



Modeling fine scale urchin and kelp dynamics: Implications for management of the Maine sea urchin fishery

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ABSTRACT

The Maine sea urchin fishery is a classic boom–bust fishery in which efforts to sustain the resource failed despite the creation of a co-management system. We report on ethnographic work undertaken to assist in the development of a fine scale model of the natural system of this fishery. The development of the natural system model required understanding the key linkages between the biology and ecology of the sea urchin and the behavior of fishermen. Information was gathered from the primary scientific literature and from interviews with sea urchin industry members and scientists. Urchin–kelp interactions at a very fine scale create patchy, almost sedentary aggregations of urchins. Settlement of larval urchins appears to be ubiquitous; however, after settlement patches of urchins operate as nearly independent demographic units. In the short term – months to several years – the abundance of urchins in any patch and the spatial dynamics within these patches are determined largely by the actions of fishermen. Consequently, the resource can be characterized as a dynamic fitness landscape in which the spatial structure of urchin patches is the principal determinant of fishermen's harvesting strategies and fishermen's activities are the principal determinant of the spatial structure of urchin patches. While doing the interviews for the natural system model, we developed a fine scale alternative to the usual theoretical explanation of overfishing. The scale of management in the fishery occurs at a much broader scale than the demographically relevant scale of urchin patches. This results in a mismatch of ecological and management scales that leave each patch in the fishery in an open access state, resulting in a very fine scale form of serial overfishing that removes, piece-by-piece, discrete, local aggregations of sea urchins.

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1. Introduction

The Maine sea urchin (*Strongylocentrotus droebachiensis*) fishery is a classic boom and bust fishery. Landings began in 1987 when urchins were first exported to Japan. Landings peaked in 1992 and, in spite of a co-management system implemented in 1994, have declined since then to very low levels (Fig. 1). There are two, scale related, theories that have been offered for the analysis and management of the fishery. The first is what might be called the traditional model in which overfishing is seen as a rate of catch that exceeds the growth of the resource over its range. Restraints on fishing that reduce the rate of catch are seen as the appropriate remedy. This was the approach the state adopted in the early 1990s,

using nearly uniform rules over the extent of the fishery. An alternative theory argues that the urchin resource is really composed of a large number of local patches whose dynamics are nearly independent of nearby patches and, for that matter, the broad state of the resource. A peculiarity of these patches is that they tend to have two stable states; one in which kelp and predators dominate with few or no urchins present and another in which (starving) urchins dominate with little or no kelp (Steneck et al., 2004).¹ Harvesting appears to mediate the transition between these two states. Too much harvesting leads to the growth of kelp and predators and a stable kelp-dominated state, while too little harvesting leads to a stable urchin dominated state. The transition state in which harvesting maintains a balance of urchin and kelp abundance appears, from the fishery perspective, to be the desirable sustainable state.

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¹ For simplicity, we use the term “kelp” to refer to macroalgae (primarily *Laminaria* sp.) and other seaweeds.

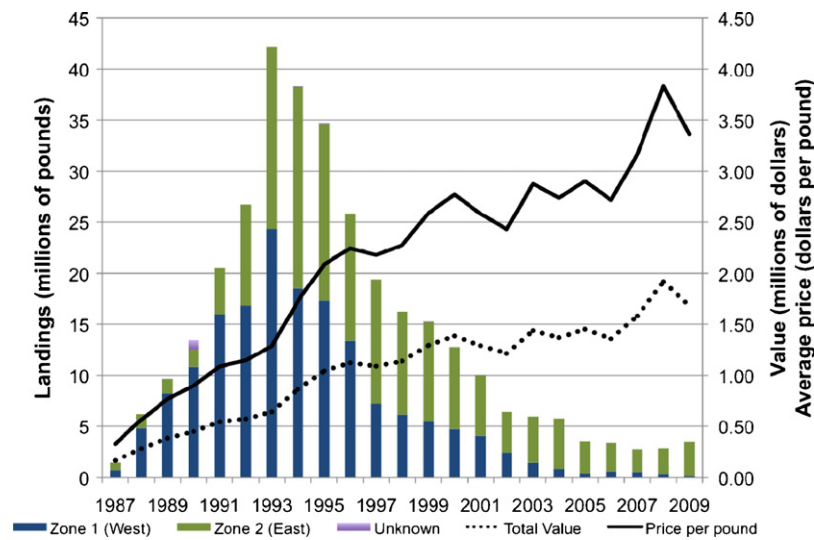


Fig. 1. Maine sea urchin landings by zone and value and prices from 1987 to 2009.

Source: Maine Department of Marine Resources.

The work we report on here describes our efforts to model the fine scale coupled natural and human system dynamics that are characterized by this alternative theory. Our research is guided by the idea that the spatial and temporal circumstances of different fisheries create different search and learning problems for fishermen. By search and learning, we refer to the challenge of knowing when, where, and how to fish, which is especially difficult in dynamic, patchy marine ecosystems. The different search problems fishermen encounter lead to different forms of cooperation (or non-cooperation) and, consequently, to different kinds of individual relationships, informal groups, and networks. The particular structure and dynamics of this emergent social organization are important indicators of the feasibility of self-governance and sustainable resource management (Ostrom, 2007; Wilson et al., 2007). We explore this broad hypothesis in order to better understand the factors influencing sustainability in the Maine sea urchin fishery.

To explore our hypothesis, we draw from complex adaptive systems theory (e.g., Levin, 2002; Simon, 1996) and from evolutionary, computational approaches to learning developed in computer science (Holland, 1986; Wilson, 1995). Broadly outlined, our ultimate aim is to model an adaptive agent-based model (ABM) of a coupled natural and human system. The first component of this adaptive ABM is the focus of this paper, the natural system model, a dynamic, multiscale simulation of the resource, in this instance, sea urchins.² The point of the natural system model is to create a qualitative, multiscale representation of the dynamic spatial patterns, the patchiness, of the resource.³ These patterns are affected by changing natural conditions – seasons, depth, bottom type, etc.,

² We use the term “natural system” to include not only the ecological conditions (i.e., interactions among species and between species and their environment), but also to the particular oceanographic, geological, and biological conditions that influence dynamics in marine ecosystems.

³ Urchin–kelp dynamics have been modeled extensively elsewhere, as a few examples: In Atlantic Canada, Lauzon-Guay et al. (2008, 2009) developed models based on empirical information to investigate feeding front formation and destructive grazing and transitions between the kelp bed and barrens state. Lauzon-Guay and Scheibling (2010) further developed a coupled map lattice model to explore the process of urchin aggregation within kelp beds that leads to the shift to barrens. In Tasmania, Marzloff et al. (2011) produced a qualitative model of rocky-reef communities to predict alternative states in ecosystems. The purpose our natural system model differs from other efforts with its focus on capturing the patterns fishermen must learn in order to be successful.

as described below – and harvesting. The problem fishermen face is learning these patterns, including the way they are altered by other fishermen.

The second component of the adaptive ABM, the human system model, is still in development, but it will be coupled with the natural system model. The human system model (Section 1.5) will be simulated using a method called a learning classifier system (LCS) (Holland, 1986; Wilson, 1995; Wilson et al., 2007) in which heterogeneous agents are able to explore their environment and, as a result of that experience, are able to learn and adapt. (Wilson et al., 2007 is an early example of this approach.) The result is a co-evolving, non-equilibrating system of agents who imperfectly learn the dynamics of the natural system and the ways their agent competitors affect that environment (Wilson et al., 2007; Wilson and Yan, 2009). Although the human system model is still in development, the natural system model stands on its own as an example of an interdisciplinary modeling effort, combining social science, natural science, and computer science, as well as fishermen’s experience-based knowledge (Fig. 5).

In this paper, we report the way we combined ethnographic research (Section 1.4) documenting fishermen’s observations and fishing strategies and scientific information from the literature and from interviews with scientists (Section 1.2) to create a dynamic simulation of the natural system in the urchin fishery. The development of the natural system model requires understanding key linkages between the biology and ecology of the sea urchin, *Strongylocentrotus droebachiensis*, and the behavior of fishermen. We gathered information for this model from interviews with sea urchin industry members and scientists, as well as a review of the scientific literature.

The natural system model illustrates how urchin–kelp–human interactions occurring at a very fine scale create patchy, sedentary aggregations of urchins and kelp. These aggregations occur at a very fine scale (tens of meters) within a larger patch and at a broader scale across patches (thousands of meters). Our interviews indicate that the changing spatial structure of these patterns is the principal determinant of fishermen’s search and learning problem and, hence, the particular harvesting strategies and social relationships they adopt. Fishermen’s strategies and urchin–kelp dynamics at fine scales lead to important broader scale effects. When fine scale fishing is combined with broad scale management, the resulting

mismatch of scales leaves each patch in an open access state with few meaningful restraints on fishing. This leads to a very fine scale form of serial overfishing that removes, one at a time, discrete, local aggregations of sea urchins.

1.1. History of sea urchin fishery and management

The birth and near death of the sea urchin fishery in Maine was part of a global sequential depletion of this resource (Andrew et al., 2002; Berkes et al., 2006). This global depletion began with the collapse of the Japanese resource in the mid-1970s. With the loss of domestic supplies, imports to the Japanese market began to arrive from increasingly distant locations. In 1987, the market reached Maine and instigated an explosive growth in harvesting. Before that time, the resource in Maine was marginally exploited, groundfish predators of urchins had been nearly extirpated and, as a result, urchins were extremely abundant and covered extensive areas of shallow, near-shore ocean bottom; these areas were characterized as urchin barrens (Steneck et al., 2004).

With the sudden opening of the Japanese market, licensed divers (using SCUBA) and druggers (using light bottom trawl gear) quickly began to target the resource. By 1994, there were nearly 3000 licensed divers and druggers (Fig. 2). The incredible abundance at this time made harvesting very easy and, even with relatively low prices, generated large incomes leading to very rapid growth in the fishery. Initial harvests concentrated in the southwestern region of the state, near the location of the first buyers, but rapidly spread eastward. Previously formed business relationships enabled rapid distribution of knowledge about the market opportunity and required little or no new local infrastructure (Laur, 2001, 2005).

In the early 1990s, the Maine Department of Marine Resources (Maine DMR), the agency responsible for managing the state's fisheries, created an informal, advisory committee that included scientists and members of the industry. Managers first required a license to harvest urchins in 1992. The following year more rules came into effect, including a 5.1 cm minimum size, a diver and tender license requirement, a closed season during the summer, and a size limit on urchin drag gear. In 1994, the state implemented a moratorium on licenses and created two fishing zones (Fig. 3). The two management zones were justified because of the differences in the time of spawning along the coast (Vadas and Beal, 1999). Except for the different seasons in the two zones, management rules applied uniformly along the entire coast.

In 1996, a formal co-management system was established with the creation of the Sea Urchin Zone Council. Initially the Council consisted of 18 members. Seven members were elected by the industry and the rest appointed by the Commissioner of the Maine DMR. Industry members included 3 druggers, 3 divers, 1 buyer, and 1 processor from each zone. In addition, two independent (non-government) scientists were appointed to the Council. In the same year, open and closed seasons were established (Zone 1, 150 days open; Zone 2, 170). Regulations tend to be restricted to measures that are enforceable given the limited financial resources of the state.

Based on advice from the Council, the fishery has been managed exclusively through input controls, such as allowable fishing days and minimum and maximum size limits. In addition, there are data reporting requirements and fees to support research and management. Neither total nor individual catch limits have been used. The number of allowable fishing days and seasons vary by zone due to geographic differences in abundance and timing of reproduction.

Prior to the boom in the fishery, landings prices (~\$0.07 per pound) and total value (~\$3,000) were very low (Maine DMR Landings Data). In 1987, however, with the advent of the Japanese market, 1.4 million pounds were landed at an average price of \$0.16 per pound and a total value of \$236,391 (Fig. 1; Maine DMR

Landings Data). Total landings peaked in 1993 at around 42 million pounds, while revenues reached their highest point in 1995 at \$35.5 million, with a price of \$0.64 per pound. In 1996 statewide landings were 25.8 million pounds, valued at \$29 million (Fig. 1). Landings continued to decline and in 2009 only 3.5 million pounds were landed, worth about \$5.8 million (Fig. 1; Maine DMR Landings Data). Most landings are now taken from Zone 2 because urchins are nearly economically extinct in western Maine (Fig. 1). As the decline in landings, value, participation, and stock biomass indicate (Figs. 1 and 2; Chen and Hunter, 2003), the co-management system did not stop and certainly has not reversed the depletion of the fishery.

1.2. Sea urchin biology and life history

In this section, we briefly describe the aspects of the biology and life history of the sea urchin most relevant to understanding the feedback fishermen receive from their interaction with the resource system. It is this feedback that drives fishermen's strategies, their response to change, and the conditions under which they are likely to cooperate or otherwise engage in practices necessary for the sustainability of the resource.

Sea urchins live at depths ranging from 0 m [in tide pools in the low intertidal zone] to 300 m, although they are most common in the shallow subtidal zone to 50 m (Scheibling and Hatcher, 2006). Urchins are patchily distributed; they are found most often in rocky bottom areas, but also on gravel bottoms in deep water and occasionally on sand (Scheibling and Hatcher, 2006). Scientists and divers also report finding them on mud where they appear to feed on patchy growths of diatoms (R.L. Vadas, personal observation). Densities decline below depths of 20–30 m, which is often the lower limit of the rocky subtidal zone. Their upper limit varies seasonally with wave action and ice scouring in especially cold winters (Scheibling and Hatcher, 2006).

The types and amount of food available affect urchin growth and reproduction. Urchins are generally omnivores, but they exhibit clear food preferences for large brown algae, which forms their primary diet either as attached fronds or drift kelp (Larson et al., 1980; Vadas et al., 2000). Urchins can detect food from a distance of several meters and aggregate around it in response (Vadas and Beal, 1999). The ability to feed on drift kelp allows them to survive in areas where their preferred food does not grow (e.g., in places below the photic zone where drift kelp might collect). In the absence of macroalgae, they can survive by feeding on other items but with reduced growth and reproduction (Larson et al., 1980).

Well-fed urchins in kelp grazing aggregations have high somatic growth rates and gonad indices (Scheibling and Hatcher, 2006; Wahle and Peckham, 1999). Urchin roe swells in fall and early winter, while spawning occurs in the spring (Vadas and Beal, 1999). The roe is most valuable in the late fall and winter when it is the color, texture, and taste favored by the Japanese market. Urchins usually spawn in their third year, when their diameter is 2.5–3.8 cm. Females can produce up to 10 million eggs for an 8.0 cm urchin.

The strong interaction between urchins and kelp communities is well documented (e.g., Harris and Tyrrell, 2001; McNaught, 1999; Miller, 1985; Scheibling and Hatcher, 2006; Steneck et al., 2002, 2004). Meidel and Scheibling (2001) describe shifts in the community state due to changes in urchin abundance and feeding behavior. When urchins are in low abundance and small, kelp beds thrive. Large urchins aggregate into “grazing fronts” along the edges of kelp beds (Brady and Scheibling, 2005; Scheibling and Hatcher, 2006; Wahle and Peckham, 1999). Urchins show a strong preference for and feed extensively on the kelp at this time, along what is known as the feedline. Eventually, with a reduction in kelp and other seaweeds and an increase in the local urchin population, a stable state emerges known as an urchin barren (Miller, 1985). In this state,

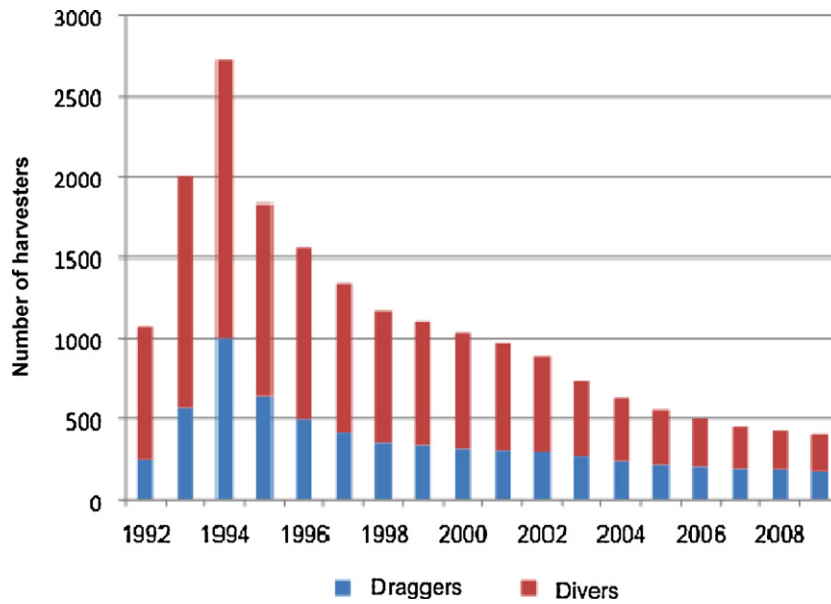


Fig. 2. Numbers and type of Maine sea urchin fishermen from 1992 to 2009.

Source: Maine Department of Marine Resources.

the nutritional state of the urchins declines leading to reductions in growth and reproduction (Botsford et al., 2004).

The urchin barrens persist until urchins are removed by disease (Miller, 1985; Scheibling, 1986), harvesting (McNaught, 1999), or ice scouring (Gagnon et al., 2004), although this is an infrequent event in Maine. Once urchins are eliminated, diatoms and then macroalgae grow rapidly (Vadas and Elner, 1992); kelp beds can become reestablished within 2–3 years if urchins do not repopulate the area (Scheibling, 1986; Scheibling and Hatcher, 2006). The relevant spatial scale of these processes is on the order of tens to a couple hundred meters. In an unharvested system, the state of nearby sites can differ substantially due to the differing effects of water motion, storms, and ice.

Recolonization of the kelp beds by urchins occurs via larval settlement, local population growth from increased algal production, and, if they are present, migration of nearby urchins from deeper waters (Brady and Scheibling, 2005, 2006; Miller and Nolan, 2008).

There does not appear to be any shortage of spat production in Maine, even in areas where shallow water urchins have been economically extinct for over a decade (McNaught, 1999; Vavrinec, 2003). Repopulation of urchin areas, however, can be limited due to predation on new recruits (Scheibling, 1986; Steneck et al., 2002). Steneck et al. (2004) describe local system flips in Maine that occur as a result of urchin removal via intensive harvesting. Local extirpation of urchins allows for increased growth of kelp providing favorable habitat for crabs (McNaught, 1999; Steneck et al., 2002). Steneck et al. (2002) noted the kelp-dominated state is relatively long-lived and stable; a decade later this conclusion appears even more valid.

On the eastern shore of neighboring Nova Scotia scientists describe a migration in response to widespread, recurrent mortality events caused by a paramoeba that can eliminate sea urchins to depths of 25 m (Miller, 1986; Miller and Nolan, 2008; Scheibling and Hatcher, 2006). Miller and Nolan (2008:929) describe urchins

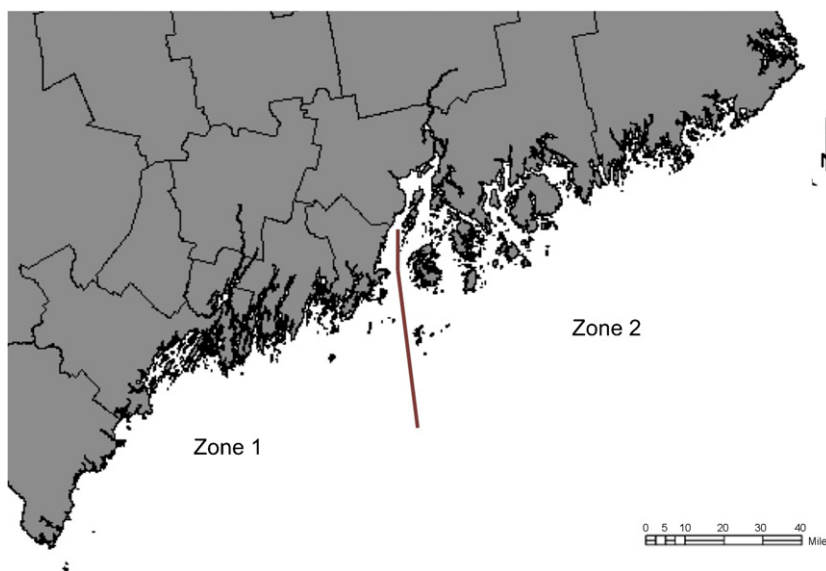


Fig. 3. Map of the Sea Urchin Zone Council boundaries.

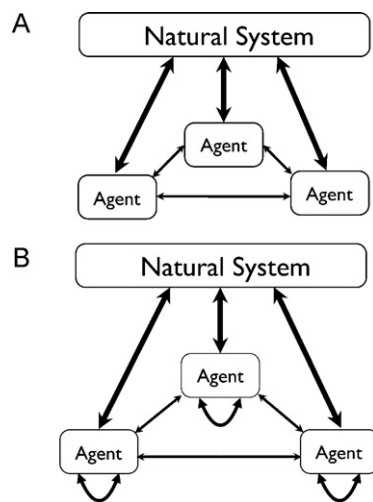


Fig. 4. Two agent based modeling approaches. (A) Non-adaptive agent-based model with human agents: a natural population aggregate (e.g., urchins) and multiple individuals, interact with one another and the natural population. Modeler specifies behavior and dynamics. (B) Adaptive agent based-model with human agents: a natural population aggregate (e.g., urchins) and multiple individuals who interact with one another and the natural environment and learn through experience (indicated through circular arrows). Modeler supplies the dynamics of the natural system, but the model evolves the behavioral rules of the agents using a learning classifier system (LCS).

forming “a slow-moving belt from deep water to the edge of macrophyte beds [in shallower waters] where harvesting takes place” (see also Scheibling et al., 1999). Although we cannot state how extensive such migrations are in Maine, a similar pattern of movement, not associated with disease, was seen in extremely cold waters in Eastern Maine in the 1970s (R.L. Vadas, personal observation). Disease appears less prevalent in Maine than Nova Scotia due to the shallow waters being much colder in Maine, although there was an outbreak in 1999 (R.L. Vadas, personal communication; in casual conversation several fishermen also reported localized die-offs). On a finer scale, fishermen in Maine use the term ‘conveyor belt’ to describe a more local movement of urchins, generally from slightly deeper water, in response to the removal of shallow water urchins by harvesting.

Overharvesting of urchins appears to be characterized by the transition of very local patchy environments from an urchin to a kelp-dominated alternative stable state that limits the recolonization of urchins (McNaught, 1999; Steneck et al., 2002). The average decline in landings observed in each zone and across the state appears to be due to the harvest driven transition of large numbers of areas from an urchin dominated to a kelp-dominated stable state, i.e., multiple local system ‘flips’ (McNaught, 1999).

1.3. Methods

The research described here was undertaken for the purpose of developing the natural system component of an adaptive agent-based model of the coupled natural and human system of the sea urchin fishery (Fig. 4b). After describing the adaptive agent-based modeling approach that is the impetus of this research, we present our ethnographic research approach and how we integrated the social science research into the design of the natural system model. We then describe the natural system model that we produced from this integration.

1.4. Adaptive agent-based modeling approach

Non-adaptive agent-based models (ABMs) are ‘bottom-up’ models in the sense that the behavior of individual agents is the focus of the model (Fig. 4a), e.g., fishermen, fish or whatever individual agent the modeler might be interested in (Railsback and Grimm, 2012). In natural resource applications the point of these models, generally, is to explore the way in which the interactions of multiple agents emerge as broad scale social and ecological patterns such as overfishing. In these kinds of models, the modeler specifies the heuristics that govern the behavior of agents (a decision rule or heuristic follows the general form of ‘in these circumstances, take this action’). As the model unfolds agents take actions that affect the environment and one another. Their actions change their own circumstances and those of other agents. Agents detect these changes in their environment and, given these new circumstances, choose different rules to decide what to do. The weakness of this approach is that the modeler has to be very well informed about all possible, or reasonably possible, agent responses to changing circumstances; for example, the modeler has to know how a fisherman’s behavior might change in response to the imposition of a new regulation setting a maximum urchin size. To the extent that real world agents tend to figure out adaptive possibilities not anticipated by the modeler, the expectations (or predictions) generated by an ABM can be very misleading, as is true of almost any model.

The adaptive ABMs that we have been developing (Holland, 1986; Wilson et al., 2007) attempt to reduce this weakness through the use of new computational approaches borrowed from computer science (Fig. 4b).⁴ Instead of specifying the agents’ responses, the approach requires the modeler to specify the kinds of information and the broad kinds of actions agents might have at their disposal when they make their decision about, say, where and when to fish. The evolutionary computation uses these inputs to search out (compute) a broad set of adaptive possibilities, using a method of testing and selection to find well adapted rules. The data required for the design of a model of this sort are generally qualitative and relatively easy to collect through careful ethnographic fieldwork such as we described below.

The adaptive ABM approach has two major components. The first is a simulation of the dynamics of the natural environment – what we call the natural system model (Fig. 4b). In the urchin fishery this is a dynamic simulation of kelp and urchin interactions. We drew on the scientific literature to operationalize the attributes of the system that fishermen and scientists identified as important. Our objective was to create a generic model that replicated the dynamic behavior of urchin fishing sites, especially the changing patchy distributions of urchins and kelp. The point of the natural system model is to represent the kind of search problem that confronts urchin fishermen.

The second component of the model concerns human behavior, in particular the decisions fishermen make about how, when and where to fish. This part of the model employs an evolutionary computational method, specifically a learning classifier system (LCS). The LCS mimics a Darwinian evolutionary process, except the evolutionary process is used to simulate the evolution of agents’ behavior as they learn through experience. The LCS uses algorithms that are close analogs of heritability with variation and selection to develop and find decision rules that best fit the agents’ interest (Holland, 1986; Wilson et al., 2007). In other words, as the simulation proceeds the rules the agent uses to govern its interaction with the natural system model and other agents yield better or worse outcomes. From these outcomes the agent learns

⁴ We are also developing similar adaptive agent-based models of the groundfish and lobster fisheries.

which rules work well in what kinds of environmental circumstances. The result is an evolving set of decision rules that, at any time, are the equivalent of the behavioral rules specified by the modeler in a non-adaptive ABM. The important difference when compared with a non-adaptive ABM is that the adaptive ABM does not require that the modeler know all the adaptive possibilities open to agents. Nevertheless, the point of an adaptive ABM is the same as a non-adaptive ABM: to get a better understanding of how multiple decisions by numerous individuals emerge as broad scale social and ecological outcomes.

1.5. Ethnographic research approach

Our social science research collected data for the design of adaptive agent-based model described above, including information for both the natural system model and human system model. We adopted an ethnographic research approach, relying on informal and semi-structured interviews, as well as our collective, long-term experience and observation of fishermen and the fishery in this region. The interviews were not intended to gather a statistically reliable profile of our study population. Rather, the point of the interviews was to gain an in-depth, qualitative understanding of the fine scale human and natural system dynamics that characterize the fishery, especially the way those dynamics are altered by fishing. We conducted a total of 18 formal interviews with past and current Maine sea urchin fishermen, scientists, managers and a buyer from June to August 2010. Also, informal discussions with two other academic fisheries scientists, a number of less extensive informal interviews with other divers and druggers, and observations and discussion at the Sea Urchin Zone Council provided additional insight into the dynamics of this fishery. The lead author is also a member of the council, and her observations and discussions at those meetings also inform this paper.

To identify key informants in the industry, we adopted a snowball sampling approach (Bernard, 2006) beginning with recommendations from Maine DMR scientists. Following a modified grounded theory approach (Glaser and Strauss, 1967; Strauss and Corbin, 1998), sampling continued until we felt we were no longer gaining new information from the interviews, what is referred to as theoretical saturation (Glaser and Strauss, 1967). We often returned to the same informants to ask questions in response to new information obtained in subsequent interviews.

All individuals interviewed are key informants (Bernard, 2006). The fishermen are considered leaders and most have experience and knowledge of the fishery since the late 1980s. We formally interviewed nine divers, one tender/captain, and one buyer. We focused on divers because in this fishery about 60–80% of all landings are from divers. All but two industry members interviewed were either past or current members of the Sea Urchin Zone Council, and the other two frequently attended meetings and were active participants in the co-management process. We believe our sample was representative of the fishery in terms of its geographic representation (both management zones and major ports were represented). All seven scientists interviewed have conducted research that has contributed directly to the management of the Maine sea urchin fishery. The scientists interviewed include three government scientists and four academic scientists involved in the science and management of the fishery. Two of the academic scientists were at one time members of the Sea Urchin Zone Council. Finally, we also interviewed two scientists and a fisherman from Atlantic Canada; although these interviews did not inform this paper directly, they did provide important insights regarding fine scale urchin–kelp dynamics.

Interviews ranged from 1.5 to 3 h and were guided by a general set of questions prepared before the interview. Rather than filling out a questionnaire, our interviews sought specific types of

information by following the conversation of the informant instead of a structured path of questions. This research protocol allows for more in-depth understanding than would be possible with a structured interview guide, because it does not require that we know all important questions before the interview; in fact, the method is designed to leave room for surprise and discovery.

At the beginning of each interview we asked questions about the history of the fishery. These questions tend to elicit memories of events that are relatively easy to check against published accounts and the memory of other interviewees. Historical questions also bring out reflections about how and why particular events happened, i.e., fishermen's theories of the forces driving the fishery and the resource, which provide insight into the feedback that informs fishermen's behavior. Fishermen were asked about the mechanics of fishing operations and markets and changes in the fishery over time as it shifted from abundance to scarcity. Interviews with scientists revealed important questions to ask fishermen and vice versa. In many instances, we went back to interviewees with follow-up questions that emerged in the interview process. All interviews were recorded and detailed notes taken from these recordings; only parts of interviews were transcribed.

Following a grounded theory approach (Glaser and Strauss, 1967; Strauss and Corbin, 1998), data analysis occurred throughout the research and involved identifying patterns and themes from the interviews and incorporating this information into the model described below. Our qualitative analysis of interviews focused on understanding the most important information fishermen use when making decisions about when, where, and how to fish (i.e., their day-to-day fishing decisions). In other words, our aim was to make sure that the natural system model generated the kind of information about the environment that fishermen use as feedback in order to learn and adapt. From scientists, we sought to understand the most important drivers of ecological change in the system; scientists' perspective often includes aspects of the environment that fishers do not observe in their activities. Examples of themes that emerged in the interviews include the qualitative characteristics of the natural system that needed to be included in the model, including characteristics of fishing behavior (e.g., bottom types, depths and seasons fished) and factors influencing kelp and urchin growth (e.g., depth, light/seasons, substrate, etc.) (Table 1). In addition, themes from the interviews also related to the observations fishers and scientists reported about major changes in the fishery system under different harvesting conditions, and these observations were important to indicate whether the model was replicating the general patterns observed in the real world (e.g., changes in kelp and urchin abundance and fishing patterns) (Table 2).

1.6. Integration of ethnographic research and modeling

Integrating the interview data into the modeling effort involved an iterative process of model development and social science research (Fig. 5). Not surprisingly, this involved extensive discussion across disciplines, where the results of the social science research (i.e., themes from the interviews) were presented to computer scientists, who then translated the findings through computer programming into a preliminary model. Translation involved looking to the scientific literature and consulting with biologists in order to add new parameters to the model. Therefore, the model development involved a similar process of iterative discussion and modeling to incorporate information from the biologists; all three components of the effort – social, biological, and computer science – worked together through all phases of data collection and model development (Fig. 5).

Once additions or refinements were made, the computer scientists would then present their progress to the research team,

Table 1
Summary of major themes from interviews included in the natural system model.

	Important factors	Influence on harvesting behavior
Biophysical and environmental conditions	<ul style="list-style-type: none"> • Wave action/exposure • Depth • Topography • Season 	<ul style="list-style-type: none"> • Harvesting limited in wave action, especially in poor weather • Harvesting limited to certain depths (~60–80 ft) • Harvesting targets urchins of high roe quality, influenced by seasons and depths where kelp found
Ecological processes	<ul style="list-style-type: none"> • Kelp growth • Urchin growth • Herbivory • Predation on urchins • Urchin movement 	<ul style="list-style-type: none"> • Harvesting targets urchins with high roe quality (in the feedline); avoids urchin barrens due to low quality roe • Harvesting avoids kelp-dominated areas; these harbor urchin predators, few urchins available • Herbivory limits excessive kelp growth and predator abundance (transition to kelp-dominated state) • Harvesters report urchins moving into fished areas via conveyor belt
Market	<ul style="list-style-type: none"> • Demand (markets) • Prices (roe quality) 	<ul style="list-style-type: none"> • Demand and prices drive harvesting intensity and selectivity
Management	<ul style="list-style-type: none"> • Areas • Limited entry • Days at sea • Size limits 	<ul style="list-style-type: none"> • Limiting days and seasons/closures encourage unselective harvesting due to uncertainty of harvest and weather

Table 2
Summary of interview results describing conditions of resource and implications for harvesting and resulting incentives for collective action (i.e., information sharing and cooperative behavior).

Condition of the ledge	Urchin abundance	Roe quality/prices	Harvesting practices	Incentives for collective action
(a) Barrens state	High	Low	Non-selective, high volume due to low prices	None needed due to no competition for resource
(b) Feedlines and conveyor belts present	Moderate	High	Selective harvesting preferred, but unselective harvesting under declining abundance and open access conditions	None due to competition for limited resource
(c) Kelp-dominated state	Low	N/A	N/A	None needed because state is not targeted for harvest

often with more questions for the social scientists, requiring them to return to the field for follow-up interviews. This process of data collection, modeling, and more data collection repeated itself until all project members were satisfied that the dynamics of the natural system model were consistent with what was known about the biology and ecology of the resource.

1.7. Natural system model

Based on the major themes and patterns that emerged in the interviews and their analysis, we constructed a simple model of the natural system. The dominant drivers in natural system model are the different rates of kelp growth (which vary by depth), herbivory (grazing by urchins is influenced by the numbers and size of urchins), predation of urchins (enhanced under conditions of high kelp abundance), and harvesting (removal of a portion of available

biomass) (Table 1). Topography is also important because it has a strong influence on the rate and location of kelp growth, it determines the distance urchins have to move to graze new kelp growth, and it affects the extent to which urchins are excluded from parts of the area due to wave action and harvesting (i.e., a spatial refuge for kelp). For example, a long shoal area tends to produce a very different pattern of kelp and urchin patches than an area with a steep edge that falls off quickly to deeper water. Depending on the shape of the area, this dynamic plays out as a unique, changing and patchy pattern of urchins and kelp. At the scale of the urchin patch, the fisherman's search problem consists of learning the dynamic patterns of this patchiness and, especially, how to quickly find the feedline or other fine scale aggregations on a patch. Without these dense aggregations, a given site is not efficient or profitable for harvesting.

The point of the natural system model is to provide a reasonable simulation of the urchin diver's search problem; i.e., the different ways urchins aggregate in different topographic conditions and with different harvesting patterns. The basic model, described here, is a generic model that can be applied to any area.⁵ The area is divided into a grid in which each cell is approximately 20 m on a side and is populated with kelp and urchins. When the simulation begins urchins are placed randomly in dense clusters and kelp is distributed as if there was no herbivory. Kelp growth is modeled in terms of both plant height and ground coverage and varies with depth and season. Urchin movement is simple; urchins move along a chemical gradient toward a food source, but when the signal is weak or nonexistent, urchins move randomly, if at all. Herbivory

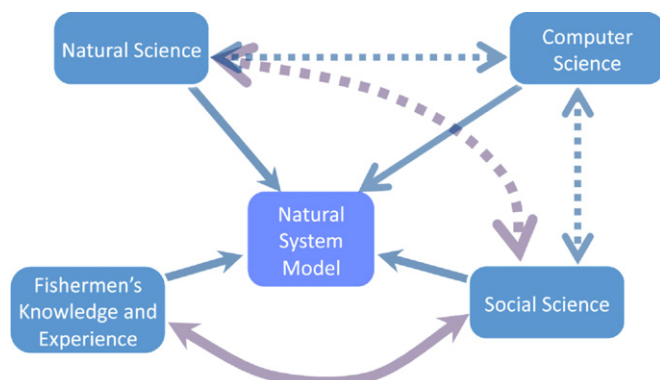


Fig. 5. An interdisciplinary approach to modeling fine scale coupled natural and human system dynamics in the Maine sea urchin fishery.

⁵ When the natural system model is combined with the LCS approximately 150–200 instances of the natural system model will be implemented. The point is to provide a reasonable simulation of the diver's search problem at a much broader scale.

is a function of local urchin biomass and season. Predation simulates the effects of crabs, lobsters, and fish feeding upon smaller urchins and varies with kelp coverage. The dynamic interactions between urchins and kelp and the patchy patterns they form vary with their starting configurations, the shape of the area, and the driving factors mentioned above. The variations are often nonlinear and unpredictable.

We model urchin growth, roe quality, mortality and recruitment. The urchin population is age structured and growth is dependent on the very local availability of kelp and the urchins' nutritional state (Chen and Hunter, 2003). The gonad index of the urchins also varies according to the urchins' nutritional state. Predation, on smaller urchins only, and natural mortality are the only forces that reduce the urchin population. Recruitment occurs stochastically throughout a two-month period during each simulated year.

Harvest patterns and volume will be determined by the LCS; nevertheless, to check the response of the natural system model we implemented a crude harvesting algorithm. This is reported in Section 2 below.

2. Results

2.1. Interview results

In addition to the factors included in the natural system model, described above (Table 1), we also report other key themes from the interviews related to changes in the resource and the implications of those changes for harvesting and collective action (i.e., information sharing and cooperative behavior) (Table 2).

When asked about the state of the resource at the beginning of the fishery, in the late 1980s, all informants described the state of the urchin barrens (Table 2a). Fishermen reported no problems finding urchins at this time; their search problem was non-existent and, hence, there was no need for reciprocal information sharing among fishermen. The market was non-discriminating; fishermen reported getting about the same price per pound regardless of quality. This led to a non-selective harvesting strategy focused on a high volume, low quality product (Table 2a).

Fishermen interviewed explained that as harvesting reduced the size of the urchin population in a given area, kelp growth led to improved quality of the remaining urchins (Table 2b). All fishermen recognized a linkage between reduction in urchin biomass, growth of kelp and improvement in roe quality. To illustrate, one fisherman explained that they would “nip at places where there were too many urchins and over time, the quality in these places became higher and higher.”

Fishermen uniformly reported targeting aggregations of high quality urchins found in the feedline (Table 2b). The shape and position of these urchin aggregations differ from place to place but in all cases they make it possible for divers to harvest higher quality urchins with much greater efficiency than they might if urchins were randomly or evenly distributed as in the usual fishery model. For example, one fisherman described feedlines as, “where the barren starts or ends depending on how you look at it. . . to one side will be the kelp bed and to the other will be the urchins.” He is describing the barrens as locations where urchins have overgrazed the kelp (and hence where urchins are of low quality); therefore, he looks for the feedlines, where kelp and urchins still co-exist, as sites for harvesting high quality urchins.

Indeed, a common harvesting strategy reported is to selectively target the feedline (Table 2b) so that the fishermen could (hopefully) return to harvest again later after new (starving, or food deprived) urchins had moved up to the kelp and achieved higher quality. As one diver explained, “You had to leave some behind

so that in a month or two you could come back to that spot to re-harvest it.” Key to this strategy was fishermen's understanding that as urchins are removed from the feedline, new urchins from deeper water replenish the area as they move up to feed; this is the ‘conveyor belt’ as described by fishermen (Table 2b). The majority of fishermen interviewed described this process, although not all used the term ‘conveyor belt.’ Although the conveyor belt is often described as a vertical movement of urchins from deep water, horizontal movement also occurs depending on the location of kelp growth and urchins in search of food. This conveyor belt differs from the deepwater migration of urchins seen following disease in Canada.

Fishermen also reported watching the shift to a kelp-dominated state after extensive harvesting (Table 2c): “You could watch kelp increase year to year. . . [T]he kelp was getting bigger and bigger. . . We worked it for quite a few years, but now it's all kelp.” Fishermen describe this state as “[j]ust masses of weed [kelp] and no urchins – more weed because it's not being eaten by urchins. You just see a huge explosion of kelp.”

Fishermen also emphasized that these changes are due to what they view as unsustainable harvesting practices. In one fisherman's words, What has really done a lot of damage is that diver who. . . keeps pounding them even if they're low quality. They just beat an area to death and the areas flip to the alternate stable state. It's a minority of divers, but some of them are well known.

The diver quoted above has worked extensively within the fishery management system, as reflected in his use of the term “alternate stable state.” As the quote above indicates, fishermen understand that unselective divers can flip a local area to the kelp-dominated state and this creates particular incentives that influence harvesting strategies. The majority of fishermen interviewed explain how the essentially open access nature of the resource at the scale of an urchin patch means that urchins left behind on the feedline are likely to be taken by others. This is reflected in the following statement: “If you know where it is, you take it. In the later years, that's what it boiled down to.” His reference to “the later years” refers to conditions where urchins were less abundant, areas were beginning to flip to the kelp-dominated state, and there were still a substantial number of fishermen fishing. Under these conditions, there was a race among fishermen to harvest urchins from areas before they flipped to the kelp-dominated state (which, of course, accelerated the flips). Not surprisingly, divers report no cooperative relationships, information sharing, or even informal rules that are important to efficient harvesting (i.e., no incentives for collective action) (Table 2).

2.2. A natural system model of urchin–kelp dynamics

Here we describe what happens when we run the natural system model without harvesting (Fig. 6a–c) and with a conventional harvesting module (Fig. 7a–c), i.e., one in which we supplied the harvesting rules rather than having them evolve with a learning classifier. The point of the conventional harvesting model was to test the response of the model to the effects of harvesting. Each version of the model was run for 650 days. The first frame shows the simulation with its original distributions of kelp and urchins (Figs. 6a and 7a). The second frame (Figs. 6b and 7b) shows the simulation after 300 days without fishing. The first simulation continues without harvesting and shows an urchin barren remains after 650 days (Fig. 6c); this is a stable state. In the second simulation, harvesting begins after day 300 and continues once every three weeks until day 650. At that time, the urchin barren is almost gone and the stable pattern that emerges appears to be that of a kelp-dominated state (Fig. 7c).

Inspecting these simulations as they proceed, we see urchins move toward their feed. However, urchins in deeper, kelp-free

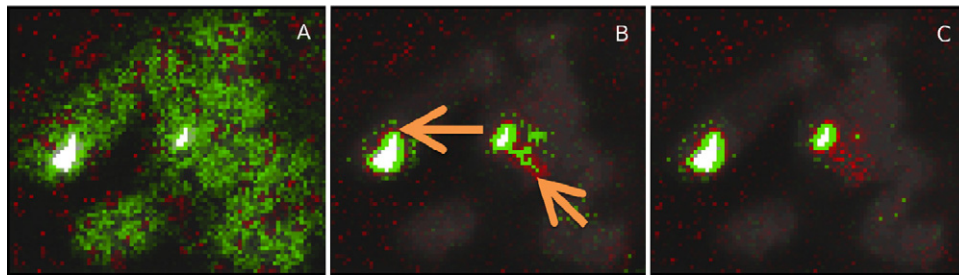


Fig. 6. No harvesting: biophysical model depicting kelp (green) and urchin (red) under no harvesting conditions. (A) Initial conditions due to random placement of urchins and kelp, (B) urchin barrens develop after 300 days and (C) remains after 350 days without harvesting. Orange arrows point to feedlines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

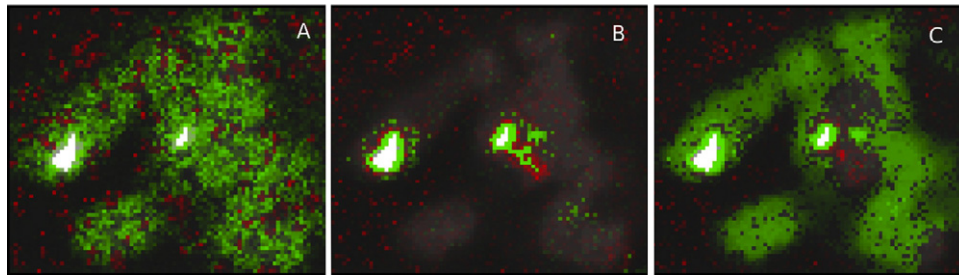


Fig. 7. Harvesting: biophysical model depicting kelp (green) and urchin (red) under harvesting conditions. (A) Initial conditions due to random placement of urchins and kelp, (B) urchin barrens develop after 300 days and (C) a kelp-dominated system emerges after 350 days of harvesting. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

zones often move randomly, or very little. However, if they happen to wander within ‘range’ of the kelp, they begin to move toward it (usually up the slope), aggregating along its edge where they feed. These aggregations are visible in the simulation (Figs. 6b and 7b). In these places, urchins are abundant and tend to consume kelp at a rate that is faster than the kelp can regenerate. Urchins overgraze their immediate area and move to adjacent kelp patches. Fishermen refer to these aggregations as ‘feedlines’ (Figs. 6b and 7b) and the movement of urchins from deeper areas to the edge of the kelp as the ‘conveyor belt’.⁶ The location and timing of these local aggregations is slightly different with each run of the model, depending on the initial random location of urchins and kelp (assuming no fixed random seed), but some effects appear stable. As explained above, after about 300 days an urchin barren always develops (Figs. 6b and 7b) and by the 650th day (in the no-harvesting case), the barren is very pronounced and stable (Fig. 6c). At this point, kelp occurs only in a very thin margin around those shallow parts of the area that are subject to strong wave action and less likely to be occupied by urchins. Urchins occupy most of the bottom but they are starving. The urchin fishery was in this state in 1986 when the commercial fishery in Maine began.

Under harvesting, the model generates the alternative kelp-dominated stable state (Fig. 7c). In the adaptive agent-based model discussed earlier, harvesting will be the result of fishermen learning how to search a multi-site environment. However, when the

natural system model is tested on its own for a single site, harvesting is simulated with a simple rule: After 300 days, a fisherman (agent) visits the area every three weeks and removes most of the legal sized urchins within the fishable depths (generally less than 60 ft). The harvest is not uniform but follows a random process somewhat like the placement of urchins and kelp when the model is initialized. This randomness is intended to model an imperfect search. Harvesting reduces the number of larger (legal size) urchins, which reduces the rate of herbivory. If fishing pressure is sufficiently high, kelp growth outpaces urchin herbivory leading to the alternative kelp-dominated stable state (Fig. 7c). In the real fishery, the aggregations along feedlines make it economical to work a patch to the point where urchin herbivory is almost non-existent. If urchins did not aggregate in this way, fishing would become uneconomical at much higher population densities. At low urchin population densities, there is rapid growth of kelp cover, an increase in the abundance of urchin predators and a further decline in the urchin population, leading in the end to a stable state in which kelp dominates and urchins are absent. Today, this stable state is characteristic of almost all of the areas previously populated by urchins in the western part and much of the eastern part of the Maine coast.

3. Discussion

In this paper, we described the ethnographic research we used (1) to help design a computational model of the fine scale, ‘patch’ level dynamics of urchins and kelp, what we refer to as the natural system model, and (2) to better understand human interactions with this natural system. The point of the natural system model is to generate an environment with spatial and temporal patterns that are qualitative replicas of the real world patterns a fisherman has to learn to be successful. Our interviews of fishermen, scientists and managers were used to identify (a) a set of very simple rules governing urchin and kelp dynamics and (b) the patterns of kelp and urchins typically observed in a variety of patch states. We find that a relatively simple set of rules governing urchin behavior and

⁶ The ‘conveyor belt’ represents an interesting modeling problem. Fishermen describe a directed movement but actually observe the position of urchins only at well separated intervals, weeks and months. The continuous upward movement implied by fishermen’s idea of a very local conveyor belt appears to require sensory and cognitive abilities beyond those possessed by urchins. The scientific literature, on the other hand, is clear that urchin movement is random unless the urchin is within range of food. There is no reason to see a discrepancy in these two different observations. The simplest way to model this and the way that assumes the least sensory and cognitive ability in urchins is just as described by scientists. Nevertheless, it turns out the two ideas are fairly consistent. Random movements observed at extended intervals show a net movement towards the kelp and are entirely consistent with the conveyor belt as described by fishermen.

kelp growth can replicate the typical states of a patch or area, i.e., a stable urchin barren, a kelp-dominated stable state and the unstable transition state in which neither urchins nor kelp dominate. In the transition state, with or without simulated harvesting, the natural system model generates typical patterns of feedlines and 'conveyor belts' at locations and times that are qualitatively similar to those described by fishermen, scientists and the scientific literature.

As has been suggested for Atlantic Canada (Miller and Nolan, 2008), our interviews and the scientific literature make it clear that the mechanisms that eventually emerge as widespread depletion in Maine occur at the scale of the individual harvesting site. In Maine, the unique dynamics of urchin, kelp, and fishermen interactions on each patch combined with broad scale restraints not adapted to the circumstances of each patch create open access incentives at the scale of the patch. The result has been overfishing; but in this case, overfishing is a relatively fine scale process that causes each area to flip to stable kelp-dominated, urchin-depleted state. Over the course of the history of the fishery this process has removed, piece-by-piece, discrete, local aggregations.

Our interviews also suggest that under these conditions, the fine scale open access incentives that emerge in this fishery make it nearly impossible for individual fishermen to conserve the resource because they cannot be assured that others will do so also. The harvesting restrictions in place are not onerous, nevertheless, even if a draconian quota were imposed for the entire coast, each urchin patch would remain in an open access state and the process of overharvesting described above would continue. In addition, the sedentary nature of urchins means divers have little to be gained and much to be lost by sharing information about the spatial attributes of the resource. Consequently, there is no basis for self-organizing social structure that might provide the foundation for successful collective action. On the other hand, one could imagine institutional arrangements in which appropriate incentives might exist. Fishermen might fish more selectively and leave some urchins behind if they believed that they could catch the same urchins at a later time before others harvested them. However, a strategy like this could work only if the density of divers was very low or if fishermen had exclusive rights over a spatially defined area of the resource at the scale of an individual fishing site. Under those conditions, fishermen might expect that they could leave urchins behind and return to them another time. Interestingly, an area-based approach like this was attempted in Nova Scotia, but the effects of disease apparently ended the management experiment (Miller and Nolan, 2008). It is unknown if such a system would work under conditions where urchins appear less susceptible to disease.

Nevertheless, our findings suggest that sustainability requires rules that would constrain harvesting at the scale of the 'conveyor belt' on each fishing area, where the system has not yet flipped to the kelp-dominated state and a balance between urchin and kelp biomass persists. Under these circumstances, it would appear that the appropriate management system would be one in which it was possible – economical – to manage the very fine scale dynamics of each urchin fishing site. However, it is clear that the scale of the 'conveyor belt' is far smaller than the relevant scale of an individual harvesting operation (which might be on the order of 10–15 areas or more depending on harvesting success at any one patch) and certainly much smaller than the 100 or more mile extent of each of the current sea urchin co-management zones.

We also theorize that the types of management restrictions matter. Reducing the number of allowable fishing days and limiting harvesting to specific days may only increase unselective fishing behavior and exacerbate the flipping of patches to the stable kelp-dominated, urchin depleted state. Under these conditions, fishermen have no incentive to leave any urchins behind because

they cannot be assured they will get them in the future, not only because others might get them first, but also because weather conditions might limit the use of future fishing days. It is rational to take what one can get, when one can get it. Allowing fishermen a set number of fishing days that they can use at their discretion may reduce the "race for the fish" in the short-term and allow fishermen the opportunity to fish selectively for higher prices, but in the long run there is no assurance that fishermen will not continue to remove, piece-by-piece, discrete, local aggregations. Similarly, restrictions on individual catches, such as total allowable catches or individual quotas, are only likely to work if assigned at the scale of individual urchin fishing areas, the feasibility of which would be exceedingly difficult, if not impossible, to enforce. However, if property rights were assigned (and enforced) at the scale of individual fishing sites, we speculate fishermen would have more incentives to manage their harvest than currently exist under the present system of open access at the scale of the patch. The trick is to determine the appropriate spatial extent over which fishermen can manage (and enforce) the resource.

As explained, we will couple the natural system model with a human system model to create an adaptive, agent-based model. The human system model will be simulated using a method called a learning classifier system (LCS) (Holland, 1986; Wilson, 1995; Wilson et al., 2007). The data produced from the fieldwork described here is also being used to develop the human system model. Together, the natural and human system models will simulate a co-evolving, non-equilibrating system of fishermen who imperfectly learn the dynamics of the natural system and the ways their agent competitors affect that environment (Wilson et al., 2007; Wilson and Yan, 2009). From this model, we will be able to test some of the fine-scale hypotheses that have emerged in the more simple natural system model presented here, as well as in the interview process.

The combination of ethnographic work and scientific literature strongly suggest the broad scale collapse of the sea urchin fishery observed was the result of the serial extirpation of a large number of individual, very local patches. Overfishing on each patch of urchins was possible because the peculiar patterns of urchin aggregation gave divers the ability to harvest local urchin patches to very low levels of abundance. This appeared to occur because the broad scale of management restraints was inappropriate for the local scale of the biology, maintaining for all practical purposes an open access system even though the fishery had all the trappings of co-management, limited entry, and scientific support. The particular human and natural system conditions of this fishery suggest the individual fishing sites, rather than the broad scale co-management zones as currently defined, is the appropriate scale of management. More research, however, is needed to identify the particular design of such a fine-scale management approach. Possibilities include the small-scale leaseholds, as implemented in Nova Scotia (Miller and Nolan, 2008), or multi-species, territorial user fishing rights, such as those in Chile (Moreno et al., 2007). Regardless, management rules and monitoring will need to pay closer attention to the fine scale dynamics that are at present invisible in the current broad scale management approach.

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