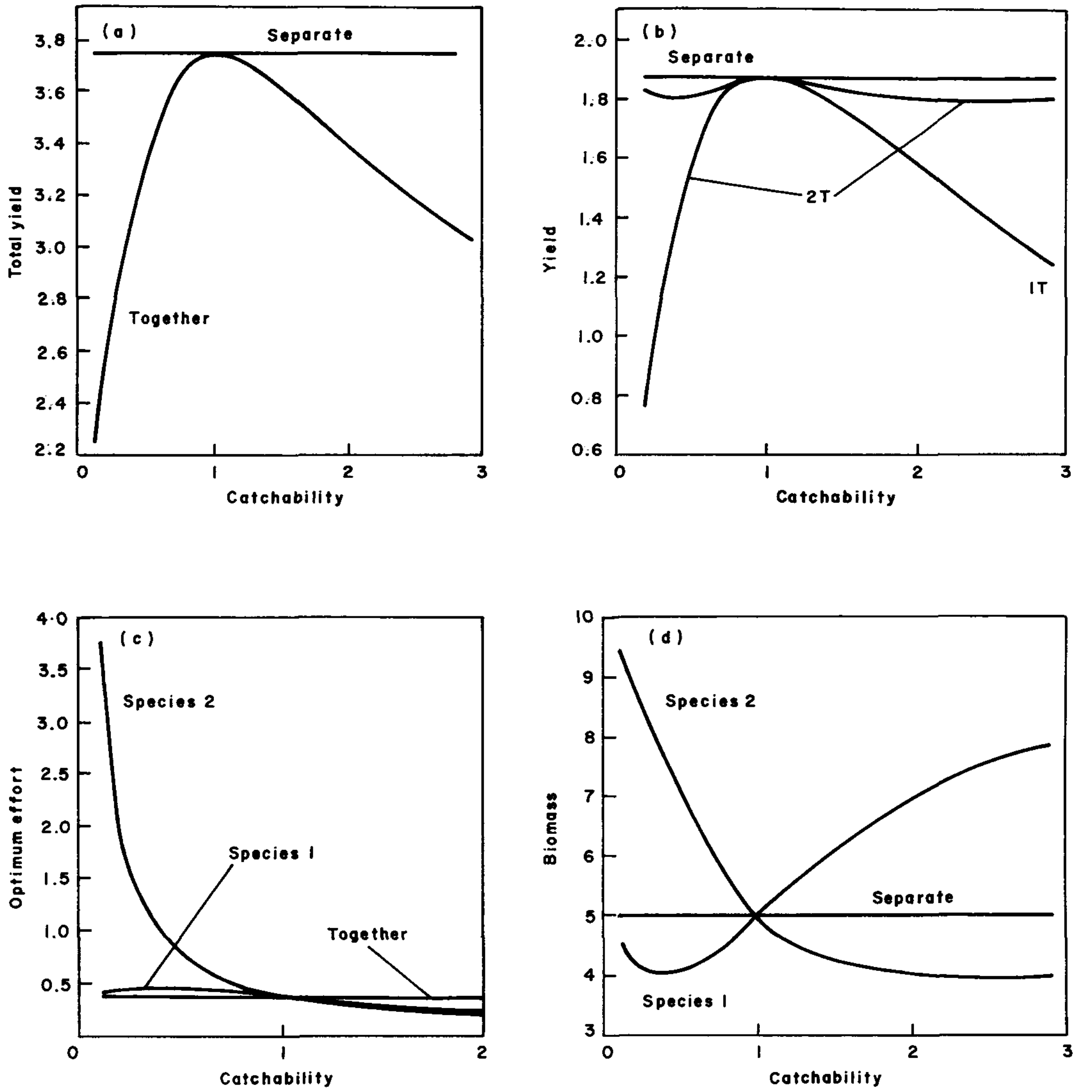

Figure 1. (a) Total yield as a function of catchability coefficient for species exploited separately and together. (b) Yield as a function of catchability coefficient for species exploited separately, for species 1 exploited with species 2 (1T), and for species 2 exploited with species 1 (2T). (c) Optimum effort as a function of catchability coefficient for species 1 and species 2 exploited separately and together. (d) Biomass as a function of catchability for species 1 and species 2 exploited separately and together.

Lake trout and lake whitefish

The logistic surplus production model was applied separately to lake whitefish (Jensen, 1976) and lake trout (Jensen, 1978).

The parameter estimates for lake whitefish are listed in Table 1; the optimum effort was 100,000 units, the optimum fishing mortality coefficient was 0.30, the MSY was 1050 Mt, and the biomass at the MSY was 3500 Mt.

The parameter estimates for lake trout are also listed in Table 1; the optimum effort was 17 500 units, the optimum fishing mortality coefficient was 0.35, the MSY was 122 Mt, and the biomass at the MSY was 350 Mt.

Fishing effort for the two species together cannot be determined exactly. Although the same fishing gear was used for both species, a unit of effort was reported as a unit of effort for a species only if that species happened to be caught. Hence, the same unit of gear could be counted twice; once for lake trout and once for lake whitefish. In addition, if the fishermen intended to catch lake whitefish rather than lake trout, the gear was used in somewhat different areas. But lake whitefish cannot be caught without catching lake trout, and there was a close association between lake trout and lake whitefish fishing effort ($r=0.74$).

Both fishing effort and catch for lake whitefish were much larger than for lake trout. On the assumption that

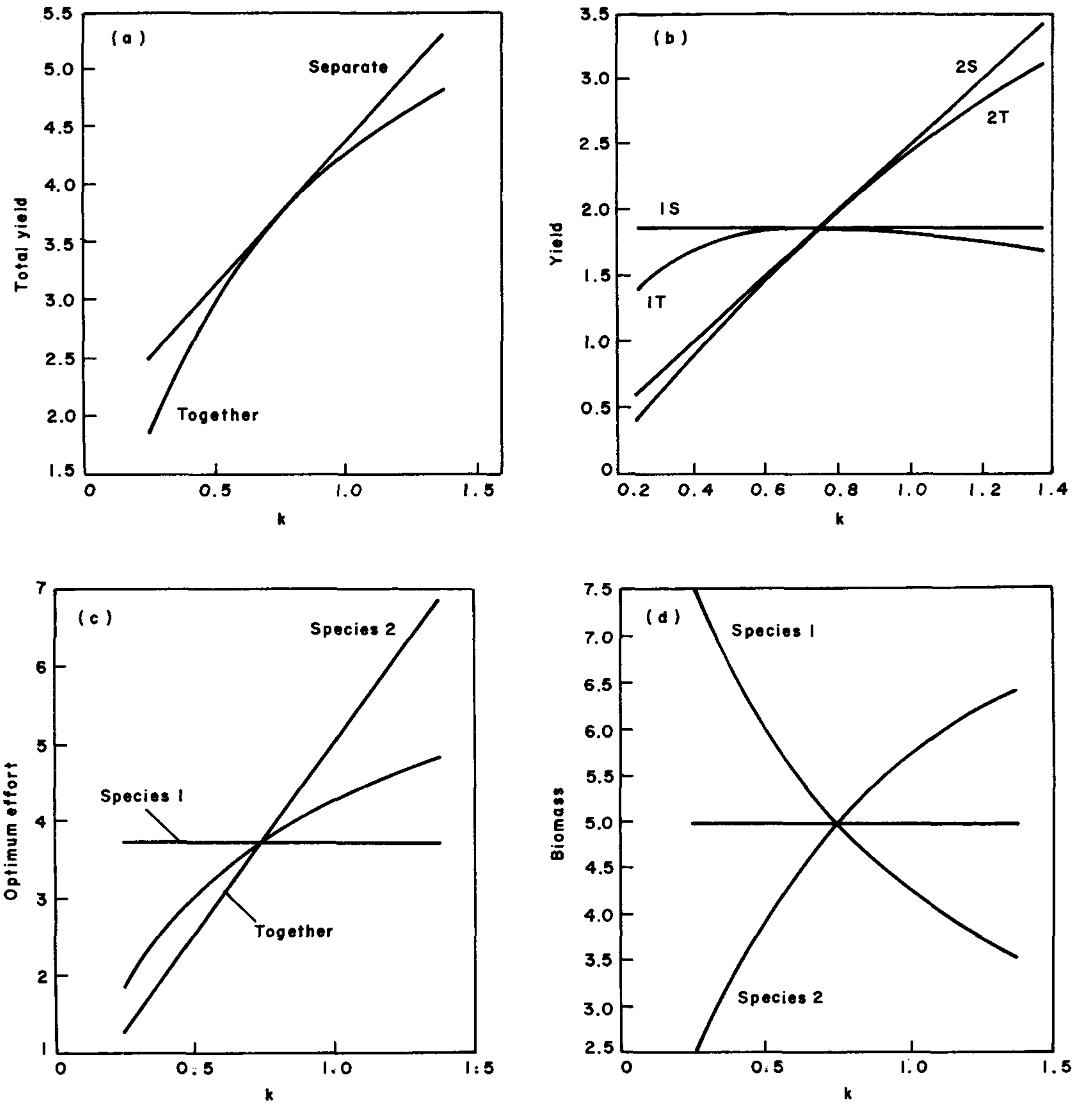

Figure 2. (a) Total yield for two species exploited together and separately as a function of the population growth coefficient. (b) Yields for each species when optimized separately (1S and 2S) and when optimized together (1T and 2T) as a function of the population growth coefficient. (c) Optimum effort as a function of the population growth coefficient for species 1 and species 2 optimized separately and together. (d) Biomass as a function of population growth coefficient for species 1 and species 2 optimized separately (straight line) and for each species when optimized together.

Table 1. Surplus production model parameter estimates for lake trout and lake whitefish optimized separately.

Parameter	Lake trout	Lake whitefish
k (per year)	0.70	0.60
K (Mt)	700	7000
q (per 1000 feet of gillnet)	0.2×10^{-5}	0.3×10^{-6}
R^2	0.62	0.66
E_{opt}	17 500	100 000
F_{opt}	0.35	0.30
MSY (Mt)	122	1050
B_{MSY} (Mt)	350	3500

all lake whitefish effort fished simultaneously for lake trout and lake whitefish, the optimum fishing effort for the two fisheries together was 34 653 units while the MSY was 606 Mt. The yields of lake whitefish and lake trout are 601.62 Mt and 4.81 Mt, the biomasses are 5787 Mt and 6.94 Mt, and the instantaneous fishing mortality coefficients are 0.10 and 0.69 per year. These results are summarized in Table 2.

For lake whitefish the optimum fishing mortality coefficient for exploitation of the two fisheries together is about one-third that for exploitation of lake whitefish alone, and for lake trout the optimum fishing mortality

Table 2. Results for simultaneous optimization of lake whitefish and lake trout.

Parameter	Lake trout	Lake whitefish	Total
E_{opt}	–	–	34 653
Yield (Mt)	4.81	601.62	606
Biomass (Mt)	6.94	5787	–
F (per year)	0.69	0.10	–

coefficient for exploitation of the fisheries together is about twice that for exploitation of lake trout alone. Although the carrying capacities do not affect the optimum fishing effort, the impact of fishing on the populations does depend on the carrying capacities, and the low carrying capacity of lake trout combined with its higher catchability coefficient results in under-utilization of lake whitefish and severe over-exploitation of lake trout when they are optimized together.

It is unlikely that all lake whitefish gear fished simultaneously for both lake trout and lake whitefish, but, when the lake trout fishery was closed to commercial exploitation, incidental catch of lake trout by gillnets fishing for lake whitefish was substantial and this led to a gillnet ban in State of Michigan waters of the Great Lakes (pers. comm., Meryl Keller, Michigan Department of Natural Resources). The above two-species surplus production model indicates that lake trout and lake whitefish cannot be exploited together with the same fishing gear without severe over-exploitation of lake trout, unless gear such as trapnets is used that allows release of the lake trout.

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