

Spatial Competition in Overlapping Seasonal Fisheries: A Bioeconomic Model of Fishermen and Regulators

Joshua K. Abbott
University of California, Davis
abbott@primal.ucdavis.edu

*Selected Paper prepared for presentation at the American Agricultural Economics Association
Annual Meeting, Denver, Colorado, August 1-4, 2004*

*Copyright 2004 by Joshua Abbott. All rights reserved. Readers may make verbatim copies of
this document for non-commercial purposes by any means, provided that this copyright notice
appears on all such copies.*

Abstract

Those familiar with the recent literature on fisheries economics have undoubtedly noticed a gradual trend toward the incorporation of an explicit spatial dimension in the description of both biological and economic processes. Most of these models have expanded the conventional Gordon-Scott-Schaefer industry model of the fishery to include a notion of spatial equilibrium (basically a no-arbitrage condition) to predict the long-run economic and biological status of discrete resource patches in an open access property regime.

Despite the usefulness of such approaches, there is a need for richer agent-level models in which fishermen compete in an endogenous regulatory environment and make decisions about how to allocate effort across spatially and temporally scattered fish populations. Such models are especially appropriate in fisheries such as the Alaskan salmon and groundfish fisheries where small numbers of fishermen compete across several distinct resource patches in the space of a single season – all while subject to the watchful eye of regulators.

This paper develops a simple short-run dynamic game between regulators and fishermen in a two-site, seasonal fishery. In this single-season model, fishermen have a single indivisible unit of effort (i.e. a boat) to allocate to one site or the other at the start of each period. Profits depend not only upon the biomass present at each site but the fishing decisions of other participants and the site closure decisions of regulators. Fishermen reduce each other's profits by contributing to congestion externalities, thereby reducing the productivity of effort. Participants may choose to move from one site to another at any time, but must incur a constant adjustment cost in the process.

The regulators for each site act upon biological goals that are expressed by cumulative harvest ceilings for each fishery. Each regulator is able to perfectly observe the cumulative

harvest for their site at the beginning of each period and must then decide whether to close the fishery or let it remain open. The regulators' preferences are such that they will 1) never set a season closing date such that the quota is exceeded and 2) always pursue an optimal stopping strategy such that a closed site is never reopened.

This interaction between fishermen and the regulators can be expressed as a finite difference game and solved for a Markov perfect equilibrium through a nested backwards-recursive algorithm. This is done in the case of a two-fishermen, two-site model with symmetric, parabolic abundance equations. The model is first analyzed in the simple unregulated case in which both sites are always open before proceeding to the fully regulated case.

Simulation results for the unregulated case show how differences in fishing technology (as expressed through the strength of congestion externalities and the magnitude of adjustment costs) can dramatically influence the timing and pattern of movement in the fishery. The results are particularly striking when high congestion externalities and relatively low adjustment costs produce strong incentives for averting behavior.

Results for the model with regulators show how the effects of congestion combined with the temporally coincident nature of the fisheries can lead to feedback between the strategic behavior of fishermen and the equilibrium closing dates of the regulators. This feedback can induce asymmetries in the strategies of regulators with otherwise identical goals and biological systems.

Finally, a policy experiment is conducted to show that a simple, spatially delineated policy instrument may reduce the burden of congestion and congestion-averting movement expenditures, leading to an outcome that achieves a higher net present value of profits without compromising the harvest goals of the regulators.

Introduction

Those familiar with the recent literature on fisheries economics have undoubtedly noticed a gradual trend toward the incorporation of an explicit spatial dimension in the description of both biological and economic processes.¹ Most of these models have expanded the conventional Gordon-Scott-Schaefer industry model of the fishery to include a notion of spatial equilibrium (basically a no-arbitrage condition) to predict the long-run economic and biological status of discrete resource patches in an open access property regime.

Despite the usefulness of such approaches, there is a need for richer agent-level models in which fishermen compete in an endogenous regulatory environment and make decisions about how to allocate effort across spatially and temporally scattered fish populations. Such models are especially appropriate in fisheries such as the Alaskan salmon and groundfish fisheries where small numbers of fishermen compete across several distinct resource patches in the space of a single season – all while subject to the watchful eye of regulators.

The following section develops a simple short-run game-theoretic model between regulators and fishermen in a two site, seasonal fishery. The second section reports some simulation results from the model's solution and discusses the possibility of policy improvements by taking account of the spatial/strategic nature of competition. The third section concludes the analysis.

I. Model

The total fishing season is of length T . Within this season are two spatially distinct fish populations ($i=1,2$) with their own biological (as opposed to regulatory) season start and ending dates (\underline{t}^i and \bar{t}^i respectively). During the season, the population of each site evolves

¹ Notable examples of this literature include the seminal work by Sanchirico and Wilen (1999) as well as earlier but less general papers by Brown and Roughgarden (1997) and Tuck and Possingham (1994). See also the literature on marine reserves; Sanchirico and Wilen (2001) is a good example of the current state of the art.

exogenously according to the common-knowledge equation $g^i(t)$ (where $g^i(t \leq \bar{t}^i) = g^i(t \geq \bar{t}^i) = 0$); this entails that the harvest decisions of fishermen at a site have no impact on the availability of fish for future catch.² Such a description is suitable for fugitive populations such as spawning salmon that are either caught today or unavailable for catch tomorrow.

At the beginning of each discrete time period the fishermen ($j=1, \dots, J$) each have a fixed, indivisible unit of effort, E^i (normalized to 1) to allocate to either site 1 or site 2. Since this is a short-run model, we can be sure that effort is employed at all times in order to help cover fixed costs. The instantaneous harvest function at time t for a fisherman j at a particular site i is:

$$\dot{h}_{j,t}^i(E_{j,t}^i, E_{-j,t}^i, g^i(t), d_t^i) = (1 - d_t^i) \times q_j g^i(t) E_{j,t}^i (1 + E_{-j,t}^i)^{\alpha_j}, \quad i=1,2 \quad j=1, \dots, J \quad t=1, \dots, T$$

where $d_t^i \in \{0,1\}$ is a variable indicating the regulatory status of the fishing site (= 0 for open and 1 for closed), q_j is the catchability coefficient, $E_{j,t}^i \in \{0,1\}$ is own effort in site i , $E_{-j,t}^i = \sum_{k \neq j} E_{k,t}^i$ is the sum of all other effort at site i , and $\alpha_j (< 0)$ describes the sensitivity to congestion effects of fisherman j . Since $g^i(t)$ is the only continuously varying component of $\dot{h}_{j,t}^i$, the harvest from t to $t+1$ can be written as:

$$h_{j,t}^i(E_{j,t}^i, E_{-j,t}^i, X_t^i, d_t^i) = (1 - d_t^i) \times q_j X_t^i E_{j,t}^i (1 + E_{-j,t}^i)^{\alpha_j}, \quad i=1,2 \quad j=1, \dots, J \quad t=1, \dots, T$$

where $X_t^i = \int_t^{t+1} g^i(t)$.

Fishermen are price takers in the output market (with the price invariant across sites and normalized to 1). Additionally, fishermen face a constant adjustment cost of moving between

² This assumption is made in order to focus upon the unique strategic and spatial aspects of the problem rather than the ubiquitous stock effects. A harvest-dependent fish stock may be added with little effort to the analytical model but increases the complexity of the solution algorithm (and the use of computer time) considerably. Of course, the exogeneity of the fish stock will necessarily break down if the model is extended beyond the single-season case.

sites that is invariant with respect to site of origin:

$$c_{j,t}(E_{j,t}^1, E_{j,t-1}^1) = \gamma_j (E_{j,t}^1 - E_{j,t-1}^1)^2, \quad j=1, \dots, J \quad t = 1, \dots, T$$

where $\gamma_j > 0$.³ Note that costs are only incurred when a change of location is made. Since

$E_{j,t}^2 = 1 - E_{j,t}^1$, it is now possible to express per-period profits in terms of a single choice

variable, $E_{j,t}^1$:

$$\pi_{j,t}(d_t^1, d_t^2, E_{j,t}^1, E_{j,t-1}^1, E_{-j,t}^1) = h_{j,t}^1(E_{j,t}^1, E_{j,t-1}^1, X_t^1, d_t^1) + h_{j,t}^2(E_{j,t}^1, E_{-j,t}^1, X_t^2, d_t^2) - c_{j,t}(E_{j,t}^1, E_{j,t-1}^1),$$

$$j = 1, \dots, J.$$

Note that due to indivisibility of effort that harvest for a particular individual can only be nonzero in one site at a given time.

There are two regulators – one for each site. This article follows the example of Homans and Wilen (1995) by assuming that the regulators independently set a target cumulative harvest quota \bar{h}^i and strive to achieve this goal by controlling the site closure date. Unlike their work, however, I assume that managers perfectly observe cumulative harvest at the beginning of each period and need not declare the closure date at the beginning of the season.⁴ Instead each site is assumed open at the start ($d_0^i = 0$) and regulators can then close it at any discrete breakpoint ($d_t^i = 1$). Once the site is closed, it remains closed for the remainder of the season. The regulators' goal structure may be given a utility theoretic description as follows:

$$u_t^i(d_{t-1}^i, d_t^i, h_{cum,t}^i) = (1 - d_{t-1}^i) d_t^i \times w(h_{cum,t}^i - \bar{h}^i) + d_{t-1}^i (1 - d_t^i) \Psi, \quad i = 1, 2 \quad t = 1, \dots, T$$

$$d_0^i = 0, \quad w(\bullet) > 0 \quad \& \quad w' > 0 \quad \text{for } h_{cum,t}^i \leq \bar{h}^i, \quad w(\bullet) = 0 \quad \text{for } h_{cum,t}^i > \bar{h}^i$$

³ This lumped cost may include physical costs of movement (i.e. gasoline) and the monetized opportunity cost of time.

⁴ The realism of this assumption is open to debate. However, in many near-shore fisheries (such as the Alaskan salmon fisheries) where the number of participants is small and fisheries managers maintain a presence, this assumption is likely appropriate.

where $h_{cum,t}^i$ is the total cumulative harvest to date and Ψ is a large negative constant (which is the cost to the regulator of reopening a previously closed fishery).⁵

Having described the important aspects of the regulators and fishermen, we are now free to expound the structure of the dynamic game and characterize its solution. At the beginning of each period, each regulator perfectly observes the vector (s_t) of relevant state variables of the system (cumulative harvests, $h_{cum,t}^1$ and $h_{cum,t}^2$, the previous closure statuses, d_{t-1}^1 and d_{t-1}^2 , and the current locations of all fishermen, $E_{j,t-1}^1$ for $j = 1, \dots, J$) and decides whether to open or close their site. Simultaneously, the fishermen (who also observe the same state vector) decide whether to allocate their effort to site 1 or site 2. This dynamic game can be expressed via the typical extensive form game tree, but is handled with much greater flexibility by expressing it as a difference game and using the tools of dynamic programming to obtain a solution.

The Markov perfect equilibrium (MPE) strategies, $d_t^{i,*}(s_t)$ and $E_{j,t}^{1,*}(s_t)$, are complete, state-contingent descriptions of the players' best responses to the current observed state of the system given that all other players pursue their best line of action.⁶ Fishermen maximize the present discounted value of short-run profits and regulators maximize the sum of their "utilities". The equilibria resulting from their joint behavior may be characterized by the following set of Bellman equations (for fishermen and regulators, respectively):

$$V_{j,t}(s_t) = \max_{E_{j,t}^1 \in \{0,1\}} \{ \pi_{j,t}(d_t^{1,*}(s_t), d_t^{2,*}(s_t), E_{j,t}^1, s_t, E_{-j,t}^{1,*}(s_t)) + \beta V_{j,t+1}(s_{t+1}) \}$$

$$j=1, \dots, J \quad t = 1, \dots, T$$

⁵ The reader should not be unduly preoccupied with the details of this function. This is simply one of many utility-theoretic descriptions that yield the described regulatory behavior.

⁶ The concept of Markov perfect equilibrium is basically an extension of subgame perfect Nash equilibrium to differential and difference games. The key property is that the best response functions represent a credible strategy at every proper subgame, regardless of whether the subgame lies on the equilibrium path. See Dockner, et al. (2000).

$$V_t^i(s_t) = \max_{d_t^i \in \{0,1\}} \{u_t^i(s_t, d_t^i) + V_{t+1}^i(s_{t+1})\},$$

$$i = 1,2 \quad t = 1, \dots, T.$$

where the states evolve according to the following deterministic relationship:

$$s_{t+1} = [h_{cum,t+1}^1, h_{cum,t+1}^2, d_t^1, d_t^2, E_{1,t}^1, \dots, E_{J,t}^1] =$$

$$[h_{cum,t}^1 + \sum_{j=1}^J h_{j,t}^1, h_{cum,t}^2 + \sum_{j=1}^J h_{j,t}^2, d_t^1, d_t^2, E_{1,t}^1, \dots, E_{J,t}^1].$$

II. Solution and Analysis

Although the previous equations fully characterize the equilibrium of the dynamic game, this system of Bellman equations generally lacks a closed-form solution. Nevertheless, given the functions to describe the exogenous population dynamics of the seasonal fish stock, values for all parameters, and terminal conditions for the $V_{j,t}(s_t)$ (here set equal to zero), it is fairly easy to achieve numerical solutions via a nested backwards-recursive algorithm.⁷

Upon obtaining the Markov perfect strategies, it is then possible to simulate from any initial state (i.e. locations of fishing effort at $t=0$) the equilibrium effort allocation decisions and season closure dates. Yet, in many fisheries, this initial location status is likely endogenous and dependent on fishermen's perceptions of opponents' and regulators' strategies. This factor is encompassed in the model solution by allowing the game to be played in two stages. In stage 1 (occurring in time zero) the fishermen simultaneously decide how to allocate themselves in space based on the MPE payoffs in the second stage resulting from their (and their opponents') decision.⁸ The Nash equilibrium resulting from this static game decides the initial state of the second stage dynamic game beginning at $t=1$.

⁷ Details of this algorithm are omitted due to space considerations. Full MATLAB code is available from the author.

⁸ It is assumed that the initial cost of reaching one site vs. another is equal – all that matters is the NPV of future payoffs in the second stage game. This is likely fairly accurate for many non-resident fleets where the relative distance from port of various sites in a general region are relatively negligible. It may be less appropriate for resident fleets with relatively slow and inefficient technology. Nevertheless, this assumption is easily modified.

The instantaneous population of fish available for catch at any given time ($g^i(t)$) is given by a set of overlapping parabolic relationships (see Figure 1) where the parabolas have been expressed in terms of the biological season parameters (\underline{t}^i and \bar{t}^i) and the population maximum g_{\max}^i .⁹

Figure 1: Parabolic Fish Biomass by Site

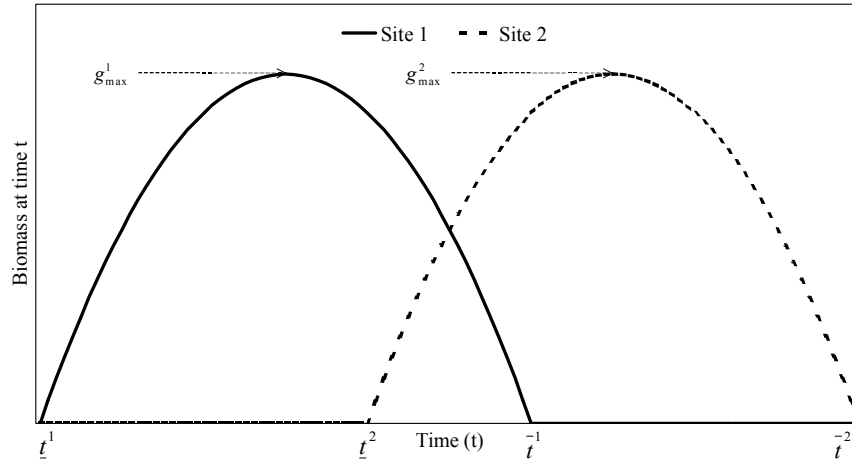


Table 1: Parameter Values for Simulations

Biological Parameters			Economic Parameters		
	Site 1	Site 2		Fisherman 1	Fisherman 2
\underline{t}^i	1	5	β	1	1
\bar{t}^i	7	11	q	0.5	0.5
g_{\max}^i	10	10			

For the purposes of the ensuing analysis, certain parameters are held fixed throughout (see Table I). These parameter values are fixed in order to more closely discern the impact of changes in congestion externalities and adjustment costs.¹⁰ It is important to note that the given parameter values imply that the two sites have staggered but identical abundance relationships.

⁹ Note that these biological relationships are *not* the differential equations representing the long-run reproduction/mortality of the fish population -- rather they are the perceived intra-seasonal fluctuation of a local stock. The parabolic functional form is a crude but reasonably accurate characterization of the seasonal abundance for many transient species -- particularly anadromous fish.

¹⁰ These parameter values have not been calibrated to any real-world system and thus the results have only qualitative significance.

Also, the β values entail that fishermen simply maximize the sums of their profits.¹¹ The following simulations fall into two broad categories: 1) unregulated fisheries (i.e. no constraints on site choice), and 2) regulated fisheries.

Unregulated Fisheries

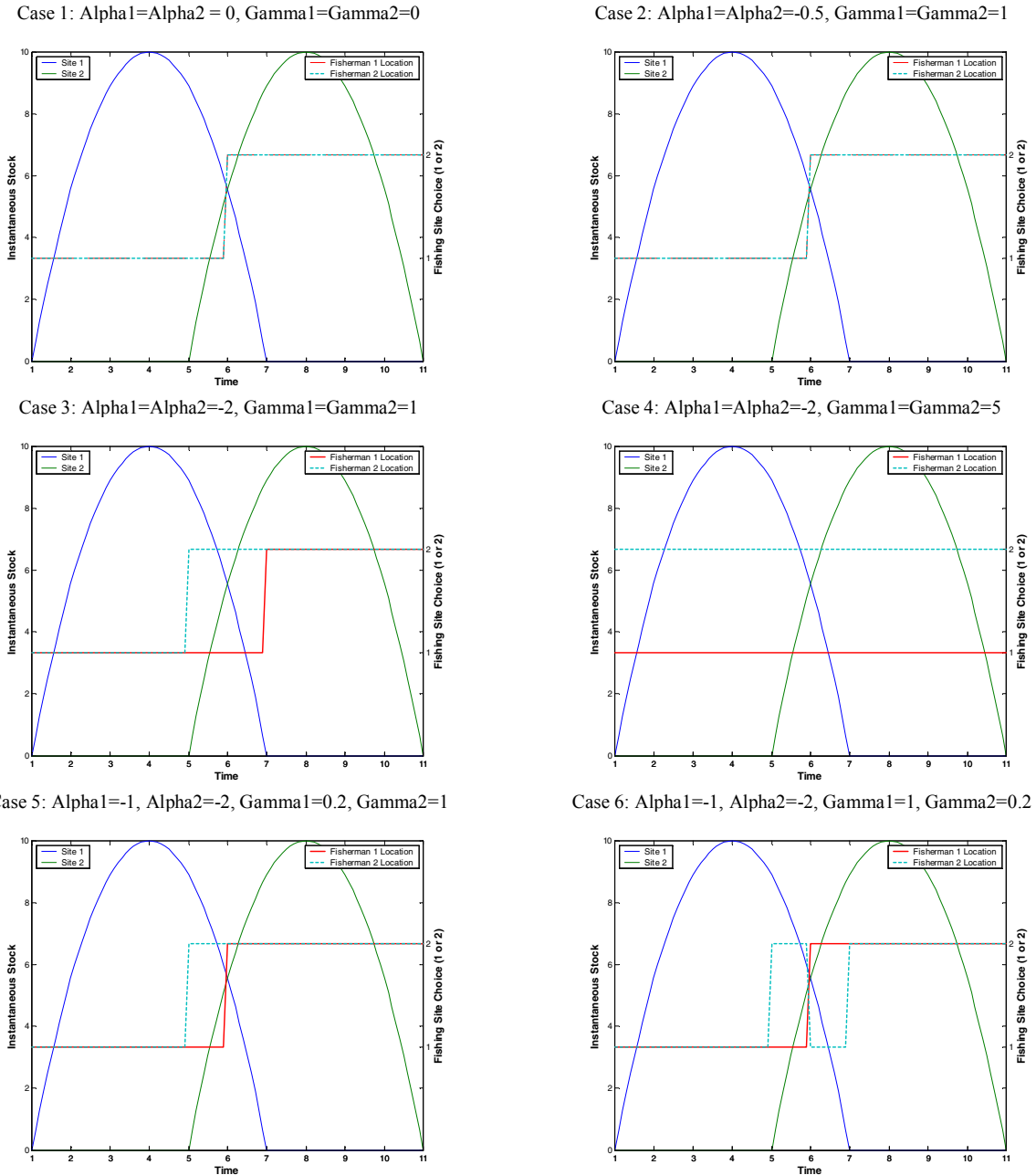
The graphical results of the simulations under various parameter values are given in Figure 2. Case 1 is the most basic of scenarios, one with no congestion externalities and zero adjustment costs; in this case there is no real strategic interaction, and so switching behavior is driven entirely by the relative biological abundance between sites. Case 2 describes a fishery with mild externalities and moderate adjustment costs. Notice that there is no change in behavior from that of Case 1; the costs of congestion are not sufficiently onerous to motivate either fisherman to change his behavior from that of the zero-congestion cost scenario. Case 3 shows a fishery in which congestion externalities are more intense (perhaps due to oceanographic or biological features that lead to clumping of harvestable biomass) while movement costs remain relatively low. In this case, it is now a Markov perfect outcome for one player to move to the second fishery as soon as possible (at $t=5$) while the other remains in site 1 for 2 more periods – this despite the initially lower abundance in the second fishing site.¹² Case 4 is an extreme case in which fishermen face not only considerable congestion but also very high costs of adjustment, perhaps from a large geographical distance between sites or slow boats. In this scenario, neither participant can afford to move from site 1 to site 2 given the high adjustment costs and depressed catch stemming from congestion externalities. Since fishermen perceive this at the start of the

¹¹ This is a fairly benign assumption for a short season. Simulations over alternative discount rates revealed little change in simulated behavior within a reasonable range of variation.

¹² Even though the graph shows Player 2 switching at $t=5$, it is also a MPE for Player 1 and 2 to reverse roles. This is to be expected given the symmetry of congestion externalities and adjustment costs between fishermen. Nevertheless, it is generally difficult to rule out the possibility of multiple equilibria. Despite this difficulty it is possible in many cases (especially with heterogeneous fishermen) to either demonstrate uniqueness or find alternative equilibria.

game, they allocate their effort to opposite sites, effectively choosing to let effort lie idle for a portion of the season in exchange for a larger harvest over a shorter time horizon.

Figure 2: Simulation Results for Unregulated Fisheries



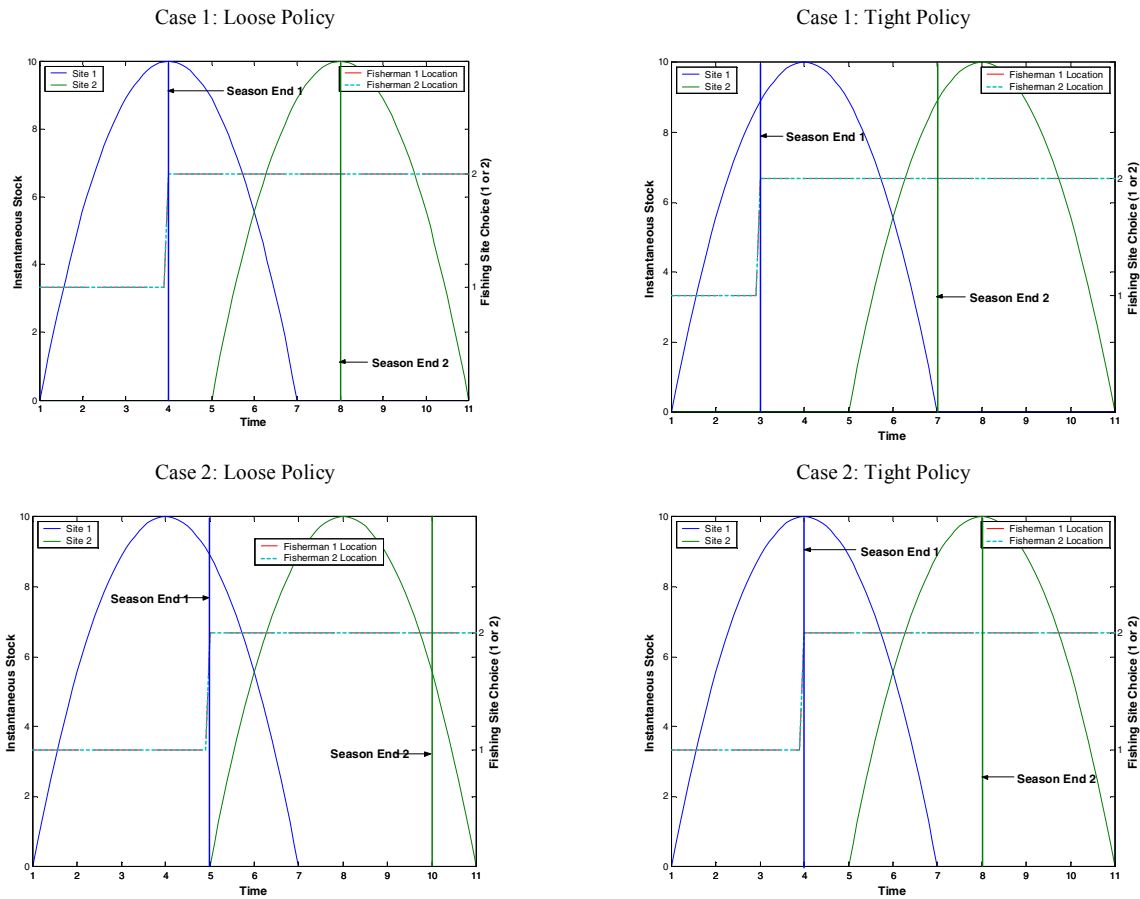
The first four scenarios in Figure 2 all presume symmetric harvesting technology – clearly a heroic assumption. There are many cases in which the patterns of behavior observed in Cases 1-4 are mimicked by simulations with nonsymmetrical α_j and γ_j , but there are many

others which produce patterns of behavior that do not occur in the symmetric cases. In Case 5, we see an instance in which fisherman 2 has a high sensitivity to congestion relative to that of fisherman 1, but is less able than 1 (due to his higher cost of adjustment) to exhibit averting behavior. In this case fisherman 2 moves to site 2 at $t=5$ (just as in Case 3), but fisherman 1 moves at an earlier date than in Case 3 due to his relatively lower sensitivity to congestion. Finally, in Case 6 we see a very intriguing case in which the (unique) MPE depicts fisherman 2 bouncing back and forth between site 1 and 2 for the span of three periods. This occurs due to a combination of the overlapping pattern of biomass in the two sites, the relatively high movement cost of fisherman 1, and the combination of high congestion costs and low adjustment costs for fisherman 2. This result shows that the moving back and forth that is often associated with the search behavior of fishermen in a world of imperfect information and uncertainty can be explained (in an admittedly special case) by a model of perfect foresight.

Regulated Fisheries

As in the unregulated case, there are numerous scenarios that may be investigated within the structure of this model; however, for the sake of brevity, only two simple cases are considered. The first is a fishery characterized by symmetric participants with mild congestion externalities and a moderate cost of adjustment (i.e. exactly as in the previous Case 2). The second has the same costs of adjustment, but with higher (and symmetric) impacts from congestion (which implies the parameter values from the unregulated Case 3). Within each of these two cases lie two sub cases – one in which the site regulators follow a “loose” or a “tight” policy ($\bar{h}^i = 75\%$ or 50% respectively of the unregulated MPE cumulative harvest). Figure 3 shows the results of these simulations, where the vertical lines indicate the equilibrium site closure dates.

Figure 3: Simulation Results for Regulated Fisheries



A glance at the results for Case 1 reveals little in terms of interesting behavioral implications for fishermen. Switching is simultaneous, as in the regulated case, but occurs earlier for both policies than in the nonregulated scenario due to the external stimulus of the regulator. Also, the total season length is the same across sites for each regulatory policy (3 periods for the “loose” policy and 2 for the “tight” policy). The regularity of this situation is not surprising given the smallness of the distortion from congestion externalities. A perusal of the results for Case 2 is more enlightening. Note, for both policy choices, that the once divergent switching paths evidenced in Case 3 for the unregulated fishery now occur contemporaneously. There is also an interesting asymmetry in the season lengths for each site in the “loose” policy case (4 periods for site 1 and 5 for site 2) – this despite the fundamental sameness of the biology,

economic parameters, and regulatory goals. This longer season for the second site is induced by the fact that if the regulator in site 1 sets a closing date of 6 instead of 5, this will result in the movement of one fisherman from site 1 to site 2, leaving a fisherman behind to harvest without the impact of congestion. The ensuing increase in catch leads to a violation of the harvest ceiling. This example demonstrates just one of the many potential feedbacks between strategic behavior and policy instruments that may be analyzed within this general modeling framework.¹³

Given the previous results, how then might the regulators seek to improve the economic welfare of the fishery as a whole? Given the spatial nature of congestion externalities, it may be possible to construct policy instruments to achieve the biological objectives of fishery managers while increasing aggregate surplus by reducing the burden of congestion externalities and minimizing resource-diverting averting expenditures. This can be illustrated by a simple example. Suppose that a fishery has parameter values like those seen in Case 3 of the unregulated fishery. There is, therefore, a fairly large and symmetric congestion externality and a moderate cost of movement. Supposing regulators in each fishery have a cumulative harvest cap of 10, is there a simple policy prescription that might lead to a higher NPV of profits without exceeding the biological targets?

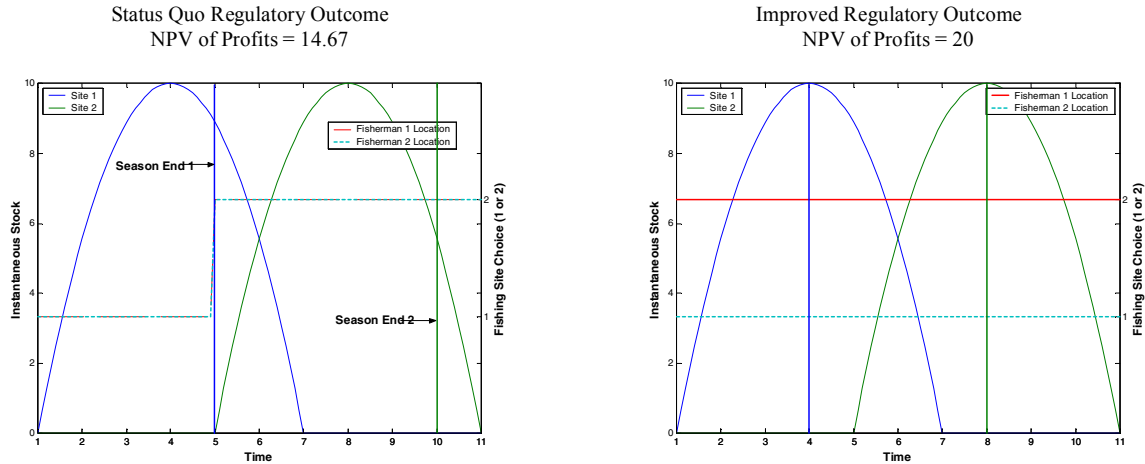
Figure 4 shows the regulatory MPE and the NPV of profits under a single policy instrument (season stop date) and an alternative equilibrium in which the regulators (jointly) control both closing dates and the spatial allocation of effort. Note that by simply restricting each fisherman to one site, the aggregate (short-run) surplus is substantially increased.¹⁴ These gains are divided between reductions in congestion costs (3.33 units to be exact) and avoidance

¹³ Such asymmetries are ultimately the product of the rigidities introduced into the regulatory decision problem by the discrete time framework; in the limit, no such asymmetries should exist. However, the realism of a continuous model may be suspect given the associated high costs of rapidly updating information on relevant state variables.

¹⁴ Some ways this spatial allocation might be made are through simple mandate or through more imaginative instruments such as spatially delimited permits, site auctions, or even “entry fees”.

of adjustment costs (2 units). Clearly such naive spatial “zoning” will not succeed in general, yet this case is suggestive of the potential of spatially delineated policy instruments, particularly in multi-site problems with substantial congestion externalities.

Figure 4: Comparison of Status Quo and Improved Regulatory Outcomes



The apparent increase in profits observed in this example, while impressive, is purely transitory. Excess rents in a fishery will, in a repeated-game context, be dissipated by increased entry or augmentation of existing capital. Regulations that merely reallocate fishermen across space may yield substantial short run benefits by reducing congestion and averting expenditures, but they are doomed to ultimate economic failure unless the fundamental problem of excess entry is addressed. Indeed, the increased efficiency of harvest resulting from simple spatial policies may exacerbate the possibility of biological overexploitation.

III. Conclusion

The existence of strategic interplay between the site-choice decisions of fishermen and the management decisions of regulators appears both theoretically and empirically probable.¹⁵ This model, although admittedly highly stylized, nonetheless demonstrates the tremendous usefulness of dynamic game theory in addressing strategic and spatial interactions within a

¹⁵ The empirical evaluation of such behavior is the topic of ongoing research.

disaggregated context. Clearly there are limitations to such an analysis; chief among them are 1) the computational difficulty of obtaining solutions in many real-world cases with multiple sites and fishermen, and 2) the scarcity of easily generalized results, even in relatively straightforward scenarios. Indeed, one may even balk at the cognitive burden entailed by a game-theoretic model as a description for such an intrinsically complex web of fishing and regulatory decisions. These criticisms notwithstanding, the ability of such models to generate an impressive array of predictions from a relatively simple framework may prove quite useful in increasing our understanding of fishing behavior and improving the state of fishery management.

References

- Brown, G.M. and J. Roughgarden. 1997. "A Metapopulation Model with Private Property and a Common Pool." *Ecological Economics* 22(1): 65-71.
- Dockner, E. et al. 2000. *Differential Games in Economics and Management Science*. Cambridge University Press. Cambridge, UK.
- Homans, F.R. and J.E. Wilen. 1997. "A Model of Regulated Open Access Resource Use." *Journal of Environmental Economics and Management* 32: 1-21.
- Sanchirico, J.N. and J.E. Wilen. 1999. "Bioeconomics of Spatial Exploitation in a Patchy Environment." *Journal of Environmental Economics and Management* 37: 129-150.
- Sanchirico, J.N. and J.E. Wilen. 2001. "A Bioeconomic Model of Marine Reserve Creation." *Journal of Environmental Economics and Management* 42: 257-276.
- Tuck, G.N. and H.P. Possingham. 1994. "Optimal Harvesting Strategies for a Metapopulation." *Bulletin of Mathematical Biology* 56(1): 107-127.