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Benthic fisheries ecology in a changing environment: Unraveling process to achieve prediction

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Abstract – Marine fisheries and the ecosystems that sustain them are increasingly beset by environmental deterioration, and the problem is particularly acute in coastal zones where human populations are increasing. In the best of circumstances, fishery managers are faced with the multiple, often conflicting, demands of resource users, politicians, and scientists when considering strategies for resource management. A further challenge is that management decisions must be made against a backdrop of a deteriorating environment and the shifting status of coastal ecosystem integrity. Traditional tools for single-species management may be inadequate in these settings. Furthermore, the necessary empirical data to appropriately parameterize models with vital rates representative of an altered environment are often lacking. Thus, we need approaches that better approximate the complicated dynamics between environmental conditions, fishery impacts, and multi-species interactions. Spatially-explicit, individual-based simulation modeling potentially permits this kind of integration, but it has seen limited use in marine resource management, especially with respect to benthic resources. My colleagues and I have used this approach, combined with targeted experimental work, to explore the impacts of nursery habitat deterioration, coastal freshwater management, and fishery activities on Caribbean spiny lobster populations and sponge community structure in the Florida Keys, Florida (USA). Although not applicable for all resource management situations, our experiences provide an example of the potential use of spatially-explicit, individual-based modeling and targeted empirical science in predicting resource conditions in a dynamic environment.

Key words: Marine Ecosystem Management / Benthic / Fisheries / Lobster /
Spatially-explicit individual-based modeling

Résumé – Écologie des pêches benthiques dans un environnement changeant : éclaircir un processus pour réussir une prévision. Les pêches maritimes et les écosystèmes qui les supportent sont assaillis par la détérioration de l'environnement, et le problème est particulièrement aigu dans les zones côtières où les populations humaines augmentent. Dans les meilleurs des cas, les gestionnaires des pêches sont face à de multiples, et souvent conflictuelles, demandes des usagers des ressources, des politiciens, et des scientifiques lors de la mise en œuvre de stratégies pour la gestion des ressources. Un plus grand défi existe lorsque les décisions de gestion doivent être prises contre une détoriation de l'environnement et le changement de statut de l'intégrité de l'écosystème côtier. Les outils traditionnels pour la gestion d'une seule espèce peuvent être inadéquats dans ces montages. De plus, les données nécessairement empiriques pour paramétrer des modèles avec des taux vitaux représentatifs d'un environnement altéré font souvent défaut. Ainsi, nous avons besoin d'approches qui estiment mieux les dynamiques complexes entre conditions environnementales, impacts de la pêche, et interactions plurispécifiques. Spatialement explicites, les simulations à partir de modèles « individus-centrés » permettent potentiellement cette intégration, mais limités à l'usage de la gestion des ressources marines et en particulier benthiques. Mes collègues et moi-même avons utilisé cette approche, combinée avec un travail expérimental ciblé, pour explorer les impacts de la détérioration des habitats, des nourriceries, de la gestion des eaux douces côtières et des activités des pêches sur les populations de langoustes des Caraïbes et la structure de la communauté d'éponges de Floride Keys, Floride (USA). Bien que non applicable à toutes les situations de gestion, notre expérience donne un exemple de l'usage potentiel des modèles « individus-centrés » et de science empirique ciblée en prévoyant les conditions des ressources dans un environnement dynamique.

1 Introduction

The title of this essay and of my presentation at the 2004 meeting of the Australian Society for Fish Biology from which this essay was derived, hints at the three main points that I hope to make. Namely, that: (1) the oceans are a wreck, (2) if we are to manage fisheries under dynamic conditions we need more process-based, predictive tools at our disposal, and (3) the foundation for such tools is knowledge of the underlying ecological processes. After commenting on these points, I provide

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a brief look at how my colleagues and I are tackling the kinds of problems that are all too familiar to those with an eye on the sea. In our case, our job is not to manage the resource but to better understand the ecological processes that limit them. In so doing, we are tying experimental research on process with spatially-explicit, individual-based modeling to address questions about the potential effects of ecosystem disturbance and restoration on fishery resources, specifically spiny lobster and sponges. This glimpse into our approach is meant as an example of one tactic that may be useful in the struggle to preserve coastal fishery resources caught in the ecological turmoil caused by a degrading coastal environment. The tone of this article follows that of my presentation – it is an opinion piece, not a review or original research contribution. It is told from the perspective of a marine ecologist who studies taxa of fishery importance (i.e., spiny lobster and sponges) in a coastal region (south Florida) where fisheries are heavily exploited, the aquatic environment rapidly deteriorating, and resource managers doggedly trying to make sense of it all. The approaches now taken in attempting to manage the all too familiar fishery woes of coastal ecosystems are increasingly variable, reflecting the local ecological setting, political landscape, and available data, as well as the expertise and training of those hired to do so. Each situation is a little different. Still, I hope that this brief overview of our challenges, methods, and experiences adds depth to your perspective.

2 Dilapidated seas and failed fisheries

The modern marine realm is anything but static. Superimposed upon the age-old dynamics of marine ecosystems that has driven the boom and bust of marine fishery populations for eons, is a rapidly changing marine environment. Many marine ecosystems are now hurtling along new evolutionary trajectories due to the widespread deterioration of water and habitat quality (National Research Council 1994; Nixon 1995; Beach 2002), the infusion of exotic species (Carlton 1999; Ruiz et al. 2000), the emergence of new or trans-located pathogens (Harvell et al. 1999), and the effects of fishing on target and non-target populations (Jennings and Polunin 1997; Jennings and Kaiser 1998). The poor state of the coastal oceans and their resources is obvious to anyone who has spent time working on or enjoying the sea, and the prospect of further decline is nothing short of alarming.

The problems plaguing our seas are varied and well documented in numerous publications (US Ocean Commission 2004; FAO 2002; Field et al. 2002, and others), so the litany will not be recited in detail here. The National Research Council (1994) and the US Ocean Commission (2004) categorize the culprits similarly: (1) pollution and eutrophication, (2) habitat destruction (primarily coastal and benthic habitats), (3) over-exploitation of fishery resources, and (4) climate change. Some argue that coastal eutrophication is the most pervasive and serious problem (GESAMP 1990; National Research Council 1994), while others contend that overfishing holds this dubious distinction (Jennings and Kaiser 1998; Jackson et al. 2001). Regardless of how one ranks them, the problems are all or nearly all anthropogenically derived, their effects on coastal ecosystems synergistic, and there are few signs that they are abating (Stricklen and Gross 2000). Humans are not only the dominant species on earth, but because of our impacts on the environment and the species therein, some now consider us to be the greatest evolutionary force in the world (Palumbi 2001). Our impact on the earth's ecosystems ranks right up there with that attributable to asteroids!

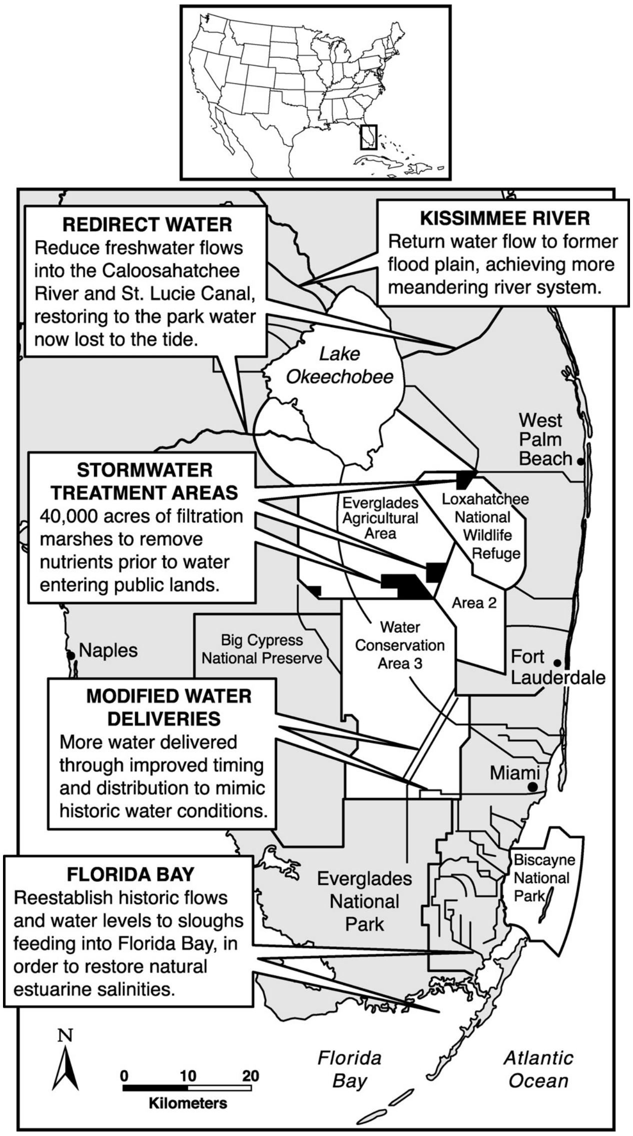
The aggregate ramification of these environmental insults is that the stability of earth's ecosystems, coastal ocean systems included, seems now at risk (Elmqvist et al. 2003; Bellwood et al. 2004). The baselines for what is considered "normal" or "typical" have changed dramatically, as coastal systems have shifted from those dominated by large fishes, mammals (e.g., sirenians, pinnepeds), sea turtles and invertebrates to systems largely populated by small fish and invertebrates (Pauly 1995; Pauly et al. 1998; Jackson et al. 2001; Jackson 2001). Around the globe, coastal marine communities appear to be on the precipice of dramatic phase shifts from ecosystems with diverse, benthic communities to biotically depauperate, plankton-dominated systems, as is occurring in the Black Sea, the "dead zone" in Gulf of Mexico, and the Chesapeake Bay to name a few (Scheffer et al. 2001). The prospect of this dim future for our seas has triggered a surge in international agreements and national initiatives pertaining to ocean management. In the United States, the Commission on Ocean Policy, which was created by congressional mandate and whose members are appointed by the President's office, have called for nothing less than complete upheaval in the way the US deals with ocean issues. A move to science-driven (as opposed to politically manipulated), ecosystem-based (as opposed to single-species) management is one of the hallmarks of the proposed restructuring of marine ecosystem management worldwide.

3 Restoring an imperiled ecosystem

> "*When one tugs at a single thing in nature, one finds it attached to the rest of the world.*"
>
> John Muir (1838–1914), naturalist

In the United States, problems in coastal resource management along the Everglades and the adjacent subtropical waters of the south Florida peninsula are indicative of those in coastal marine systems elsewhere (see papers in Porter and Porter 2002 for a review). Yet, nowhere in the US is more effort and money being spent to solve those problems. Over $8 billion (US) will be spent over the next 25 yrs on the Comprehensive Everglades Restoration Plan (CERP) in what is touted as the world's largest environmental restoration effort (Fig. 1; see: `http://www.evergladesplan.org/about/rest_plan.cfm`).

When most people think of the Everglades they picture a vast freshwater marsh infested with alligators. But the Everglades are, in fact, a series of interlinked aquatic ecosystems stretching over 500 km from the Kissimmee River watershed north of Orlando to Florida Bay southwest of Miami. It is fresh water, both surface and groundwater, that link the river, marsh, cypress swamp, mangrove forest, and coastal marine ecosystems of the Everglades. Extensive hydro-engineering of the



REDIRECT WATER
Reduce freshwater flows into the Caloosahatchee River and St. Lucie Canal, restoring to the park water now lost to the tide.

KISSIMMEE RIVER
Return water flow to former flood plain, achieving more meandering river system.

STORMWATER TREATMENT AREAS
40,000 acres of filtration marshes to remove nutrients prior to water entering public lands.

MODIFIED WATER DELIVERIES
More water delivered through improved timing and distribution to mimic historic water conditions.

FLORIDA BAY
Reestablish historic flows and water levels to sloughs feeding into Florida Bay, in order to restore natural estuarine salinities.

Fig. 1. Map of the United States (at top) and south Florida (at bottom) providing an overview of the types of project planned as part of the Comprehensive Everglades Restoration Plan (CERP), as well as their general locations and restoration goals. Modified from CERP website; see the CERP website for full details and a comprehensive list of projects: `http://www.evergladesplan.org`

Everglades began in the early 1900s for flood control and to provide water for agricultural and urban use, culminating in what now is one of the world' s largest freshwater management systems. Although a successful feat of engineering, the system of canals, dykes, levees, and pumping stations has significantly altered the quality, quantity, and seasonal periodicity of freshwater that flows from the Everglades into the sea (Fig. 2), and threatens the ecological integrity of this subtropical ecosystem (see papers in Porter and Porter 2002 for a review). For example, natural variation in rainfall along with alterations to the Everglades natural hydrography have resulted in dramatic annual and sub-annual differences in salinity and water temperature in Florida Bay (Brewster-Wingard and Ishman 1999). Portions of Florida Bay that were historically estuarine are now marine, and other areas vacillate dramatically in salinity by as much as 50 psu or more a year.

The Everglades has had a long history of environmental champions, many of whom were non-scientist citizens who recognized the intrinsic value of this enormous aquatic ecosystem. Marjory Stoneman-Douglas's classic work "*The River of Grass*" (1947) is the most famous. However, it was not troubles within the Everglades proper that prompted this latest and largest restoration action, it was downstream in Florida Bay, the shallow coastal lagoon lodged between the marshlands of the Everglades and the islands of the Florida Keys archipelago. This is where signs of an ailing ecosystem most recently emerged; evidence of the intimate linkage between land and sea.

Fishermen and scientists who had worked in the region for years had a sense that the south Florida marine ecosystem was changing, the most noticeable differences being diminished water quality and the health of the coral reef communities (see Boesch et al. 1993; Fourqurean and Robblee 1999; Porter and Porter 2002 for a review). Then, a decade ago, an unprecedented series of perturbations struck Florida Bay in what has been described as a "cascade of disturbances" (Butler et al. 1995; Fig. 3). Details are sketchy and not all causal relationships confirmed, but the evidence for what tipped the ecological balance of the system is compelling and points to human activity in the Everglades. Briefly, changes in the flow and quality of freshwater emanating from the Everglades resulted in the overproduction of seagrass throughout much of the western basin. Density-dependent declines in the health of seagrasses coupled with high temperature and an outbreak of a slime mold pathogen (*Labyrinthula* sp.) resulted in the die-off of thousands of hectares of seagrass (Robblee et al. 1991; Zieman et al. 1999; Fourqurean et al. 2003). The release of nutrients from decaying seagrass and the suspension of sediments in the water column is thought to have fueled the subsequent and repeated occurrence of harmful algal blooms that persisted for months. The blooms loomed over hundreds of kilometers of seagrass and tropical hard-bottom habitat, and at times were swept out to sea, threatening coral reefs (Butler et al. 1995; Phlips et al. 1999). Inexplicably, the cyanobacterial blooms triggered a massive mortality of sponges, resulting in the decimation of the sponge community – commercial and non-commercial species alike – over most of the afflicted region (Butler et al. 1995; Herrnkind et al. 1997; Lynch and Phlips 2000). The cascade went on. The rapid loss of seagrass and sponges resulted in a reconfiguration of nursery habitat for spiny lobster on a grand scale. Approximately 20% of the area used by spiny lobster as a nursery in Florida was destroyed, which translated into significant local declines in lobster recruitment (Herrnkind et al. 1997).

This series of events highlighted an intricate and unexpected set of ecological linkages in the system: both terrestrial to marine and within the marine communities themselves. Understanding the cause of the seagrass die-off alone revealed a complicated set of processes at work that interact in maintaining the integrity of the seagrass community (Durako and Kuss 1994; Carlson et al. 1994; Zieman et al. 1999). The dramatic and rapid alteration of a highly visible ecosystem got

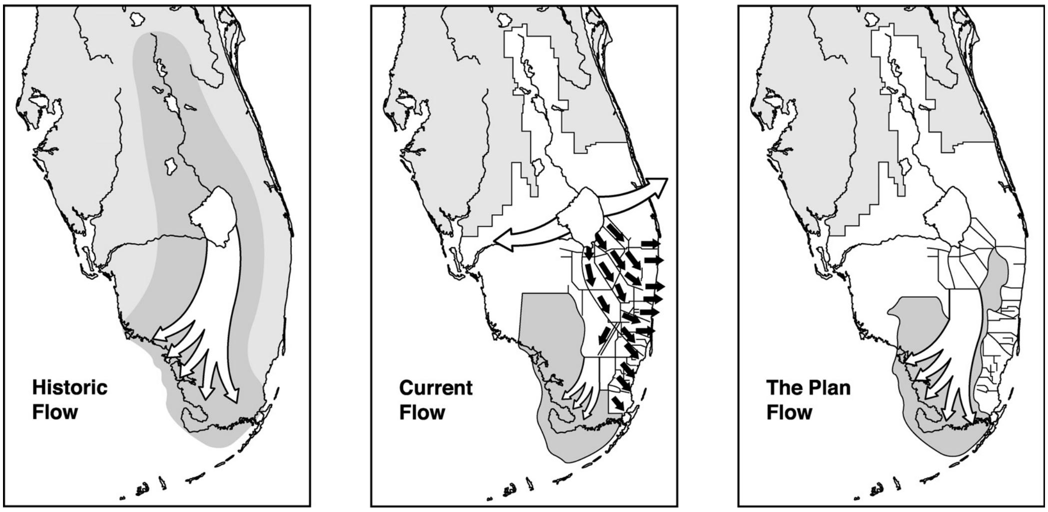


Fig. 2. Generalization of the historic flow of freshwater through the Everglades ecosystem and out to sea (left panel), the current pattern of flow (center panel), and the proposed pattern of flow under the CERP (right panel). Modified from CERP website.

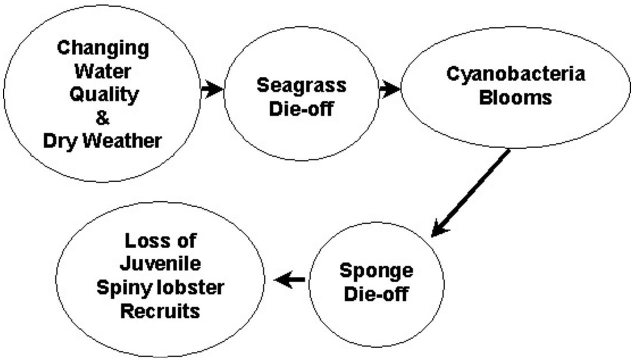


Fig. 3. Overview of the cascade of disturbances that took place in Florida Bay ecosystem in the early 1990's, as described in Butler et al. (1995).

the attention of the media, the public, local politicians, and several influential individuals – including friends of the President of the United States. Their concerns led to the Comprehensive Everglades Restoration Plan (CERP). For the burgeoning number of marine scientists in the region, CERP signaled an opportunity to conduct ecosystem-based studies that provide the science necessary for managing what had become a steamroller-like initiative to "replumb" the Everglades and "fix" the environmental problems plaguing the region.

Perhaps the central question for the marine scientists and managers, whose realm lies "downstream" of where most restoration efforts will occur, is: what kinds of changes might be expected in the coastal ecosystems adjacent to the Everglades? For the public and for coastal resource managers, an equally important question is whether a "restored" Florida Bay would be equally desirable to the thousands of fishermen, residents, and tourists who use it annually. The marine ecosystem in the area has almost certainly changed in the hundred years or so that freshwater flow has been altered.

To address these and other questions, the science plan for CERP includes support for targeted environmental research, modeling, and monitoring. It also calls for "feasibility studies", that is, small scale engineering projects linked with environmental monitoring to provide empirical "what if" tests of restoration scenarios (for a detailed description of these and other Everglades restoration issues see: `http://www.evergladesplan.org/about/rest_plan.cfm`). A small part of this enormous effort involves research on the potential impact that Everglades restoration may have on the hard-bottom communities in the shallow waters of Florida Bay and the Florida Keys. In particular, there were concerns about consequences for spiny lobster, which are the focus of Florida's most valuable fishery. A large fraction of Florida's lobster nursery lies in a region at risk. Our previous work had shown that hard-bottom communities within Florida Bay, in particular the sponges and lobsters found there, were sensitive to changes in water quality (Field and Butler 1994; Butler et al. 1995; Herrnkind et al. 1997). Those findings, along with the commercial and recreational value of the lobster fishery and the perceived ecological importance of sponges in this shallow ecosystem, set the stage for a new phase in our research, one directed toward prediction of restoration impacts.

4 New tools for ecosystem management?

The dismal status of the seas and our inability to protect fishery resources using traditional management methods have been catalysts for development of "new" approaches for managing ocean resources. The concepts of "ecosystem-based" management (including but not limited to marine protected areas), "adaptive management", and "managing with uncertainty" are all the rage in marine management circles. Predictably, the marine science literature is filled with debate over the utility and feasibility of these approaches to coastal resource management (Larkin 1996; Botsford 1997; Mooney 1998; Salvanas et al. 1998 and others). Regardless of the philosophical approach one embraces as a management strategy, the need for new ecosystem-oriented management tools is ubiquitous and, increasingly, those tools center on modeling.

We desire predictive models that operate on scales large enough to encompass ecosystem-level changes, yet are specific enough in spatial resolution to investigate the consequences of spatially heterogeneous impacts on spatially heterogeneous ecological systems. Ultimately what we seek are integrated fishery management models that link interactions among fishery resources, the fisheries for them, and the changing nature of the marine environment. Attempts to do so have been successful to a point, but most have fallen short in how they deal with aspects of ecosystem ecology that shape the dynamics of fishery resources (Benaka 1999; Rose 2000). Perhaps, the best known ecosystem model is ECOPATH (and its various versions), which has seen wide use as a standard means of comparing the trophic structure, trophic pathways, energy flux, and efficiencies among ecosystems or time periods within an ecosystem (see Pauly et al. 1993; Christensen and Pauly 1993). The demand for more general ecosystem models that incorporate dynamic conditions, and thus the allure of predictive capability, has led to more dynamic trophic models such as ECOSIM (Walters et al. 1997).

Ideally, we also need models that explicitly incorporate the effects of local environmental features (e.g., turbulence, prey abundance, water quality, habitat structure) on marine population dynamics (Moore 1972; Mazeaud et al. 1977; Jaworski et al. 1997; LePage and Cury 1997; Schreck 1999), and models that do so in a way that recognizes individual variation in response. Individual-based modeling (IBM) that integrates relevant spatially-explicit features of the environment is one possible approach. The unification of IBM with spatial modeling was a long overdue computational tool, judging by the number of studies that have applied this approach in the past decade. This has been especially true among biological oceanographers, whereas spatially-explicit IBM has seen only limited use in benthic marine systems. An electronic search of Cambridge Scientific's Aquatic Sciences and Fisheries Abstracts and Oceanic Abstracts for papers employing individual-based (or agent-based), spatial approaches yielded 177 papers published over the past 10 years. When only marine papers are considered, the list drops to 29 only four of which describe spatial IBMs of benthic systems (Breitburg et al. 1999, 2003; Butler et al. 2001; Butler 2003).

Spatial models combine population dynamics with a landscape depicting the spatial distribution of salient environmental features that may vary among habitat "boxes" or "cells" (see Steyaert et al. 1997). The spatial resolution or detail in marine IBMs varies considerably, from those incorporating only a few spatial cells (e.g., three vertical water mass strata) to more recent formulations with thousands of cells, each with its unique physical properties. Werner et al. (2001) detail the progression of marine spatial IBMs in their recent review, but their coverage of the topic is limited to pelagic models that describe larval-oceanographic dynamics, and therefore their spatial structure is defined primarily by velocity fields, temperature, salinity, or prey density.

Spatial models can be married to population dynamics in several ways. In their most simple form, population dynamics may be described by state variables defined separately for each spatial cell, whereas stage-based models permit separate formulations of important life history processes that often exist among different age or size classes (see Caswell 2000). In contrast, IBMs follow the status of each individual in the population, whose survival, growth and reproduction (i.e., fitness) is affected by individual characteristics, local conditions in the habitat cell, and stochastic processes (see reviews by DeAngelis and Gross 1992; Van Winkle et al. 1993a,b; Uchmanski and Grimm 1996; Grimm 1999). The underlying rationale for the use of IBMs is that the properties of ecological systems (i.e., communities, populations) emerge from consideration of the properties and interactions of the individuals that constitute them. In the case of behaviorally complex organisms, such as spiny lobsters, the notion is that individuals respond uniquely to their surroundings based on genotypically variable sets of behaviors and physiologies, which in turn depend appreciably on contingencies in the environment (e.g., temperature, salinity, habitat heterogeneity, predators, prey, conspecifics, etc.). The spatial dynamics of the composite population thus arises out of the interplay of individual behaviors in this complex environment in ways that could not be anticipated from simpler models. Thus, the distribution of individual characteristics and responses matters, not just their mean value – this is the very essence of ecology, of natural selection, of evolution. IBMs are attractive not only for their heuristic appeal, but also because they are easily parameterized and readily permit the investigation of "what if" scenarios. These complex models can produce quantities of output that can be difficult to manage, although thoughtful consideration of the necessary output and new visualization tools minimize this problem (Megrey et al. 2002). On the downside, bias or omission of key processes may render these data-rich models suspect and they are rarely validated – a trait shared by many fishery models. Therefore, we seldom expect our models to produce absolute truths, but their predictions may reveal unexpected consequences and can help to set the bounds or probable consequences of our actions – or inaction – in a changing and uncertain environment.

5 Fisheries ecology and ecosystem restoration: An example

The approach that my colleagues and I have taken in addressing the effects of ecosystem-level change on lobster recruitment and hard-bottom community structure in the Florida Keys is multi-faceted and engenders many of the key aspects called for by proponents of ecosystem-based management. The overall question driving our research is whether changes in salinity resulting from Everglades restoration appreciably affect hard-bottom communities in Florida Bay and the fishery resources that they sustain? The foundation of our project is the empirical study of ecological processes that effect the populations of ecologically pivotal species, and the effect of environmental change on these processes. We chose to focus on a suite of prominent hard-bottom dwelling species of both ecological and economic importance. That is, the primary structure-forming benthic animals (sponges and octocorals); the functionally important and ecologically dominant benthic predators (spiny lobster) and filter feeders (sponges and octocorals); and species (spiny lobster and sponges) of special

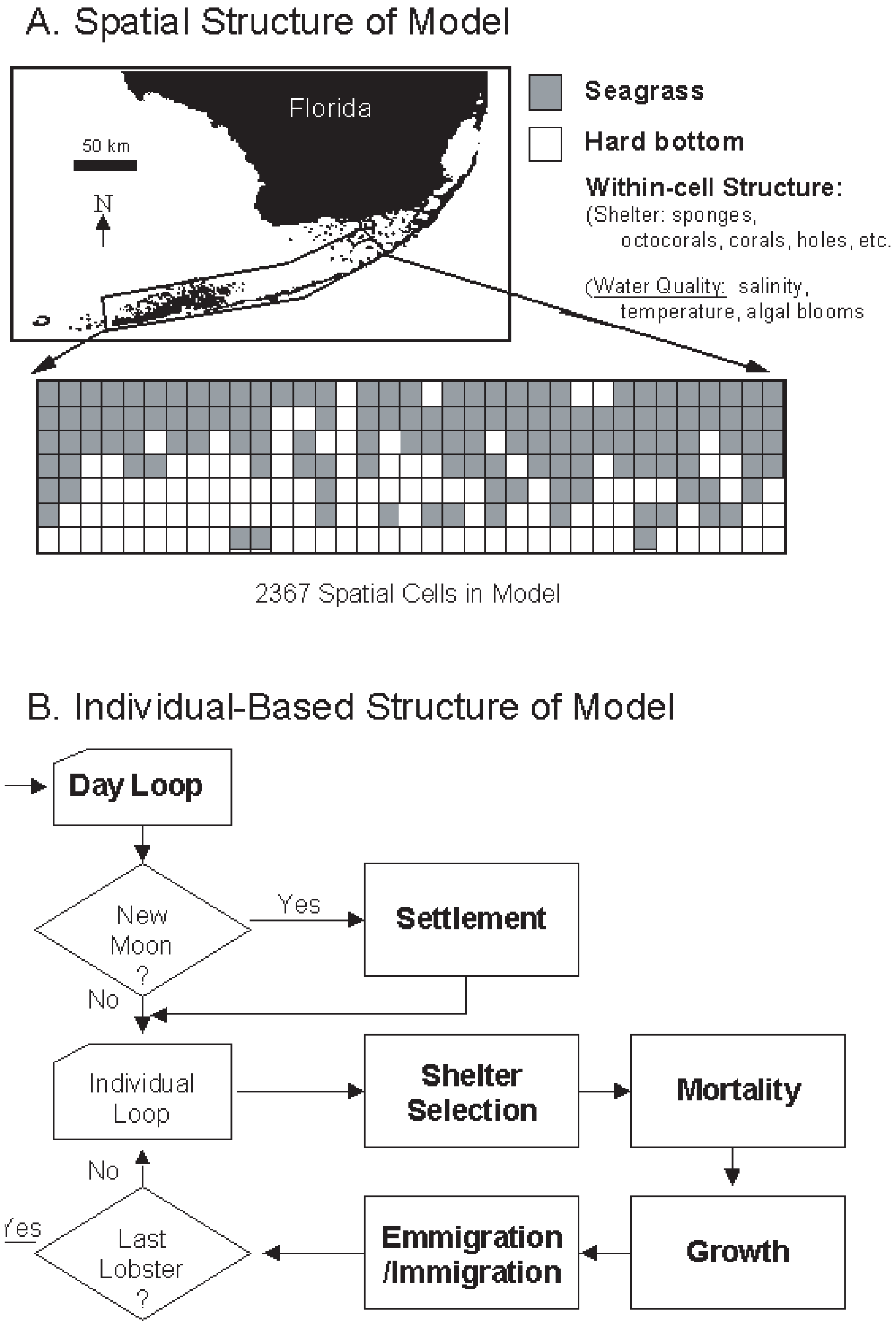


Fig. 4. Graphical summary of the spatial structure (A) and population dynamics (B) included in the spatially-explicit, individual-based model of spiny lobster recruitment and hard-bottom habitat structure in the Florida Keys, FL (USA).

economic importance to commercial, recreational, and artisinal fishing interests.

Linking disparate sources of data in a meaningful, quantitative way and scaling up from narrowly focused laboratory experiments and small scale field studies so as to investigate ecosystem-level questions is a challenge, but a worthy goal if we are to achieve the predictive capability needed for ecosystem management. Our approach has been to meld data from field surveys of existing community structure over the entire target seascape with the results of focused laboratory and field studies of ecological processes within the context of a spatially-explicit, individual-based model.

Our model is ecosystem-based in the sense that it incorporates multiple levels of ecosystem organization, although not all to the same degree (Fig. 4). The model's clear focus is on lobster population dynamics, but it also includes dynamic

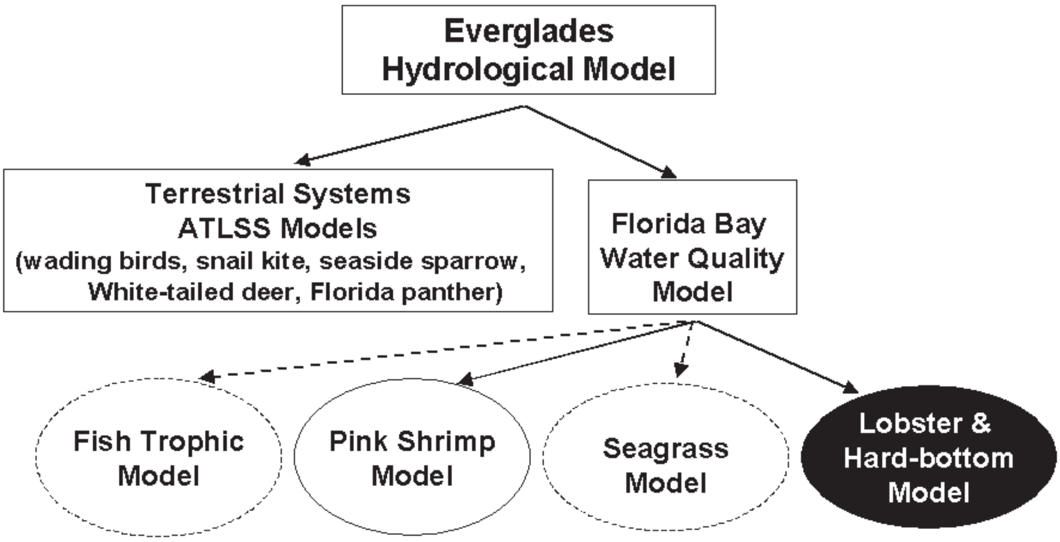


Fig. 5. Conceptualization of the linkages among models developed (solid lines) or proposed (dashed lines) for examining the effects of the CERP on the south Florida ecosystem. The lobster – hard-bottom model, which is the focus of this essay, is highlighted by the darkened circle.

changes in biotic nursery habitat features (i.e., sponges, octocorals, seagrass, and macroalgae) that occur in response to abiotic alterations such as: temperature, salinity, or harmful algal blooms. In turn, our model is structured so it can be driven by spatio-temporally dynamic model projections of salinity in Florida Bay (e.g., FATHOM model; Nuttle et al. 2000) that might be expected under different water flow regimes (Fig. 5). Changes in water quality in Florida Bay are also expressed within a model for pink shrimp (Browder et al. 1999) and those that have been proposed for fishes and seagrass. The Florida Bay water quality model is in turn dependent on Everglades hydrology modeling, which also has ties to a large multi-trophic level model (ATLSS) depicting the population dynamics of various upland biota (e.g., wading birds, snail kite, seaside sparrow, white-tailed deer, Florida panther: see DeAngelis et al. 2002 for a review). At present, most of the proposed inter-model linkages are as yet unrealized, each of the models having been constructed independently by and for different agencies and purposes. What follows is a glimpse at how we developed the lobster – hard-bottom community part of this puzzle.

5.1 Laboratory experiments

5.1.1 Methods

At the start of the project about a decade ago, we were perplexed that literally nothing was known about the salinity, and to a lesser extent, temperature tolerances of the prominent hard-bottom species we chose for study. In retrospect, one can see that whereas these kinds of data may be common for estuarine species, there is little call for such studies on true marine species not typically subject to massive or persistent doses of seawater. Therefore, we began by assessing, in rather straightforward laboratory exposure trials, the lethal and sublethal effects of different salinity-temperature regimes on: Caribbean spiny lobster (*Panulirus argus*), five sponge species (loggerhead sponge, *Speciospongia vesparia*; vase sponge, *Ircinia campana*; brown-brancing sponge, *Ircinia* sp.; golfball sponge, *Cinachyra alloclada;* sheepswool sponge, *Hippospongia lachne)*, and two species of octocoral (angular seawhip, *Pterogorgia anceps;* purple seaplume, *Pseudopterogorgia acerosa)*. In brief, individuals of each species were independently exposed to salinities of 15, 25, 35, or 45 psu at typical summer (28−30 °C) and winter (16−18 °C) water temperatures. Salinity in each tank was gradually changed (using peristaltic pumps; 4 psu/day) over several days until the target salinity was attained. Later, we repeated the experiment but instead exposed each species to a rapid, single day pulse of the proposed salinity mimicking a flash flood or emergency freshwater water release from the water management system. In terms of responses, we measured the obvious and perhaps not so obvious. For sponges and octocorals, we monitored survival but also wound healing as an indicator of sub-lethal responses. In the case of lobster, we recorded size-specific differences in survival, growth, movement, and susceptibility to disease. The methods we used to assess the latter two measures of sub-lethal response bear further mention.

Unlike their sessile sponge and octocoral counterparts, lobsters and fishes can potentially emigrate from an area where conditions are inappropriate and this response is likely to vary with individual size. We tested this for *P. argus* juveniles of varying sizes by exposing individuals, placed in large (2 m diameter) raceways, to gradually changing salinities at summer and winter water temperatures (same treatment conditions as described above). During each five-day experiment, we recorded each individual's relative rates of movement using an event recorder wired to a mechanical tripping mechanism. To assess whether changes in salinity might alter the transmission of disease, we tested the transmission of a newly discovered, pathogenic, and ultimately lethal viral disease (Behringer and Shields 2003) at the same series of salinities and temperatures and across a range of juvenile lobster sizes.

5.1.2 Results

Our laboratory studies indicated that postlarval and early benthic juvenile spiny lobsters are intolerant of salinity change and experience high mortality, especially at high summer temperatures (Field and Butler 1994; Butler unpubl. data). In contrast, the survival and growth of larger juvenile lobsters was unaffected by salinity, but their movement was. When salinities change, lobsters initially respond by increasing their walking for a day or two, presumably to escape the changing environmental condition. Whether they maintain their trek depends on the salinity. With intermediate changes in salinity (e.g., from 35 to 25 psu) they indeed continue higher than normal walking for days. However, if salinity changes more drastically (e.g., from 35 to 15 or 45 psu), then their movements return to normal or lower levels after the first day of heightened response. These results parallel exactly those found in the clawed American lobster (*Homarus americanus*), where the initial increase in walking following by decreased walking in response to large changes in salinity are attributed to metabolic exhaustion (Jury et al. 1994).

The five species of sponge that we tested varied in their tolerance to low salinity, although none survived the 15 psu treatment at winter temperatures and none survived any low salinity during high summer temperatures. The least tolerant species was the commercial sponge (*Hippospongia lachne*) and the most tolerant were the brown-branching sponge (*Ircinia* sp.) and the golfball sponge (*Cinachyra alloclada*). Our field observations match these laboratory results in that the latter species appear to be "weedy" species: good colonizers and tolerant of a wide range of conditions. Although the sponges varied considerably in their response to changing salinities, both species of octocoral that we tested experienced 100% mortality at salinities below 35 psu at all temperatures. Our efforts to measure sub-lethal impacts on sponges and octocorals were thwarted by heavy mortality, suggesting that wound healing may only be a factor at more modest changes in salinity (i.e., <10 psu).

5.2 Modeling

5.2.1 Model description

Details of our modeling approach are given elsewhere (Butler et al. 2001, 2005; Butler 2003), thus only an overview is provided here. The spatial framework of our model is a matrix of 2367 habitat cells (each ~ 1 km^2) that simulate the Florida Keys (Fig. 4). It includes virtually all of Florida's spiny lobster nursery habitat. The habitat designation for each cell (i.e., hard-bottom, sand/mud, and seagrass) corresponds with the actual spatial distribution of habitats in the region as determined from GIS-based habitat layers and dive surveys. Habitat structure within each hard-bottom cell, the preferred nursery habitat for *P. argus*, is also spatially-explicit and reflects the natural abundance, diversity, and within-cell proximity of shelters typically used by juvenile lobsters (e.g., sponges, stony corals, octocorals, solution holes, etc.). Lobster "carrying capacity" within a cell is thus a function of the size and density of each shelter type and the number of lobsters that typically inhabit each. We also specify cell-specific temporal changes in salinity, temperature, and exposure to harmful algal blooms that potentially affect lobster growth, movement, and survival, and the survival of living crevice shelters important for juvenile lobster survival (i.e., sponges and octocorals).

Superimposed on this spatial landscape are the individual-based dynamics of spiny lobster settlement, growth, shelter selection, mortality, and movement. All functions are based on empirical data and nearly all are probabilistic, a more realistic and intuitive approach that permits more direct parameterization of the functions. Settlement magnitude within cells depends on the type of settlement habitat within the cell and the location of the cell with respect to potential physical transport. Once an individual is assigned to a habitat cell, detailed depictions of individual lobster growth, mortality, foraging, movement, time spent searching for shelter, and shelter selection are played out on a daily time step. Simulations can run for any specified period of time, but typically 5−10 years. About 10 million individual lobsters are currently modeled in a single 10 year simulation.

5.2.2 Simulations

Eventually we hope to run simulations exploring the impact of various proposed hydrological restoration efforts in the Everglades on salinity in Florida Bay, and hence on lobster recruitment and the survival of sponges and octocorals. However, because of uncertainties in the reliability of the Everglades hydrological model and the Florida Bay model it feeds, we have thus far relied on empirical data. Specifically, we compared results of simulations using salinity measurements taken during weekly cruises during average, extremely wet, and extremely dry years (see Boyer et al. 1999). Thus, the spatio-temporal patterns in salinity represent upper and lower bounds, as should the resultant effects on lobster recruitment. In our simulations, lobster populations were permitted to build over 2 years, and during this initialization period, salinity fields within the model cells remained stable at 35 psu. After initialization, salinities in the model cells varied independently among cells and on a weekly time-step in accordance with empirically measured changes for the wet or dry year. The effects of salinity on lobster, sponges, and octocorals are temperature-dependent, so we also changed water temperature incrementally each day in the model reaching a maximum of 30 °C in the summer and a minimum of 18 °C in the winter. Simulations were also conducted with and without impacts on nursery habitat (i.e., sponges and octocorals), so we could examine both the direct effect of salinity change on lobsters as well as the indirect effects of salinity change propagated through nursery habitat change.

5.2.3 Results

The results of our simulations suggested that lobster recruitment during a very wet or dry year would be similar. In both cases, recruitment declined by ~25% in the area directly affected by salinity change which resulted in ~5% decline in recruitment over the entire Florida Keys region, as compared to control simulations where salinity was stable at 35 psu. Although large juveniles are capable of emigrating from areas

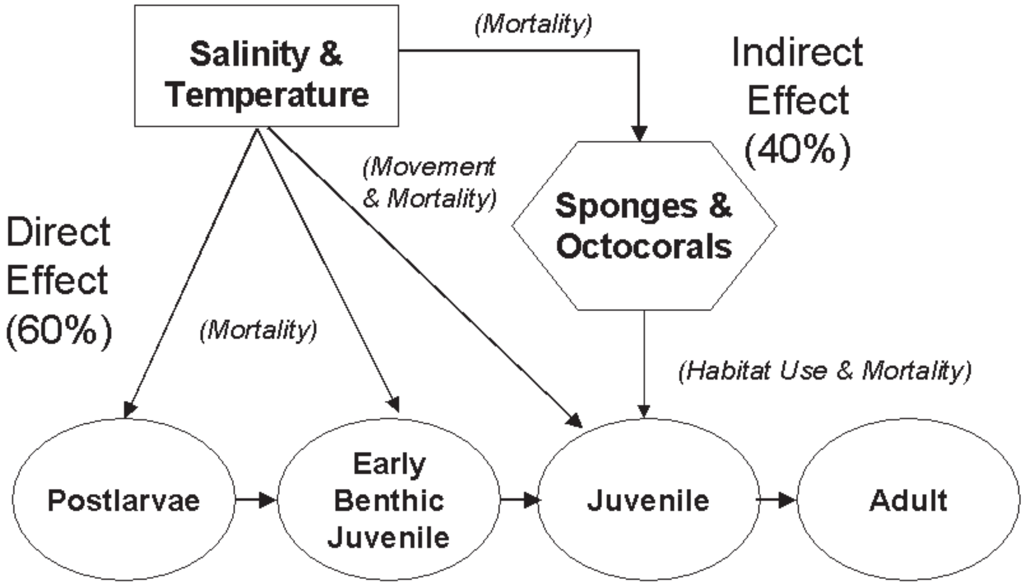


Fig. 6. A depiction of the direct and indirect effects of altered salinity on various spiny lobster life history stages as determined from empirical studies and incorporated into our model. The demographic effects of salinity change on each lobster life history stage are given in parentheses next to each interaction. Model simulations indicate that indirect effects account for approximately 40% of the lobster response (i.e., recruitment of individuals to 50 mm CL), whereas the direct effects of salinity change account for 60% of the response.

experiencing inappropriately high or low salinity and did so in the model, the effects of this movement on recruitment were inconsistent and of little overall impact. This occurred because the smallest size classes that are most effected by altered salinities cannot emigrate great distances. However, these simulations lacked some potentially important dynamics for which we have no data. For example, we did not assign any differential "costs" to large juveniles that stay in their home cell versus those that emigrate in response to changing salinity. Comparison of results with and without the indirect effect of salinity on sponges and octocorals (i.e., shelter for juvenile lobsters) suggest that the impact of ecosystem change on lobster recruitment has as much to do with indirect effects on lobster via habitat availability as it does with direct, physiological effects on lobster (Fig. 6).

Our model, like every model, has its simplifications and biases. For example, our measure of the importance of indirect effects is very conservative. It only takes into account effects on the living crevice shelters upon which large juvenile lobster depend. It does not include the potential indirect effects that altered salinity is likely to have on lobster recruitment via changes in other habitat features, such as macroalgal and seagrass settlement habitat, or the abundance of predators or prey. Quantifying those effects are future challenges for us. This particular set of simulations was also built around wet and dry year data, rather than expected hydrological changes associated with the restoration of the Everglades. We await the completion of new physical models capable of producing the appropriate salinity distributions that we can use in our model. Still, our simulations have offered managers useful predictions of the minimum impacts that might be expected for lobster, sponges, and octocorals in the region when the Everglades restoration effort is fully implemented.

6 Conclusion

There is probably no single "right" way to manage marine ecosystems because of the idiosyncrasies of the ecology, the politics, and economics of different regions. Still, we need to be explicit about the goals of ecosystem management. From such goals, one can generate questions about the potential impacts of various strategies formulated to achieve those goals. Modeling must undoubtedly play a role in this process. If so, then there is a place for flexible models that emphasize spatially-explicit, individual-based interactions among organisms and their environment.

The drive toward ecosystem-based management is growing worldwide and in principal it sounds like good management. Like a painting in progress, the form that ecosystem-based management will ultimately take is beginning to materialize in boardrooms, in print, and at meetings like the 2004 ASFB conference in Adelaide. Yet, the coastal resource managers and scientists in the trenches who are faced with fleshing out the details of ecosystem management understand that this new approach is not a simple paint-by-numbers exercise. Principals that will help guide ecosystem-based management are emerging – slowly. Yet, in light of the carnage wrought by decades of environmental compromise, it is hard to argue against the simple, guiding principal expressed by one of the great ecologists of the early twentieth century, Aldo Leopold: *"A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise"*.

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