BILLFISHES IN AN ECOSYSTEM CONTEXT

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ABSTRACT

There is a rising tenor of calls for ecosystem-based approaches to fisheries management. Many billfishes are apex predators in pelagic food webs and, therefore, of potential ecological significance as keystone predators. Most billfishes are vulnerable to exploitation effects, especially those taken as by-catch where longline fishing occurs. We developed a series of ecosystem models that serve as tools for evaluating the role of billfishes and their fisheries across a range of scales. One of those models addressed ecological questions about responses to large marine protected areas. Another developed ecological and economic forecasts of billfish responses to reduced by-catch through specific changes in longline gear. A third posits the outcome of mandatory use of circle hooks by longline fisheries as a means for reducing sea turtle mortality. Changing to circle hooks in commercial fisheries has profound effects on catch rates for many fishes and, therefore, evokes substantial changes in food web dynamics. Enhanced catch-release practices for billfishes produce an ameliorative response that reduces mortality rates and furthers the economic benefits of recreational fisheries.

Appeals for ecosystem-based management of marine resources increasingly focus on fishery effects (Browman and Stergiou, 2004; Pikitch et al., 2004; NRC, 2006). Billfishes are among the pelagic apex predator guild reduced in abundance due to exploitation by commercial fisheries (Myers and Worm, 2003; Hampton et al., 2005) which raises questions about the ecological consequences of exploitation. Members of the family Istiophoridae (marlins, spearfishes, and sailfishes) are usually at or near the apex of pelagic food webs, have broad diets, grow very rapidly, have high fecundity, and, in some cases, exhibit large-scale, trans-oceanic migrations. Economically, they are of modest market value when taken as by-catch in pelagic longline and other fisheries targeting the more highly valued tuna species. Pelagic longline (hereafter called longline) vessels constitute the major source of fishery mortality for billfishes (> 90%; Cox et al., 2002b,c). Recreational fisheries for billfishes can have a profound economic impact (Holland et al., 1998; Ditton and Stoll, 2003) and recent analyses argue that fishery management efforts should increase their focus on recreational fisheries (Coleman et al., 2004).

In some ecosystems, responses to fishery effects can be revealed through experimental manipulation (Pace et al., 1999), management actions (e.g., stocking, Kitchell et al., 2000) and/or dramatic changes evoked by introduced species (Kitchell et al., 1997). Unfortunately, clear evidence of ecological responses to fisheries is more difficult for the large marine ecosystems where billfishes exist. Instead, models must be among the primary tools for evaluation of responses that may derive from fishery effects (Essington et al., 2002; Hinke et al., 2004, Walters and Martell, 2004). Actually developing practices for ecosystem management requires a conceptual framework or vision, appropriately-scaled models and data analyses, plus opportunity to develop insightful tests (Walters and Martell, 2004).

This paper offers an abbreviated review of examples as our modeling efforts underwent an ontogeny of development and were used to address a diversity of questions about apex predators and their prey. We focus on the role of billfishes as apex predators plus the possible consequences of fishery management actions that would affect both billfish abundance and their role in an ecosystem context.

The Models

Ecosystem-scale models represent a complex set of hypotheses about population dynamics and trophic interactions. They are fueled by parameter estimates derived from basic life history characteristics, food habits data, and estimates of mortality rates, including those for exploitation. They are criticized as being disquietingly complex for some biologists (including many of the modelers) and often constrained by the quality of data employed in their development. Unfortunately, that fact must be accepted by both empiricists and modelers. Given the rates of exploitation for many fish populations supported by oceanic ecosystems and the need to develop policy guidelines for management, we simply cannot wait for more and better data. Readers dubious about this assertion should consider the number of times they've seen claims to the effect that we: "...have all the data we need!" and/or "...no more research is necessary." Models are imperfect generalizations, but can be a valuable way to focus on key policy issues and guide future research. Accordingly, model output should be interpreted with caution and a "broad brush" view. We adopt that view and present our results only for those simulations evoked from strong manipulation and representing large-scale responses. In general, we describe modeled responses in terms of changes from initial conditions. Those can be generally viewed as ranging from "modest" or "little" (< 10%) to "substantial" (> 25%) or "dramatic" (> 100%).

The first step in ecosystems analyses is to define the system. Our focus was on the Central North Pacific (CNP) which is bounded by the equator and the Transition Zone (35°–40°N) and longitudinal boundaries of 150°W and 130°E. The second important step involved describing food web interactions through review of the diet literature and a species level of resolution at higher trophic levels, to larger aggregations at lower trophic levels (e.g., small scombrids, mesopelagic fishes, and small squids). Our view of food web interactions in the CNP clearly focuses on the upper trophic levels (Fig. 1). We used the steps above toward developing a series of ecosystem-scale models focused through use of approaches developed by Walters et al. (1997).

Our modeling effort derives from a mass-balance approach (Ecopath) that uses estimates of biomass, production rate, feeding rates, and diet composition as the core parameters for each state variable. Ecopath develops an equilibrium state as the backbone of initial conditions (Walters et al., 1997). Ecopath can be manipulated through Ecosim to simulate alternative fishery policies and/or environmental changes (Walters et al., 2000). Results can be set in the context of spatial heterogeneity and dynamics owing to fish movement or migrations through Ecospace (Walters et al., 1999). All three models are fully described and available through the UBC Fisheries Centre website (http://www.fisheries.com). Scores of publications have employed this set of modeling approaches (Christensen et al., 2000). Here we review a series of steps in model development for the CNP. In each case the cited source includes parameter tables used in that specific application.
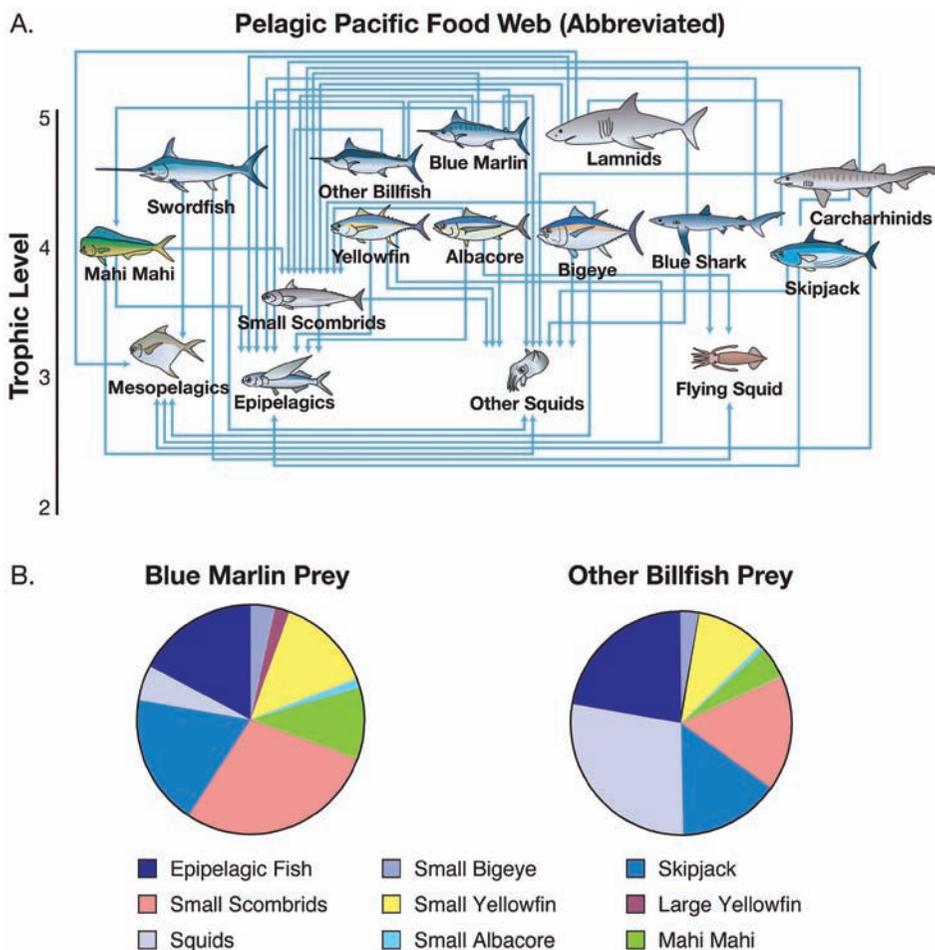
Figure 1. (A) A general description of trophic level and food web interactions for apex predators and their prey in the Central North Pacific ecosystem. The pie diagrams describe relative importance of prey for (B) blue marlin and other billfishes.

Keystone Predators

We often read concerns about the removal of apex predators and consequent effects on the "delicate balance" of "fragile" ecosystems. Recent claims to that effect have assumed major visibility (Myers and Worm, 2003). Among these claims are assertions that billfishes may be keystone predators (Hinman, 1998), i.e., consumers whose effects on ecosystem structure and function are substantially greater than their abundance would suggest. This concept (Paine, 1969) found favor in a large, diverse set of studies and is central to the "top-down" principle employed in describing trophic cascades (Pace et al., 1999).

The original Ecosim model of the CNP was used to test for the role of billfishes as keystone predators (Kitchell et al., 1999). As the equivalent of an experimental manipulation, we increased or decreased fishery mortality for each of a series of apex predator species (billfishes, sharks, and tunas) and analyzed results from a 30-yr simulation that approximated a new equilibrium state.

Removal of sharks evoked a modest effect with long lag periods representative of their life history characteristics (Schindler et al., 2002). Removal of billfishes evoked a more modest and more rapid response, but with little effect on food web structure. Removal of yellowfin tuna (*Thunnus albacares* Bonnaterre, 1788) produced a rapid and substantial effect—a widespread change in trophic structure owing to their role as both predator and prey (Essington et al., 2002). Removing all forms of fishery mortality (longline, purse seine, troll, pole and line, and drift net fisheries) produced the most dramatic effects. Predators (billfishes, sharks, and tunas) increased and their prey decreased. Tunas increased by about 2 to 3-fold and sharks increased by about 3 to 4-fold. The magnitude of these responses were more modest and certainly not in accord with the 90% depletion of all apex predators argued by Myers and Worm (2003) but, in the case of tunas, more in keeping with the exploitation effects asserted by Hampton et al. (2005) and Polachek (2005).

The most dramatic response to removal of all fishing mortality was by blue marlin (*Makaira nigricans* Lacépède, 1802) which increased 8-fold within the 30-yr period. This owes primarily to the fact that marlin mortality due to by-catch by commercial fisheries had greatly reduced adult abundance (Cox et al., 2002b,c). In other words, removing the fisheries allowed blue marlin to recover to previous abundances. Removing fishery impacts on the community also had an amplifying effect on marlin recovery, as several other species initially recovered from fishing and then declined as their role as prey fueled a continued marlin rebound. This combination of direct and indirect effects is broadly apparent in analyses of many ecosystems (Walters et al., 2005). In this case, the role of keystone predator was obviously that of the fisheries. As a test of that assertion, fishery mortality for the CNP model was doubled to represent the equivalent of current effort in the Gulf of Mexico. Comparison of species composition for catches in the latter demonstrate further reduction of apex predators accompanied by substantial increase in smaller tunas and fishes of lower trophic levels (e.g., mahi mahi) which confirms the widespread effect of increased fishery mortality (Kitchell et al., 1999).

Ecological Economics

As stated above, the economic importance of angling for billfishes substantially exceeds their ecological role as predators. Mortality rates associated with recreational catches remain a subject of debate (Kitchell et al., 2004), but they are certainly less than those derived from by-catch in commercial fisheries which account for more than 90% of fishery mortality for marlin species (The Billfish Foundation, http://www.billfish.org). The recent petition for listing of Atlantic white marlin, *Tetrapturus albidus* Poey, 1860 (Federal Register, 2001) as an endangered species derives from evidence that the current population is at about 7% of pre-fishery abundance. If the white marlin is listed by the US Endangered Species Act, an ironic situation develops. Virtually no landings will be allowed in the US. In fact, the US fleet comprises about 5% of total longline effort and any assessment of stock status must come from reporting by other national fleets. Their governments would have lessened or little incentive to participate in our restrictive actions or the data sharing they require. Thus, enacting the ESA will likely cause us to know even less about the status of this species. Blue marlin in the CNP are estimated by Cox et al. (2002b,c) to be at 15%–20% of virgin stock abundance. We can imagine a similar ESA-listing effort

directed toward their protection and, unfortunately, a similar increase in our lack of knowledge.

Conservation organizations such as The Billfish Foundation are among the leaders in promoting catch-release as a protective measure. While a growing practice among recreational anglers, its effects are relatively modest compared to the mortality imposed by by-catch in commercial fisheries. We can, however, imagine the development of international cooperation in reducing marlin mortality through changes in gear that might reduce marlin by-catch and be enacted for all longline fleets. This could prove to have strong economic benefits expressed through the positive feedback of higher marlin survival rates and increased recreational catch rates that would follow.

The most recent modification of a CNP model was developed by Cox et al. (2002b, c) and differs from previous modeling efforts in that it was based on stock assessment analyses including all fisheries, then calibrated by the ability of the model to reconstruct trajectories from pre-fishery abundances for major species to those of the present. In other words, the model was evaluated through its ability to recover the past. This process is the preferred method for reconstructing pre-fishery abundances and providing parameter values that account for changes in trophic interactions (Walters and Martell, 2004). The fit to blue marlin abundance changes over a 50-yr period was particularly good, providing some confidence in its potential for simulating the future. We used that model to simulate both ecological changes and economic benefits as outcomes of a change in methods practiced by fisheries in the CNP.

Boggs (1992) studied catch rates on each hook deployed in fishing practices representative of longline gear in CNP waters. More than half of all marlin were caught on the two hooks nearest the floats, (i.e., those that are most likely to fish in near-surface waters) of a standard 13-hook "basket" between the floats. If those hooks were removed, or more practically, fished at greater depth, marlin mortality could be reduced by roughly half. We developed a simulation that represented those changes by expanding the economic benefits (in present dollars) derived from studies of chartered recreational fisheries (O'Malley and Glazier, 2003), estimating angling effort responses from a model developed by Cox et al. (2002a) and simulated effects by assuming a 54% decrease in marlin catch rates (Boggs, 1992) extended over a 30-yr period. A key assumption in all this is that all fishes and fisheries are mobile and interacting in a well-mixed system referred to as the CNP.

Highlights of the results were:
- Blue marlin abundance approximately tripled over the 30-yr period following changes in fishing practices.
- Abundance of "other billfishes" increased by 1.8×. In the CNP model, this group is an aggregate of smaller billfish species, but dominated by striped marlin, *Tetrapturus audax* (Philippi, 1887).
- Angling effort doubled as a result of increased catch rates.
- Economic benefits to the Hawaii-based recreational fishery increased by 280 million dollars. We have no estimates for recreational fisheries based elsewhere in the CNP.
- As a result of greater marlin predation on valuable tuna species, major economic losses occurred in the commercial section. For the entire CNP, those were estimated at 1.7 billion dollars.

• In general, if shallow hooks were removed or fished at greater depth, food web effects were modest compared to those owing to changes in marlin catch rates.

Clearly, conservation approaches focused on reducing marlin mortality can have profound economic and ecological effects. Making economic forecasts over a 30-yr period is certainly questionable, as is the assumption of a durable, widespread change in fishing practices. Nevertheless, there is obvious potential for tradeoffs between local benefits and larger scale losses owing to the food web effects of higher marlin survival rates. The benefits are scaled in dollars while most of the losses should be scaled in yen or yuan. In this case, we can have more confidence in the ecological forecasts owing to changes in billfish abundance because we know that juvenile tunas are both a major prey of marlin and a valuable resource as adults. Expansions such as this are limited by our knowledge of local or large-scale movement and abundance patterns for both billfishes and tunas. This is a clear call for more research effort in this area.

Collateral Damage

Conservation efforts for billfishes correspond with similar efforts to protect pelagic sharks, sea birds, and sea turtles. Management actions intended to reduce mortality rates for one group can produce benefit or debit for another. The CNP model was used to evaluate the trade-offs that might develop in two case studies—one for sharks and the other for sea turtles.

Prior to about 1990, most pelagic fisheries treated sharks as by-catch; they were discarded and released which caused relatively low mortality rates (He and Laurs, 1998). In the 1990s, development of shark fin markets raised that mortality rate so that > 80% of sharks caught were killed (WPFMC, 1998; Camhi, 1999). In response to growing concern over shark conservation, some countries (e.g., US and Australia) enacted legislative limitations on landings of shark fin. This type of legislation will probably produce a significant reduction in mortality rates for coastal sharks from the EEZ of countries that limit shark landings. However, there will be a much more modest reduction in mortality rates for pelagic sharks taken in longline gear because Asian fleets dominate these fisheries in the international waters of all of the world's oceans and many markets remain for shark fins.

In a second evaluation of the role of sharks as apex predators, Kitchell et al. (2002) attempted three model manipulations: (A) Reconstruction of shark diets as they might have been before longline fisheries developed (another keystone predator test), (B) Closure of all longline fishing in the CNP, and (C) Two-fold increase in CNP longline fishing. Some general conclusions of this effort were:

• Sharks are neither keystone predators nor strong competitors with tunas and billfishes (Essington et al., 2002). Owing to shark life history characteristics (Musick, 1999), fisheries can have profound, negative effects on their populations.

• Cannibalism among sharks bears further evaluation as a component of natural mortality rates.

• Predation on billfishes by large, piscivorous sharks has declined due to the advent of longline fisheries.

Sea turtle conservation has recently surged to the forefront of complex policy issues in the CNP. Loggerhead *Caretta caretta* (Linnaeus, 1758) and leatherback *Dermochelys coriacea* (Vandelli, 1761) turtles are listed as endangered species in the US and both are taken as by-catch by longline fisheries. Recent court actions have alter-

nately closed, then re-opened some waters of the CNP as US-based longliners are directly affected by suits intended to conserve turtles (US Dept. Commerce, 1999, 2004). Asian fleets are not affected by the US ESA; hence, management actions apply to only about 5% of the longline fishery effort in international waters. On the other hand, a new international body commonly referred to as the Western and Central Pacific Fishery Commission (Commission for the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean) is developing to facilitate collective data sharing and management of high seas fisheries throughout the Pacific. Thus, the institutional structure is in place for evaluating possible and collective conservation efforts.

Billfish conservation organizations such as TBF actively promote use of circle hooks in recreational fisheries because post-release mortality rates are substantially lower than those from other hook types (Domeier et al., 2003; Horodysky and Graves, 2005). In addition, results from the Atlantic (Watson et al., 2005) and similar results from the Pacific (Boggs, 2004, Largacha et al., 2005) reveal that changes in longline hook types may effect major reductions in sea turtle by-catch. If the traditional "J" hook or the similar Japanese or "tuna-style" hook were replaced by large (size 18/0) circle hooks and a change in baiting practices, sea turtle by-catch could be reduced by as much as 90%. Voices for sea turtle conservation call for a mandatory conversion to circle hooks by all U.S. longline fleets and the tenor of demand is rising in the international forum. Unlike many recreational fisheries, captured fishes are typically retained by commercial fisheries. Thus, the proposed change in gear raises questions about catchability of targeted fishes, effects on their abundances, and consequent effects on trophic interactions.

Kaplan (2004) used the Cox et al. (2002 a,b) model to construct simulations of a CNP-wide conversion to circle hooks. There are many hook comparison studies in recreational fisheries (Prince et al., 2002) and a series of recent and ongoing large-scale experiments with alternative hook types and/or baits (Watson et al., 2005, Gilson et al., 2006). At the time of Kaplan's work, there were very few published and thorough documentations of effects of hook types on catch rates for target and other species taken in commercial longline fisheries, with one important exception. Hoey (1996) compared catch rates from circle hooks versus traditional tuna-style hooks for 352 longline sets in the Gulf of Mexico. Catch rates on traditional hooks were 25.5 fish per set while those for circle hooks were 32.9 fish per set. In other words, circle hooks catch about 30% more fish. If the current fishing effort is maintained and all catch retained over a 30-yr period, the increased mortality rates cause major changes for species that are directly affected and for potential indirect effects expressed in food web structure. In general, nearly all apex predators declined in response to the higher catch rates of circle hooks, but there were differences from the simple expectation based on 30% greater catch rates. Major changes reported by Kaplan are as follows:

- Abundances declined for blue marlin (–50%), bigeye tuna (–40%), large, piscivorous sharks (–40%), and other billfishes (–33%) owing to the higher catch rates of circle hooks.
- Abundance increased modestly for yellowfin tuna (+12%) and juvenile blue sharks (+15%) due to changes in food web interactions. Mortality rates for yellowfin tuna and juvenile blue sharks declined due to reduction of their predators.

Kaplan also simulated the effects of catch-release for billfishes if required in commercial fisheries and estimated a post-release survival rate of about 50%. For traditional tuna-style hooks, the results were similar to those approximated in the Kitchell et al. (2004) study, blue marlin increased by 2.7-fold, other billfishes by 1.8-fold, and there were modest decreases in yellowfin tuna. If circle hooks were mandated and all marlin released, responses were similar for blue marlin (2.4-fold increase) and other billfishes (1.7-fold increase), but the responses of other species were more akin to those reported for universal use of circle hooks without billfish release. Some reduction in yellowfin tuna, a primary prey of marlin, was the only, but modest, exception.

If the catch-release focus were on sharks instead of billfishes and shark post-release survival rates were as reported (about 73%; Kaplan 2004), then all adult shark populations increased by 1.5–2.7 times. Billfish populations declined even more substantially owing to the joint effects of higher catch rates on circle hooks and enhanced predation by an increased population of their predators, the large sharks. If both sharks and billfishes were released, tuna populations were further reduced owing to circle hook effects coupled with enhanced predator populations. Again, shark effects reduced billfish abundance increases, but only modestly; blue marlin increased by 2.2-fold and other billfishes by 1.5-fold.

The central message from this pioneering simulation study is that changes in fishery practices intended to promote survival of sea turtles may create a substantial and negative effect on many other species. Those representing new catch-release practices for billfishes and/or sharks can have similarly profound effects among the commercially valuable tuna species. Alternative modeling approaches may differ to varying degrees and applications to other billfishes may require more specific data such as that derived from studies of white marlin mortality owing to recreational fisheries (Horodysky and Graves, 2005), but the central assumptions about trophic interactions are probably appropriate. Conducting field trials as a set of experimental fishery ventures would require decades before unequivocal results were apparent. In this case, the modeling results clearly call for immediate and substantial increase in studies of hook type comparisons in the CNP. Longline fishing practices differ in other ecosystems and will likely produce very different results if circle hooks are widely adopted (Watson et al., 2005, Gilman et al., 2006). The key requisites are documentation of changes in catch rates for target species, catches of other species, and the models required to set those in the larger context of food web interactions.

Spatial Dynamics

The merits and debits of Marine Protected Areas (aka Marine Reserves) is a focus of increasing interest as one means for reducing large-scale effects of fishery exploitation and consequent changes in food web structure and ecosystem function (Micheli et al., 2004). While most of the effort to date has been directed to coastal systems, there are analogs in the proposals for time and area closures in protecting pelagic fishes (Goodyear 1999, 2003). Responses for individual species can be gauged by known dispersal rates, but the expression of those in a larger context is unexplored.

Martell et al. (2005) envisioned a large MPA for the CNP and used the Ecospace model to evaluate its effects. This effort employed the Cox et al. (2002a,b) model but

with some important modifications. Fishing effort was assumed to increase at the present rates of growth for a simulated 50-yr period but was prohibited within the MPA. Migration rates were scaled by known swimming velocities for all adult apex predators and their juveniles. Both were treated as aggregate groups. Environmental variability effects and fish distribution responses were tested through two basic modeling approaches. One was based on the advection-diffusion approach which can account for behavioral changes in a gradient of productivity and consequent prey abundance (Lehodey et al., 1997). A second, novel approach was based on behavioral changes that might evoke if fish responded positively to increasing prey abundance, but negatively to higher predator abundance. This "fitness function" derives from extensive behavioral observations and experimental studies on predation risk conducted in a miscellany of ecological settings (Walters and Kitchell, 2001; Martell et al., 2005). In addition, Martell et al. (2005) used an effort response for fishing fleets as a response to abundance of the targeted fishes. Tests of the two distribution models were portrayed as outcomes for alternatives owing to productivity gradients, alternative current effects, and convergence-divergence zones.

One important contrast of results from the two distribution models is summarized in Figure 2. The advection-diffusion model predicts that both adult and juvenile abundances will generally increase in response to a productivity gradient. Juvenile fishes respond as expected. Adult fishes are the target of fisheries, increase in abundance within the MPA, and, as seen in many cases, fishing effort accumulates at the MPA boundaries. In this case, greater effort accumulates at the more productive edge of the MPA.

The role of trade-offs between access to prey and risk of predation is evident in results from the fitness function hypothesis. Adult fishes and fishing effort develop as in the advection-diffusion case, but juvenile distributions are very different. Within the MPA where predation risk is high, juvenile abundance is much reduced. Instead, maximum juvenile abundances occur outside the edges of the MPA with a greater accumulation evident in the region of higher productivity. As a result, we should expect substantial asymmetry in the food web effects exhibited within the MPA boundaries as compared with those outside its edges.

The fitness function employed in this case is a theoretical construct and a testable hypothesis. Although billfishes are not presented as separate groups in this analysis, two somewhat different results will appear for this group, especially for blue marlin. Because of high swimming velocities, there are more modest changes in relative abundance inside and outside the MPA. Adult billfishes are relatively less abundant than other apex predators inside the MPA because their predators, more slowly swimming large sharks, accumulate inside and predator avoidance behaviors cause greater dispersal rates for the rapidly swimming billfishes.

This analysis offers a very important message. If protection of pelagic fishes is the MPA goal, the area must be very large.

DISCUSSION

A search for keystone predators at the top of the CNP food web revealed that no single species is essential to ecosystem function. Diets broadly overlap and habitats are generally similar. By-catch of billfishes has generally reduced their abundance more than that observed for the targeted tuna species. Ecological compensatory re-
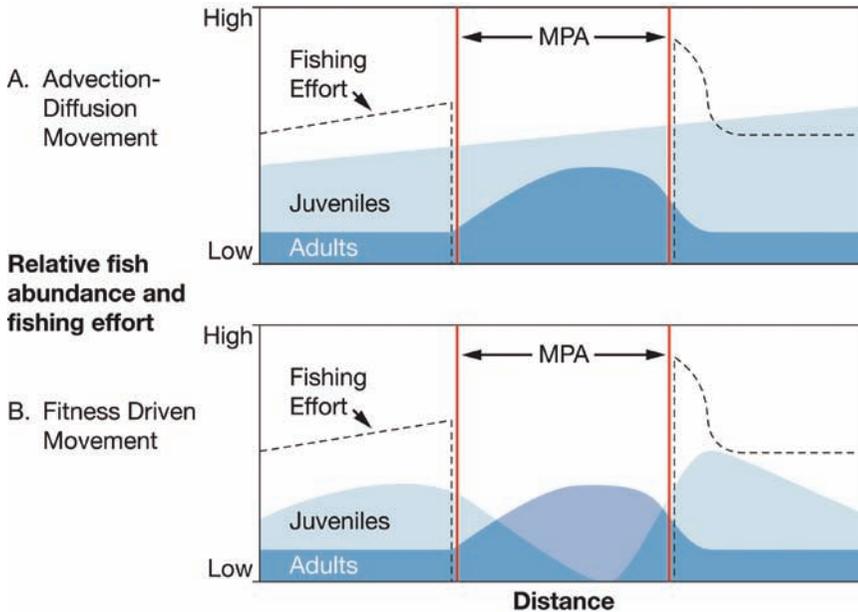
Figure 2. Responses of adult and juvenile apex predators and their fisheries in the Ecospace model of a Marine Protected Area represented within the Central North Pacific ecosystem. Two distribution models are presented: (A) the advection-diffusion model for behaviors in a gradient of prey abundance, and (B) the fitness function model where predator avoidance is balanced against prey abundance. Both panels are redrawn from Martell et al. (2005).

sponses are to be expected for this subset of the apex predator guild. Thus, conservation efforts directed toward billfishes have some important justification at the ecosystem scale because they are indicators of the intensity of fishery exploitation with consequent potential changes in food web dynamics and because recreational fisheries for billfishes offer major economic benefits. Billfishes prey on tunas, hence there are economic trade-offs to be considered as billfish populations are altered through management efforts. In addition, of course, these species are magnificent expressions of the evolutionary process and as such deserve attention as important expressions of biodiversity in pelagic systems (Holland, 2003).

Ecological compensation has developed among this set of species (Cox et al., 2002a,b). As predator populations are reduced through exploitation, their prey should increase. The potential magnitude of those responses is one of the major motivations for using ecosystem-scale models. Myers and Worm (2003) assert that increases in catch per effort of small billfishes and smaller tuna species are due to reductions of their predators and competitors as larger billfish (especially blue marlin) and larger tunas were reduced by fisheries. Ward et al. (2005) reported similar results based on comparison of catch rates for early and recent longline fisheries near Hawaii. Changes in fishery targeting practices, improvements in fishery methods, and debate about interpreting catch rate data confound those analyses (Walters, 2003), but the basic ecological expectations are appropriate and are widely expressed in our efforts at modeling these interactions.

Unanticipated effects on billfish populations can derive from conservation efforts directed toward reductions in sea turtle mortality and adopted through modification of longline gear. While there are compelling reasons to encourage use of circle hooks

in recreational fisheries, a mandated switch to circle hooks by commercial fisheries can effect major changes in food web structure with strong, negative impact on billfish populations and those of other target species (Gilman et al., 2006).

Time and area closures designed to protect pelagic stocks can have strong local effects, but may be of lesser value in protecting the highly mobile pelagic billfishes. Marine protected areas must be very large and their effectiveness may be modified by important behavioral responses that create strong gradients of predator and prey abundance.

Few, if any, of the modeling results presented above could be exclusively and properly represented through either experimental studies or data analyses. Experimental studies would require scales of endeavor beyond the capacity of current institutions. Retrospective data analyses are confounded because of changes in both targeting behavior and fishery technologies employed in the past. Those are interactive in time and space. Thus, the modeling approach offers a means for considering both as drivers of ecological change in complex food webs.

Our modeling approach also reveals specific areas where targeted experimental assessments may be of greatest value in improving our understanding, especially as focused on billfishes. For example:

- Comparison of data about large-scale differences in fishing effort can help reveal more about the suite of ecological changes evoked by increased mortality of apex predators. In this case, analysts must seek ways to remove bias induced by changes in fishery efficiency and targeting.
- A straightforward comparison of site-specific early data on billfish diets with those evidenced since fishing has increased would be instructive in helping assess food web changes from the view of the predator.
- More studies of catch rates as a function of hook type are clearly of value. Mortality rates associated with catch-release practices are essential, both for recreational and commercial fisheries.
- Archival tags offer the benefit of revealing habitat use as defined by the fish, not by the fishery. These can provide major insights at all scales.
- Two modeling methods are currently employed in evaluating large-scale distributional dynamics. Advection-diffusion models offer a means for evaluating tag-recapture evidence while the fitness function approach makes a strong case for considering the risk of predation in migratory behaviors and distribution. The latter is a novel and important hypothesis that needs to be tested for billfishes and/or other apex predators through creative approaches at both the local and larger spatial scales.

Our models are focused on a single conceptual approach embodied in the structure and assumptions of the Ecopath-Ecosim-Ecospace series. This method has the merit of widespread use and endorsement by a recent review (NRC, 2006), but the debit of important assumptions that can and should be challenged. Other approaches may have the merit of independence and, therefore, a means for testing alternative hypotheses. We close by inviting additional effort in the modeling arena.

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