

TRADE-OFFS BETWEEN FISH HABITAT AND FISHING MORTALITY AND THE ROLE OF RESERVES

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ABSTRACT

Ludwig (1995) argued that (1) management for sustained yield cannot be optimal and (2) effective management models cannot be realistic. I concur, and I begin with the view that sustained yield is more important than maximum yield; indeed maximum sustained yield must become a constraint rather than a target. Mangel et al. (1996) stress that we are very far from managing ecosystems; we manage human interventions in ecosystems. Following Ludwig's advice, I will use a relatively simple model to show how essential fish habitat and fishing mortality are intimately connected—loss of spawning habitat is equivalent to additional fishing mortality on adults. Reserves can help guarantee sustainability of the fishery, even when fishing mortality outside the reserve cannot be very well controlled (despite attempts to do so). In fact, in some circumstances (identified by the model) reserves can simultaneously enhance the stock, protect habitat, and increase catch. Finally, I will show how the model can be used to help resolve the reserve design question, which in this case is how we decide how much spawning habitat and how much of the fishing ground to protect.

The case for closed areas for fisheries management consolidates (Polacheck, 1990; DeMartini, 1993; Man et al., 1995; Hall, 1998; Horwood et al., 1998; Sladek Nowlis and Roberts, 1999), but the promise is not yet fulfilled, and it is essential that the design and implementation of marine protected areas be scientific (Sale, 1998). In making them so, we must keep in mind Ludwig's (1995) points that (1) management for sustained yield cannot be optimal and (2) effective management models cannot be realistic. The detailed reasons for these conclusions are related to the interplay of models and data, particularly statistical considerations; a good starting point is Ludwig's paper, backed up by Hilborn and Mangel (1997).

Furthermore, we need to recognize that maximum sustained yield is an antique phrase from the days in which Newtonian physics dominated and we viewed nature as something easily controlled (see also Isaacs, 1976). Ecosystem management is another antique phrase, which sounds as though we were somehow sitting at the controls of a big 'ecosystem machine' and tweaking the dials. We are not. We manage human intervention in ecosystems, not ecosystems. An ecosystem approach to management is possible (Fluharty et al., 1999), but ecosystem management is far off (Mangel et al., 1996). If one believes that sustained yield is more important than maximum yield, that maximum sustained yield should be a constraint rather than a target (cf. Mace, 1999), and that we control what people do more easily than we control what fish do, marine reserves have much to offer to fisheries management.

METHODS

Envision a stock that has separate fishing and spawning grounds, the latter of which I shall refer to as Essential Fish Habitat (EFH). The salmonids (*Oncorhynchus*, *Salmo*) are an excellent example of this separation (Rahr et al., 1998), but other species fit this description. Many groupers

(Serranidae) in the tropics aggregate to spawn at historically predictable sites (e.g., Nassau grouper, *Epinephelus striatus*). Pacific herring, *Clupea pallasii*, are pelagic but spawn in seagrass beds, where their eggs are harvested commercially. Some coastal sharks and rays (e.g., leopard sharks, *Triakis semifasciata*) aggregate and spawn in shallow embayments. California grunion, *Leuresthes tenuis*, are pelagic but spawn in intertidal sandy beaches, where they are fished.

The size of the fish stock at the start of year t is $N(t)$, annual mortality rate is M , reproduction occurs halfway through the season and is characterized by a Ricker stock-recruitment function. The assumption about the timing of recruitment allows compression of the age structure of the model, so that one can work with a minimum number of equations. With these assumptions, the stock dynamics in the absence of fishing are

$$N(t+1) = N(t)e^{-M} + N(t) \exp \left\{ r \left(1 - \frac{N(t)}{B_1} \right) \right\} e^{-M/2} \quad \text{Eq. 1}$$

where B_1 is the stock size at which each individual produces one offspring, which I also call the spawning habitat as a notational shorthand, and r is the maximum per capita reproductive rate (Table 1). One determines the steady-state unfished biomass by setting $N(t) = N(t+1)$ in Eq. 1; it is the larger of 0 or

$$\bar{N} = B_{\text{MAX}} = B_1 \left\{ 1 - \frac{1}{r} \log \left[e^{M/2} - e^{-M/2} \right] \right\} \quad \text{Eq. 2}$$

This quantity is also called B_{MAX} , to indicate that it is the unexploited (virgin) biomass. For each value of M , there is a minimum value of r below which the population cannot persist. Thus, the model allows many different life histories, characterized by different values of r and M , all of which achieve the same unfished biomass.

Equation 1 involves two terms for the population dynamics: survival of mature fish (first term on the right-hand side) and recruits to the population (second term). The recruitment is Ricker-like, in the sense that, if $N(t)$ exceeds B_1 , reproduction begins to decline. An alternative would be to use a Beverton-Holt-like recruitment function in which Eq. 1 would be replaced by

$$N(t+1) = N(t)e^{-M} + \frac{rN(t)}{1 + N(t)/N_{0.5}} e^{-M/2} \quad \text{Eq. 1'}$$

Table 1. Parameters in the models.

Fundamental parameters	
$r = 0.1$	Maximum per capita production
$M = 0.3$	Annual mortality rate
$B_1 = 100$	Reproductive habitat capacity
Other parameters	
$\delta B_1 = 0.05 B_1$	Amount of habitat loss when a habitat loss event occurs
$T = 40$	Time horizon
S_{max}	Number of simulations (= 500)
$\delta_v = 0.01$	Discount rate for the economic value of the fishery

where r and M have the same interpretations and $N_{0.5}$ is the population size at which per capita reproduction is 50% of its maximum value. In this case, as population size increases, reproduction saturates rather than decreases. The steady-state population is

$$\bar{N} = N_{0.5} \left(\frac{r}{e^{M/2} - e^{-M/2}} - 1 \right) \quad \text{Eq. 2'}$$

so that, as before, different combinations of r and M can lead to the same steady-state biomass. In this paper, I use Eqs. 1 and 2 rather than 1' and 2', but a similar analysis could be conducted.

If fishing mortality is F , fishing occurs after reproduction, and recruits are not fished, Eq. 1 becomes

$$N(t+1) = N(t)e^{-M-F} + N(t) \exp \left\{ r \left(1 - \frac{N(t)}{B_1} \right) \right\} e^{-M/2} \quad \text{Eq. 3}$$

and Eq. 2 becomes the larger of 0 or

$$\bar{N}(F) = B_1 \left\{ 1 - \frac{1}{r} \log \left[e^{M/2} - e^{-(M/2)-F} \right] \right\} \quad \text{Eq. 4}$$

Each life history, characterized by mortality and maximum per capita reproduction, supports a maximum level of fishing mortality F_{\max} in the sense that if $F > F_{\max}$, then the steady state population biomass is 0. This maximum value is given by

$$F_{\max} = -\log \left(e^M - e^{r+(M/2)} \right) \quad \text{Eq. 5}$$

When fishing mortality is F , the steady-state catch is (Quinn and Deriso, 1999)

$$\bar{C}(F) = \frac{F}{F+M} (1 - e^{-M-F}) \bar{N}(F) \quad \text{Eq. 6}$$

Overfishing occurs whenever fishing mortality is higher than the level at which $\bar{C}(F)$ peaks (Fig. 1).

RESULTS

SUSTAINABILITY AND CONTROLLED FISHING MORTALITY.—To begin, consider the relationship between EFH and fishing mortality. For example, suppose that spawning habitat is reduced to a fraction ξ of the original habitat and that fishing mortality is exactly controlled to be F . The question is what combination of parameters will keep the steady state level at or above a fraction κ ($= 0.6$ for the calculations) of the steady state in the absence of fishing. That is, let $\bar{N}(\xi, F)$ denote the steady state when habitat is reduced to the fraction

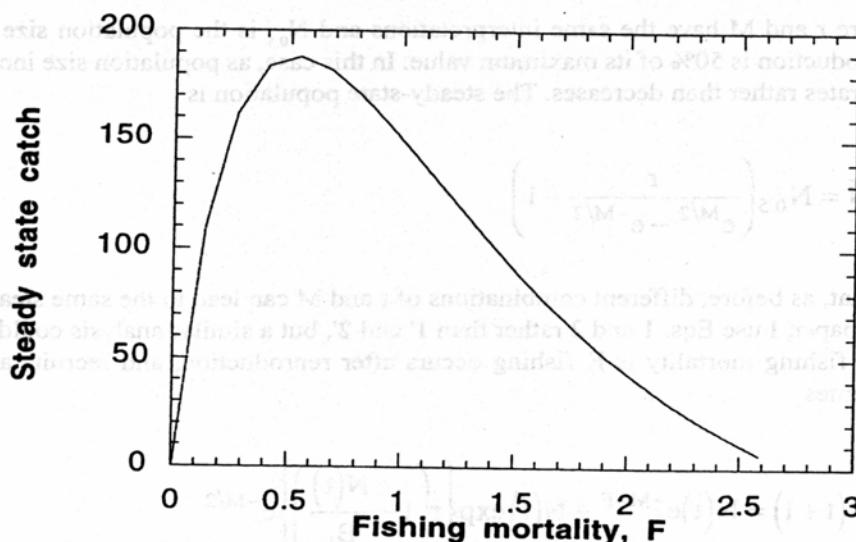


Figure 1. Steady-state catch as a function of fishing mortality for the minimalist model. Overfishing occurs whenever fishing mortality is greater than the value leading to the peak in steady-state catch, because the same catch can occur at a smaller value of fishing mortality.

ξ of the original habitat and fishing mortality is F . We then set $\bar{N}(\xi, F) = \kappa B_{\text{MAX}}$ and solve for ξ to obtain

$$\xi = \kappa \frac{\left[1 - (1/r) \log(e^M - e^{-M/2}) \right]}{\left[1 - (1/r) \log(e^M - e^{-(M/2)-F}) \right]} \quad \text{Eq. 7}$$

This equation shows us that there is a trade-off between fishing mortality and loss of spawning habitat (Fig. 2). In particular, loss of spawning habitat is equivalent to fishing mortality of the adult stock, in the sense that both cause the steady state to decrease. Thus, those interested in fishing the adults have a vested interest in protecting spawning habitat.

THE DYNAMICS AND MONITORING OF HABITAT LOSS AND RECOVERY.—Habitat will not always be lost (but see below), and restoration may occur, but lags introduced by the biological dynamics force us to be very careful when monitoring habitat change. To illustrate this point, assume that the stock starts at $N(1) = B_{\text{MAX}}$, that EFH starts at $B_1(t) = B_{10} = 100$ and that $F = 0.54$ (this choice will be explained in the next section). Furthermore, assume that, for years 1–10, habitat is consistently lost so that $B_1(t+1) = B_1(t) - \delta B_1$, where δB_1 is 5% of the original value of spawning habitat. For years 11–20, habitat recovers according to $B_1(t+1) = B_1(t) + 0.85 \delta B_1$.

The result (Fig. 3) shows that neither catch nor stock (which is directly proportional to catch) is a good indicator of what is happening to the habitat: the decline in catch or stock lags behind habitat destruction, and the recovery lags behind habitat restoration. In the years in which habitat decreases, population size decreases, but the decrease in population lags considerably behind the decrease in habitat, so the stock gives an overly optimis-

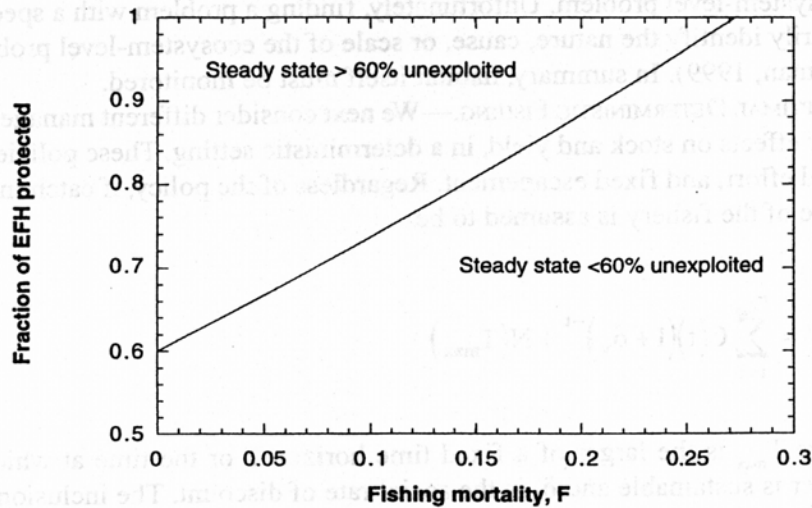


Figure 2. The trade-off between protecting EFH and fishing mortality. The boundary curve separates regions in which the steady state in the presence of habitat loss and fishing is greater or less than 60% of the unexploited biomass, determined by Eq. 7. The boundary is approximately linear but will vary with parameters of the model.

tic view of what is happening in the environment. Things are worse than they appear. The converse is also true when habitat is restored: the ecosystem, the 'health' of which is indexed by the spawning habitat of the target species, is better off than indicated by the population trend. Thus, top predators may have population dynamics that prohibit use of their abundance and productivity as effective indicators of the current health of ecosystems, although they may be good indicators of long-term effects.

In fact, it is unlikely that we can determine the health of ecosystems by monitoring any single species. A human metaphor may help: a healthy liver does not imply a healthy heart, or a healthy person for that matter. However, just as a diseased liver would indicate

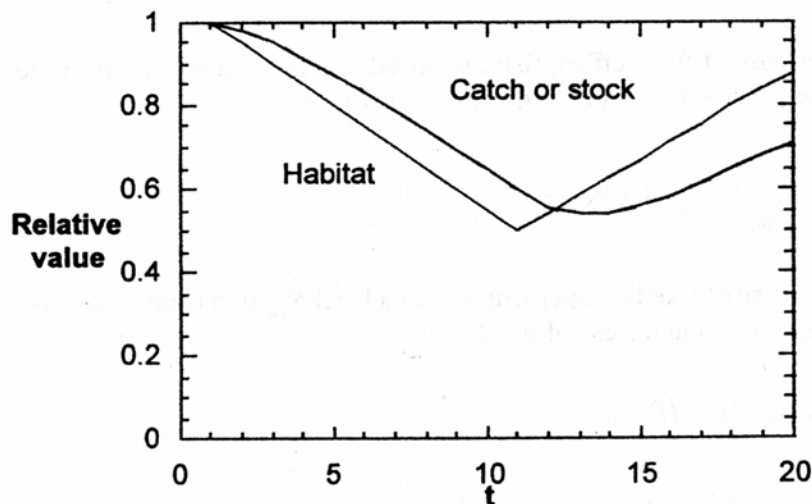


Figure 3. When habitat is lost, the stock decline lags the habitat loss, and as habitat recovers, the stock recovery lags the habitat recovery.

an unhealthy person, a problem with one particular species could indicate an ecosystem-level problem. Unfortunately, finding a problem with a species does not necessarily identify the nature, cause, or scale of the ecosystem-level problem (Mangel and Hofman, 1999). In summary, habitat itself must be monitored.

OPTIMAL DETERMINISTIC FISHING.—We next consider different management policies and their effects on stock and yield, in a deterministic setting. These policies are fixed catch, fixed effort, and fixed escapement. Regardless of the policy, if catch in year t is $C(t)$, the value of the fishery is assumed to be

$$V = \sum_{t=1}^{T_{\max}} C(t)(1 + \delta_v)^{-t} + N(T_{\max}) \quad \text{Eq. 8}$$

where T_{\max} is the larger of a fixed time horizon T or the time at which the fishery no longer is sustainable and δ_v is the social rate of discount. The inclusion of $N(T_{\max})$ takes account of the value of future options for the stock (Mangel et al., 1996); for example, future generations may determine that ecotourism is more important than harvest or future generations themselves may want the opportunity to harvest the stock.

For the case of fixed catch, the catch is

$$C = \lambda MB_0 \quad \text{Eq. 9}$$

(Beddington and Cooke, 1983), where λ is an adjustable parameter. This is a generalization of the $(1/2)MB_0$ rule common in fisheries management.

The value of λ is chosen to maximize the value of the fishery. Once C is specified by Eq. 9, fishing mortality $F(t)$ is determined by the generalization of Eq. 6

$$C = \frac{F(t)}{F(t) + M} (1 - e^{-M-F(t)}) N(t) \quad \text{Eq. 10}$$

For the case of fixed effort, fishing mortality F is constant over the time horizon. In this case catch varies according to the analogue of Eq. 10.

$$C = \frac{F}{F + M} (1 - e^{-M-F}) N(t) \quad \text{Eq. 11}$$

For the case of fixed escapement, we set a level N_{esc} that is target escapement. The catch is any population in excess of this level:

$$C(t) = \max\{0, N(t) - N_{\text{esc}}\} \quad \text{Eq. 12}$$

As before, fishing mortality must be determined from catch.

Table 2. Values of the fishery under three different management policies.

Method	Optimal parameter	Optimal value	$N(T_{\max})$
Catch	$\lambda^* = 0.4$	5,932	809
Effort	$F^* = 0.54$	7,341	512
Escapement	$N^*_{\text{esc}} = 300$	7,437	487

In each case, there is a single parameter, and the policy can be optimized by choice of the value of the parameter that maximizes the value (Table 2). For the results that follow, I assume a policy of fixed effort, under which F^* denotes the optimal value of fishing mortality.

THE CASE FOR RESERVES.—Deterministic models such as the one in the previous section are interesting and have stimulated considerable work (reviewed by Clark, 1990), but they should not be used to set management practice.

Management practice must be informed by two realities, on which the rest of this paper is focused: habitat will be lost, and fishing mortality cannot be controlled.

That is, various natural and human-caused interventions will lead to decline of essential fish habitat. Indeed, habitat loss is the single greatest threat to the decline of biodiversity (Wilcove et al., 1998). We must recognize this truth as we seek the path between no conservation and no human interventions (Minns, 1997).

Similarly, fishing mortality can be affected, but cannot be controlled precisely. Consideration of incidental mortality and discards, about which we generally know very little, is sufficient to defend this point (Gillis et al., 1995a,b).

To begin, assume that reserves are not in place, i.e., that all of the stock is available for fishing and all of the habitat is available for loss. To account for the lack of control of fishing mortality, assume that fishing mortality $F(t)$ in year t is

$$F(t) = F^* \exp\left(X_{\sigma_f} - (1/2)\sigma_f^2\right) \quad \text{Eq. 13}$$

where X_{σ_f} is a normally distributed random variable with mean 0 and standard deviation σ_f . Thus, the expected value of $F(t)$ is F^* , and the coefficient of variation of fishing mortality is related to σ_f . Using Eq. (13) allows fishing mortality to be either greater or less than the optimal level F^* , and on average the two will be the same. An alternative would be to set $F(t) = F^* \max(1, \exp\{X_{\sigma_f} - (1/2)\sigma_f^2\})$ so that fishing mortality never falls below F^* .

I allow habitat destruction to occur randomly, at rate ρ , in the sense that the probability of habitat loss in a particular year is $1 - e^{-\rho}$. Thus, when $\rho = 0$, there is no habitat loss, and as ρ becomes larger, the chance of habitat loss in a particular year approaches 1.

Because effort and habitat are now random variables, it is necessary to simulate the dynamics of the stock and habitat and the value of the fishery by Monte Carlo methods. In the simulations, I track the sizes of the population and the habitat and the value of the fishery. In addition, I introduce a success criterion: fishery management is successful over the time horizon if $N(T)$ for a particular simulation with fluctuating fishing mortality is above $0.6N(T)$ when fishing mortality is fixed and habitat destruction does not occur. A typical result is shown in Figure 4.

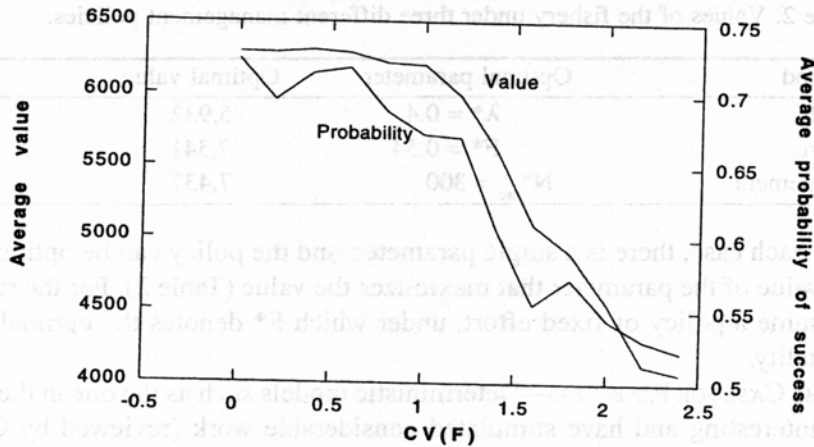


Figure 4. The average value of the fishery and probability of success when fishing mortality fluctuates and habitat destruction occurs ($\rho = 0.2$). Because sampling errors in simulations scale as $1/(\text{square root of number of simulations})$ and 500 simulations are used, differences of the order of 4% in the probability of success are not significant.

The role that reserves can play in management can now be investigated. For the calculations given here, I used $CV(F) = 0.6$ and $\rho = 0.2$. I assume that a reserve is no-take, rather than multiple use (Tisdell and Broadus, 1989; Greene et al., 1998). A reserve protects a fraction α of the habitat. This protection can be divided into a portion α_0 of the fishing grounds made into a reserve where no fishing mortality occurs and a portion α_1 of the spawning habitat that is made into a reserve so that no destruction of spawning habitat occurs. Furthermore, I assume that $B_{10} = B_1(0)$ and that the creation of reserves neither increases fishing mortality in the fished area nor increases the rate of spawning habitat destruction in the unprotected area. This is an important assumption, especially about the redistribution of fishing mortality; elsewhere (Mangel and Warner, unpubl.), I discuss the effects of redistribution of fishing mortality on the efficacy of no-take reserves.

At this point, spawning habitat consists of the protected portion $\alpha_1 B_{10}$, and the unprotected portion $U(t)$, which starts at $U(0) = (1 - \alpha_1)B_{10}$. If spawning habitat destruction does not occur in year t , then

$$B_1(t+1) = B_1(t) = \alpha_1 B_{10} + U(t) \quad \text{Eq. 14}$$

In a year in which spawning habitat destruction does occur

$$B_1(t+1) = \alpha_1 B_{10} + \max(0, U(t) - \delta B_1) \quad \text{Eq. 15}$$

Thus, $\alpha_1 B_{10}$ sets a minimum for the amount of spawning habitat by setting aside that in reserves.

The stock in the no-take reserve is $N'(t) = \alpha_0 N(t)$, and that in the fished portion of the habitat is $N''(t) = (1 - \alpha_0)N(t)$. Because both are subject to natural mortality, but only the latter is subject to fishing mortality, the stock dynamics are now

$$N(t+1) = N'(t)e^{-M} + N''(t)e^{-M-F(t)} + (N'(t) + N''(t)) \exp \left\{ r \left(1 - \frac{N'(t) + N''(t)}{B_1(t)} \right) \right\} e^{-M/2} \quad \text{Eq. 16}$$

According to the dynamics of Eq. 16, the no-take reserve provides a source of replenishment for the fishery (Dugan and Davis, 1993; Russ and Alcala, 1996). In Eq. 16, I use the simplest transfer function about movement of fish between protected and unprotected areas: I assume that the stock from the fished and unfished areas mix on the spawning ground and then redistribute themselves across the fished and unfished regions.

Repeating the same simulations as before shows the value of reserves (Table 3). In the absence of reserves, on average $B_1(T) = 63.9$; the average value of the fishery is 6245, and the probability of success is 0.7. These results in Table 3 show that reserves can simultaneously improve the value of the fishery and increase its sustainability.

Note that an intermediate mix of protected spawning and fishing habitat maximizes the value of the fishery while maintaining a very high probability of success. Thus, it is possible to think about the optimal mixture of mature and spawning habitat to protect, given an overall level of habitat protection. Figure 5 gives an example, in which the reserve mixture (spawning and mature habitat) is chosen to maximize the value of the fishery.

DISCUSSION

Clearly, this model is 'not realistic', in the sense that it does not apply to a particular species. The age structure is very simple; it could be adjusted but at the expense of its analytical simplicity and tractability and it is not clear that any understanding would be

Table 3. The value of reserves in enhancing stock, protecting habitat, and increasing catch.*

	α_0	α_1	$B_1(T)$	Value	Probability of success
Enhancing stock	0	0.1	73.6	6,457.01	0.964
	0	0.2	80.8	6,615.21	0.994
	0	0.3	85.2	6,723.48	1
	0	0.4	88.2	6,796.23	1
	0	0.5	90.2	6,863.81	1
Protecting habitat	0.05	0.05	69.7	6,671.33	0.92
	0.1	0.1	76.1	6,715.42	0.912
	0.15	0.15	77.6	7,182.53	1
	0.2	0.2	80.9	7,856.73	1
	0.25	0.25	83.2	7,858.03	1
Increasing catch	0.1	0	64.1	6,846.76	0.828
	0.2	0	64.2	5,890.87	0.996
	0.3	0	63.2	6,124.89	0.998
	0.4	0	64.2	6,456.13	0.998
	0.5	0	64.6	6,752.00	0.998

*Up to 50% of the total habitat (spawning plus fishing) is protected, divided between protecting fishing habitat (α_0) and protecting spawning habitat (α_1).

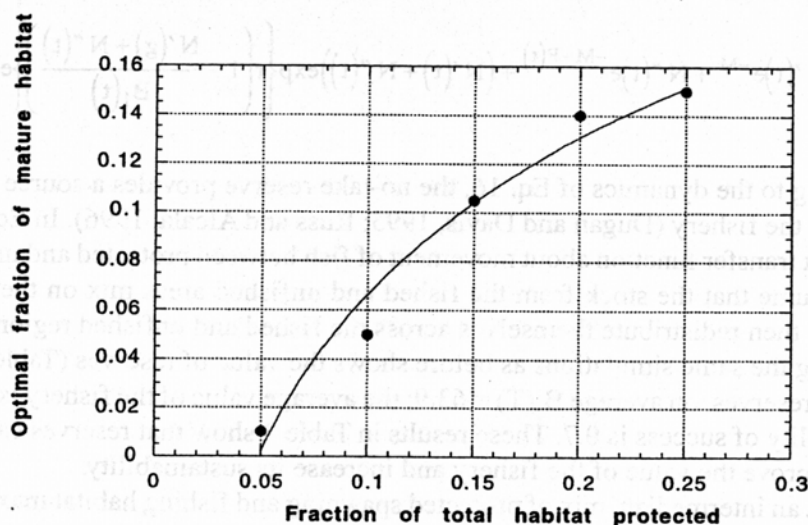


Figure 5. Optimal fraction of habitat for mature fish protected as a function of the fraction of the total habitat that is protected, chosen to maximize the value of the fishery. The key observation is that an intermediate mix of the two habitats is the best one to protect.

gained. The transfer function, albeit simple, is a useful starting point. Getting a better understanding of the transfer function is probably the next step in model design (see, e.g., Dugan and Davis, 1993; Cowen and Castro, 1994; Roberts, 1998).

Even so, remember Ludwig's second point: effective management models cannot be realistic. This model does provide a number of insights into thinking about reserve design (see also Roberts, 1997, 1998).

- Allow reproduction to take place before fishing.
- Protect an intermediate mix of the spawning and fishing grounds.
- Recognize that loss of spawning habitat is equivalent to fishing mortality of the adult stock, in the sense that both cause the steady state to decrease. This recognition can create new alliances.
- Recognize that neither catch nor stock is a good indicator of what is happening to the habitat: the decline lags behind habitat destruction and the recovery lags behind habitat restoration. Habitat itself must be monitored.
- Establish information about transfer functions (Holland et al., 1993; Roberts, 1997, 1998; Stobutzki and Bellwood, 1997).

Finally, although I did not discuss it in detail here, I stress the following design consideration that emerges from Ludwig's first point:

- Avoid the deterministic trap: establish reserves of different sizes. Otherwise, when the time comes to evaluate them, no variation in the independent variable (reserve size) will exist on which to base estimates of dependent variables (enhancement of the fishery, protection of the stock). This is the essence of adaptive management; further details can be found in Hilborn and Mangel (1997) and Parma et al. (1998).

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