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IDEA AND PERSPECTIVE

The value of coordinated management of interacting ecosystem services

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Abstract

Coordinating decisions and actions among interacting sectors is a critical component of ecosystem-based management, but uncertainty about coordinated management's effects is compromising its perceived value and use. We constructed an analytical framework for explicitly calculating how coordination affects management decisions, ecosystem state and the provision of ecosystem services in relation to ecosystem dynamics and socio-economic objectives. The central insight is that the appropriate comparison strategy to optimal coordinated management is optimal uncoordinated management, which can be identified at the game theoretic Nash equilibrium. Using this insight we can calculate coordination's effects in relation to uncoordinated management and other reference scenarios. To illustrate how this framework can help identify ecosystem and socio-economic conditions under which coordination is most influential and valuable, we applied it to a heuristic case study and a simulation model for the California Current Marine Ecosystem. Results indicate that coordinated management can more than double an ecosystem's societal value, especially when sectors can effectively manipulate resources that interact strongly. However, societal gains from coordination will need to be reconciled with observations that it also leads to strategic simplification of the ecological food web, and generates both positive and negative impacts on individual sectors and non-target species.

Keywords

Bioeconomic model, coordinated management, ecosystem-based management, ecosystem services, game theory, joint social value, natural resource management, single-sector management, species coexistence, trophic cascade.

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INTRODUCTION

Natural resource agencies and user groups (sectors) are increasingly being called upon to conduct coordinated management, or strategic structuring of their decisions and actions for achieving a common objective (Slocombe 1993; McLeod *et al.* 2005). Coordinated management in relation to ecological properties of ecosystems is important for enhancing conservation and economic outcomes in wildlife and natural resource management (Leopold 1936; Caldwell 1970; Grumbine 1994). This philosophy has since been developed into a powerfully general rule: given that individual management actions can affect multiple ecosystem properties (e.g. conservation of X affects production of Y), coordinated management can optimise the state or delivery of interacting properties and increase the joint value of an ecosystem to society (Slocombe 1998; Kappel *et al.* 2006; Granek *et al.* 2010; Tallis *et al.* 2011). This rule underlies ecosystem-based approaches to management that comprehensively account for the suite of interacting ecological resources and human activities that affect a particular place (Crowder *et al.* 2006; McLeod & Leslie 2009; Rosenberg *et al.* 2009; Obama 2010; Parliament 2010; NOC 2011).

Coordinated management has been a signature feature in integrated natural resource management (Lal *et al.* 2002), marine spatial planning (Day 2002; NOC 2011), multi-species management (Pikitch *et al.* 2004), systematic land planning (Margules & Pressey 2000; Polasky *et al.* 2008; Bode *et al.* 2011), and other proposed and actual strategies of natural resource management that instil principles of ecosystem-based management (EBM) in the conservation and exploitation of environmental resources (Slocombe 1993, 1998; Rosenberg & McLeod 2005; McLeod & Leslie 2009; Rosenberg *et al.* 2009; Parliament 2010). For example, EBM for the oceans is defined by comprehensive and integrative management decisions and actions in relation to ecosystem dynamics and the provision of interconnected ecosystem services, or human benefits (McLeod *et al.* 2005). Specifically, any EBM strategy is successful in part due to management decisions being strategically coordinated in relation to each other, their (known and unknown) interactive effects on the outcomes of ecosystem services, and the relative societal preferences for those outcomes (Pikitch *et al.* 2004; Sumaila 2005).

While the merits of coordinated management seem incontrovertible, accounting for complex ecological and socioeconomic dynamics is difficult and retrofitting natural resource management to include coordination among different sectors can be costly (Bode *et al.* 2011). Further, the specific value of coordination depends on how it affects ecosystem state and the provision of ecosystem services, and how changes in service provision levels affect the welfare of different user groups and the wider public (Granek *et al.* 2010); these welfare changes will affect the nature and strength of political support for this component to EBM. A general framework for quantifying the value of coordinated management would inform the kinds of geographies, resources, and multi-sector contexts in which it is of most importance – that is, help determine when coordination is 'worth it'. Previous theoretical and applied studies on ecosystem-based approaches have compared outcomes under coordinated management with outcomes under historic, status quo, uniform, open access, random and other reference management scenarios (Brock & Xepapadeas 2002; Wiese *et al.* 2008; Boesch & Goldman 2009; O'Boyle & Worcester 2009; Fletcher *et al.* 2010; Kellner *et al.* 2010; Jupiter & Egli 2011; Lester *et al.* In Revision). In all of these cases the reference embodies suboptimal features in addition to lack of coordinated management, such as poor enforcement, non-adaptive decision-making and overcapacity, which also degrade performance. Consequently, while these studies are well-designed and important for measuring total gains from implementing coordinated management, their results conflate coordination with other factors and so can be used only to set an upper bound of the value of coordination *per se*. More generally, to date no standardised approach and few guiding principles have emerged that isolate the conditions under which the effects of coordinated natural resource management are large or small (Bode *et al.* 2011). Even the more basic question of how much economic value coordination contributes to an overall management strategy (e.g. EBM) has not been unequivocally established (Waigner & Boyd 2009).

To gain traction on this challenge we need to quantify the effects of coordination *per se* and thus its contribution in particular to natural resource management. Doing so requires quantifying and contrasting two scenarios: optimal coordinated management and optimal uncoordinated management. The former represents an advance toward EBM in that management decisions and actions are optimally structured and coordinated among sectors (e.g. different fisheries) for maximising the joint value of their individual ecosystem services (e.g. total landings). The latter scenario is characterised by uncoordinated yet still strategic single-sector management decisions and actions within an ecosystem – that is, management conditions and outcomes arising when the interconnected sectors are each trying to optimise their private values (e.g. individual yield). In addition to being the logical benchmark against which to measure the effects of coordination, this scenario and its comparison to coordinated management is of practical importance because lack of coordination among sectors is widely prevalent in the management of ecosystems and their resources. For example, in the Peruvian upwelling region of the Humboldt Current Large Marine Ecosystem management actions by the anchovy fishery and the anchovy-consuming seabird guano extraction industry are single-sector and nearly entirely uncoordinated in relation to the joint value of these sectors in the ecosystem (Jahncke *et al.* 2004). Likewise, in the Greater Yellowstone Ecosystem game management of predatory wolves and their prey ungulate species is also largely uncoordinated, to the detriment of the ecosystem's trophic structure and productivity (Singer *et al.* 1998; Hebblewhite *et al.* 2005; Wright *et al.* 2006; Beyer *et al.* 2007). In the California Current Marine Ecosystem fisheries management has shifted toward EBM with the recent implementation of a network of no-take marine reserves; however, outside the reserves, single-sector, uncoordinated management persists despite overlap and trophic interactions among species targeted by the different fisheries (e.g. CDFG 2011). In these examples management decisions and actions are strategic yet uncoordinated and driven by single-sector objectives without explicit regard for the joint social value of the ecosystem. To date, the question of how coordinated management would affect sector values – individually and jointly – and the ecological state of these and other renewable natural resource management systems, remains largely unanswered.

At first glance, quantifying uncoordinated natural resource management may seem just as difficult to measure as outcomes under optimal coordination. However, classic results from game theory reveal that uncoordinated management will often arrive at a Nash Equilibrium – a steady state from which no sector can improve its outcome by acting unilaterally (i.e. on its own) – when individual sector management decisions and actions are driven by single-sector objectives (Nash 1951). Further, the Nash Equilibrium occurs whether or not the sector managers ignore or explicitly account for the dynamics of other sectors and their interconnectedness, thereby providing broader generality in the utility of this method for characterising uncoordinated management scenarios. In the remainder of this article we describe how these insights can be used to quantify ecological effects of coordination, and its value to society and individual sectors, relative to outcomes under single-sector, uncoordinated management and other reference management conditions. First we outline a general analytical framework that can be applied to any ecosystem for objectively evaluating how coordination *per se* affects natural resource management decisions, ecosystem state and the provision of ecosystem services and payoffs to private sectors and the public. We focus on the heart of the framework, where management actions and outcomes are driven by sector objectives that critically depend on private versus societal gains under uncoordinated versus coordinated management, respectively. We then illustrate the framework using a generic 3-species/3-sector ecosystem model to begin to identify the ecological and socio-economic contexts where effects from coordination are greatest. To provide an estimate of the effects of coordination in a realistic scenario, we then integrate our analytical framework with an Ecosim model of the Northern California Current Marine Ecosystem (NCCME) and quantify effects of coordinated management among seven fisheries that otherwise compete amongst one another for catches of a suite of ecologically interacting fishery species.

METHODS

Analytical framework

Let $\mathbf{x}$ be the vector (possibly spatially explicit) of species abundances and dynamic abiotic variables that define the state of an ecosystem. Some of the elements of $\mathbf{x}$, which we call 'resources', are converted into ecosystem services by human actors. We assume that all actors that convert a particular resource into a particular service are uniformly managed, and call them a 'sector.' We define the collection of sector-specific management actions affecting the ecosystem as $\mathbf{H}$. The ecosystem dynamics depend on the current (and possibly past) states of the ecosystem and on the current management:

$$\frac{\partial \mathbf{x}}{\partial t} = g(\mathbf{X}, \mathbf{H}). \tag{1}$$

Under any management scenario the joint social value (i.e. the value to society) of an ecosystem is a function of the private payoffs to individual sectors in the ecosystem and the social value (reflecting society's preferences) of those payoffs:

$$\Pi = u\big(\pi_1(\mathbf{x}, \mathbf{H}), \pi_2(\mathbf{x}, \mathbf{H}) \ldots \pi_Q(\mathbf{x}, \mathbf{H})\big), \tag{2}$$

where $\pi_q(\cdot)$ is the private payoff to sector q in relation to the state of the ecosystem and management actions affecting it (including those converting resources into services); and $u(\cdot)$ is the joint social value in relation to all Q sectors' private values and societal preferences for those values (see Tallis *et al.* 2011 for a discussion of these metrics). For this analytical framework we present the above equations in their most generic forms because the relationship among resources, services, management actions, private payoffs and societal preferences in an ecosystem is likely nonlinear and dependent on context (Granek *et al.* 2010). For example, resources could be associated negatively (e.g. via competition and predation) or positively (e.g. via symbioses and indirect interactions), payoffs could be measured in profits for some sectors and conservation biomass for others, and the joint social value of an ecosystem could be a weighted sum of these payoffs.

Critical to the analysis is defining explicitly and differently for coordinated versus uncoordinated management how each sector's private objective depends on the actions of all sectors. Under uncoordinated management, each sector seeks to maximise its private payoff without regard for its effect on the joint social value of the ecosystem. That is, sector q chooses the set of I management actions, $\{H_{q,1}, H_{q,2}, \ldots H_{q,I}\}$, that maximises q's private objective, taking as given the state of the resources in the ecosystem and the management actions by the other sectors,

$$obj_q = \max_{\{H_{q,1},H_{q,2}\ldots H_{q,I}\}} \pi_q(\mathbf{x},\mathbf{H}).,\text{ given } \mathbf{x} \text{ and } (\{H_{k,1},H_{k,2},\ldots H_{k,I}\})\ \forall\ \mathrm{k} \neq \mathrm{q} \tag{3}$$

In economic terms, equations 3 and 2 indicate that the social value of a sector's payoff is exogenous to (i.e. separate from) the determination of the sector's objective function, even though it is endogenous (i.e. integral) to the calculation of the joint social value of the ecosystem, respectively. When applied simultaneously across all Q sectors, the objective function above represents a strategic game by the uncoordinated sectors in the ecosystem. One likely equilibrium (i.e. steady state) set of management actions among the sectors is termed the Nash equilibrium. At the Nash equilibrium no individual sector can increase its payoff by changing its management actions unilaterally (i.e. in the absence of changes by other sectors; Nash 1951).

When one sector's actions affect another sector's opportunities, coordination may have substantial value. Under coordinated management, each sector's decisions and actions are no longer driven solely by its private payoffs but instead by how the different sector's payoffs interact and, ultimately, contribute jointly to the social value of the ecosystem. Thus, the private objectives now match the social objective, and the sectors choose a coordinated set of management actions, $\mathbf{H}$, for achieving this single, shared objective of maximising joint social value in relation to the state of the ecosystem and the sectors' private payoffs:

$$obj_C = \max_{\mathbf{H}} u\big(\pi_1(\mathbf{x},\mathbf{H}).,\pi_2(\mathbf{x},\mathbf{H})\ldots.\pi_Q(\mathbf{x},\mathbf{H}).\big) \tag{4}$$

In economic terms, the social value of each sector's private payoff is now endogenous to both the sector's private objective function (obj_C) and the calculation of the value of the ecosystem (Π).

Under both uncoordinated (eqn 3) and coordinated (eqn 4) management the sector payoffs ($\{\pi_1(\cdot),\pi_2(\cdot),\ \ldots\ \pi_Q(\cdot)\}$) can be converted to social value using eqn 2. It then follows that the value of coordinated management to society is the change in the joint social value of the ecosystem between the two management scenarios. Furthermore, coordinated and uncoordinated management can be compared with a reference management scenario that is uncoordinated and sub-optimal in other features as well (e.g. open access, status quo). The contrast among the three types of management provides an indication of how much uncoordinated management (i.e. just fixing the other sub-optimal features) versus coordinated management increase the value of the ecosystem, and thus how much coordination *per se* contributes to the total potential gains achievable over the reference. Also, individual sector preferences for or against coordinated management can be measured in relation to changes in private payoffs under coordinated management versus the uncoordinated Nash equilibrium.

Finally, while EBM in concept accounts for both market (e.g. economic; fishery profit) and non-market (e.g. conservation; fish biomass in the wild) factors affecting the value of an ecosystem, in practice the latter can be challenging to transform into sector payoffs and integrate with market factors for calculating an ecosystem's joint social value (Waigner & Boyd 2009). In such cases, effects of coordinated management among market-based sectors on non-market ecosystem properties important to EBM can be measured by comparing states of the ecosystem (eqn 1) under coordinated versus uncoordinated management. We explore these factors using the heuristic and Ecosim models below.

Heuristic model

Consider a simplified ecosystem comprised of two prey species that share common resources and a common predator, and three sectors, each harvesting a species. Resource interactions in the ecosystem include direct (via resource consumption) and indirect ('apparent', via predation) competition between the prey species, and consumption of the prey by the predator. Specifically, the predator exhibits a type II functional response, and the prey exhibit interspecific competition according to the Lotka-Volterra model, and logistic population growth in the absence of the predator. The two prey species naturally co-exist due to interspecific differences in intrinsic growth rates (R_1 and R_2) and predator capture rates (C_1 and C_2) that creates a tradeoff: if prey 2 has a lower growth rate ($R_1 > R_2$) then for coexistence to occur it must also be less susceptible to predation ($C_1 > C_2$). Normalisation of these values relative to prey species 1 (i.e. $R_1 = C_1 = 1$) enables rates R_2 and C_2 to characterise the ecosystem by defining the relative differences in growth and captures rates between the two prey species and determining all three species' natural equilibrium densities. In our assessment of the effects of coordination we considered a range of relative interaction strengths that represents 35 different 'ecosystems' with unique equilibrium prey and predator population densities (Fig. S1, Supporting Information [SI]).

Management actions were characterised by the level of exploitation (harvest rate) of each species by each sector. Each sector's private objective was to maximise long-term sustainable profit from harvest (i.e. at equilibrium), and the social objective was to maximise the sum of the three private sector profits. Profit to a sector was a function of revenue gained from yield, less the cost of harvest. Revenue to the prey species sectors was based on a fixed market price of \$1 per unit yield. Revenue to the predator sector was based on a slightly higher market price of \$1.4, reflecting a general increase in price by ~40% per trophic level (Pinnegar *et al.* 2006). We assumed marginal cost of harvest for each sector to depend inversely on the population density of its target species (the stock effect; Clark 1990), and for marginal profit of harvesting to decline to zero (i.e. marginal revenue, or price = marginal cost) when the species' population density is reduced to 10% its carrying capacity.

This heuristic model and the management scenario we analysed were chosen for two reasons. First, exact solutions could be derived for a diversity of ecosystems (i.e. combinations of R_2 and C_2 values), and across all combinations of harvest effort levels among the sectors (see SI for analytical equations; Abrams 1999). Consequently, it was feasible to quantify management outcomes across a variety of ecological and economic conditions in a reasonable amount of time. Second, while the model and management scenario are simple in comparison with the full dynamics in real ecosystems, they are sufficiently general to apply to the management of interacting prey and predator species in a variety of ecosystems. For example, fishery management of marine fish and invertebrate species (e.g. forage fish prey and a tuna predator; urchin prey and a lobster predator), game management of terrestrial species (e.g. ungulate prey and a wolf predator, as occurs in two western US States and may soon occur in a third; WGFD 2009; IDFG 2011; MFWP 2011), and agricultural pest control management in relation to parasite-parasitoid populations dynamics (Murdoch *et al.* 2006; Payne *et al.* 2011). A detailed description of the model, with equations, is presented in the SI.

To identify the Nash equilibrium under uncoordinated management, an exhaustive search was performed to identify the combination of management actions (i.e. harvest rates for each sector) that generated private equilibrium profits to each sector that could not be increased by a unilateral change in the sector's level of harvest. That is, at the Nash each sector was doing the best it can, given the actions of the other sectors and the parameter values defining the ecosystem. Given this solution the private profits to each sector and the cumulative sector profit – the joint social value of the ecosystem – were calculated and defined as $\{_H\pi^U_{q=\text{Prey1}}, {}_H\pi^U_{q=\text{Prey2}}, H\pi^U_{q=\text{Pred}}\}and_H\Pi^U$, respectively. Fixed-point iteration, typically reserved for more complex problems, was also used to identify the Nash equilibrium. Under this approach, the management actions of all but one sector were fixed, with the remaining sector choosing the management action that maximised its profit. The process was replicated for each sector, and then repeated in its entirety until there were no changes in sector management actions. Fixed-point iteration was applied using multiple initial management action and starting order conditions to verify convergence. The same solution was found to that produced using the exhaustive search, strongly suggesting that the Nash Equilibrium is unique.

For identifying outcomes under coordinated management, an exhaustive search was performed to identify the optimal combination of management actions that maximised the joint social value of the ecosystem (cumulative equilibrium profit). The same solution was also found via fixed-point iteration with all of the sectors focused on a common objective of maximising joint social value. Given this solution, the private payoff to each sector and the joint social value of the ecosystem were calculated and defined as $\{_H\pi^C_{q=Prey1}, {}_H\pi^C_{q=Prey2}, {}_H\pi^C_{q=Pred}\}and_H\Pi^C$, respectively.

We also used the heuristic model to estimate how much coordination contributes toward the total value gained when management is improved over a reference strategy that is both uncoordinated and with sub-optimal single-sector decision-making and actions. For this analysis, we set the reference as uncoordinated common pool (open access) management, where each sector harvests excessively until profits are reduced to zero (Gordon 1954). Common pool management represents an extreme reference above which even optimal uncoordinated management is expected to be a major improvement; thus in choosing this reference we are able to calculate a lower bound of how much coordination *per se* improves joint social value above that already accomplished via uncoordinated management. The proportional contribution from coordination would be expected to be larger when compared with less extreme, potentially more realistic, sub-optimal references management approaches that are closer in outcomes to optimal uncoordinated management.

Finally, coordinated natural resource management is not necessarily expected to increase conservation (e.g. certain species' population levels may be 'overexploited' to increase populations of others; Christensen & Walters 2004) especially when non-market factors such as species biomass in the wild are not explicitly represented by sector payoffs and the joint social value of the ecosystem. Accordingly, using our model we compared species biomass levels under uncoordinated versus coordinated management to test how coordinated management of market-based resources affects conservation outcomes.

Ecosim model

To estimate effects of coordinated management in a complex, realistic scenario we integrated our analytical framework with a dynamic food web model, 'Ecosim' (Christensen & Walters 2004), parameterised for the Northern Californian Current Marine Ecosystem (NCCME; Field 2004; Field *et al.* 2006). The NCCME is an eastern boundary current upwelling zone on the Western coast of the USA. The model covers ~70 000 km^2 of nearshore waters and supports several major fisheries for pelagic and demersal fish and invertebrates. The Ecosim modelling approach represents biomass dynamics of functionally equivalent groups of species, ranging from primary producers to top predators. Ecosim has been used widely for modelling marine food webs and for addressing questions about EBM (e.g. Christensen & Walters 2004; Smith *et al.* 2011). The NCCME model has 60 living functional groups, with the greatest taxonomic resolution for marine mammals and demersal and pelagic fish. Key fishery species include rockfish, hake, crab, flatfish, shrimp and salmon. There are seven fishing sectors: bottom trawl; shrimp trawl; hake trawl; line, pot and trap; salmon; crab pot; and other small fisheries (Table S1). All but the crab pot sector target multiple species. The model has been used extensively and is well accepted in the literature (cited 43 times to date), and its dynamics have been shown to produce realistic representations of biological time-series data for the California Current from the 1960s to the 2000s for a number of commercially important species and marine mammals (Field *et al.* 2006).

Management actions were characterised by the level of annual fishing effort by each sector. Annual yield to each sector was proportional to fishing effort, the current biomass of its target species and harvest efficiency. We measured each sector's private payoff as its equilibrium annual revenue per km^2, equal to species-specific equilibrium annual yields per km^2 times their market prices (Table S2). The joint social value of the ecosystem was set as the sum of the sector equilibrium revenues.

We used fixed-point iteration to identify the Nash equilibrium under uncoordinated management. As with in the heuristic model, multiple initial fishing effort and starting order conditions were conducted to verify convergence to a unique Nash equilibrium. We used a hill climbing algorithm to identify fishery effort levels under coordinated management that maximised the joint social value of the ecosystem. Private sector payoffs (revenues) and cumulative sector payoffs (joint social value) under uncoordinated and coordinated management were defined as $\{_E\pi^U_{q=1}, _E\pi^U_{q=2}, \ldots _E\pi^U_{q=7}\}$ and $_E\Pi^U$, and $\{_E\pi^C_{q=1}, _E\pi^C_{q=2}, \ldots _E\pi^C_{q=7}\}$ and $_E\Pi^C$, respectively.

We also used the Ecosim model to estimate how coordinated versus uncoordinated management affects private payoffs and the joint social value relative to outcomes generated under current (2004 status quo) fishing effort conditions (Field *et al.* 2006; see SI). Here, we chose status quo as the reference management strategy to provide realistic estimates of how much coordination actually would contribute to the expected overall gain in joint social value if fishery management of the NCCME was reformed.

We quantified the effects of moving from uncoordinated to coordinated management on key indicators of conservation value, including biomass of high trophic level groups (trophic level > 4), low-trophic level forage groups (Smith *et al.* 2011), fished groups, marine mammals, seabirds and fishery discards.

Finally, a key source of uncertainty about many ecosystems (Sinclair *et al.* 2003; Litzow & Ciannelli 2007), and in the Ecosim model in particular, is the level of predation interaction strength among species, which influences the level of trophic coupling in the food web. To account for sensitivity of our results to this uncertainty we replicated our analysis and compared results under both strong and weak predation interaction model settings. Further details about the Ecosim model and our analysis are provided in the SI.

RESULTS

The joint social value of coordination, quantified as the percentage change in cumulative sector profit (heuristic model) or revenue (Ecosim model) under coordinated (C) versus uncoordinated (U) management actions among the sectors ($100[(C–U)/U]$), ranged 13–232% across 35 ecosystems in the 3-species/3-sector heuristic model (Fig. 1a), and 42–130% across predation interaction strengths in the 60-species/7-sector Ecosim model (Fig. 2). The heuristic model revealed the value of coordination to be highly sensitive to relative differences in prey growth rate (R_2), reaching maximum values near the upper and lower bounds of relative growth rate values that allowed natural (unharvested) coexistence among all three species in the ecosystem. In the Ecosim model, the value of coordination was greatest with the strong predation interactions, which generated high trophic coupling among species dynamics in the food web.

In contrast to the consistent positive effects on the joint social value of the ecosystem, coordinated management led to both increases and decreases in private payoffs to individual sectors. Across the 35 ecosystems evaluated with the heuristic model, increases in private payoffs varied from a few percent to 610%, but only occurred for the predator and prey 1 sectors (Fig. 1b–d). Conversely, no sector was immune to negative effects of coordination, and in all cases a reduction was characterised by complete loss in profit to zero for the sector. Overall, there were more reductions (43) than increases (35) in private payoffs. In several ecosystems profit to the prey 2 sector, whose species had a slower growth rate than the other prey species, was zero under both forms of management, resulting in a zero effect of coordination on the sector's payoff. Overall, changes (positive or negative) in sectors' private payoffs were typically greatest near the parameter boundaries for natural coexistence. Finally, the private value of coordination was typically largest to sectors with the highest private payoffs under uncoordinated management (Fig. S2a).

The Ecosim model produced similar patterns: increases in private payoff to sectors ranged 5–189%, but only occurred for three of the seven sectors in the ecosystem (Fig. 2). Of the remaining 4 sectors that suffered reductions, up to 3 experienced 100% losses in revenue. For every sector, the absolute change in private payoff due to coordination was greatest under the strong predation scenario. Private gains from coordination were typically correlated with the sector's payoff under uncoordinated management (Fig. S2b).

When coordinated management was compared with open access, effects of coordination *per se* (i.e. $(C–U)/(C–OA)$) were 12–70% of the overall gain in the joint social value of the ecosystem for the heuristic model (Fig. 3a). Unsurprisingly, the gains from coordination were greatest near the perimeter of the coexistence parameter space where the value of coordinated over uncoordinated management was highest. The uncoordinated Nash equilibrium, while inferior to coordinated management, never reduced the value of an ecosystem to the level generated under open access management. In several of the evaluated ecosystems the percentage contribution from coordination exceeded 50%, indicating in those cases that optimal uncoordinated decision-making, although strategic by each sector, generated relatively minor gains over open access compared with those due to coordination.

In the Ecosim model, uncoordinated fishery management of the NCCME generated relatively minor gains in joint social value over that achieved by status quo management ($(U–SQ)/SQ$ = 12–13%), regardless of predation interaction strength (Fig. 3b, black bars). Conversely, gains from coordination over status quo were large ($(C–SQ)/SQ$ > 60%) and greatest (158%) when predation interactions were strong (Fig. 3b, white bars). The consistently small gain from optimal uncoordinated management indicates that existing fisheries management in the NCCME is approaching the limits of uncoordinated approaches. The large gains over status quo from coordination indicate that the joint social value – at least in regard to fisheries – of the NCCME could be improved substantially if coordinated, logically structured fishery management decisions and actions were adopted and implemented.

Coordinated management precipitated strong ecological changes in the ecosystems with divergent conservation implications. Relative to uncoordinated management, coordination increased total species biomass in less than half (13/35) of the 3-species heuristic ecosystems (Fig. 4a). However, the largest absolute change in total biomass observed (150%) was positive, and the average biomass change across the ecosystems was positive (5%). Species-specific gains in biomass were limited to the prey 1 and predator species only (Fig. 4b-d). Prey 1 had a higher growth rate and predator capture rate than prey 2; thus it was the more profitable of the two prey sectors and provided greater indirect value to the predator sector. The predator species had the highest market price, but for persistence required trophic support from at least one of the prey species populations. As a result, prey 1 biomass was allowed to increase across a majority of ecosystems (20/35), albeit with high variability (18–404%), or was limited to relatively minor losses (2–33%) (Fig. 4b). When joint social value is maximised by maximising payoff to the predator sector (in 3/35 ecosystems, Fig. 1d), coordination generated large increases in predator biomass (~750%, Fig. 4d); otherwise the predator was driven extinct (100% loss in biomass) to minimise its impact on the prey 1 species and sector. Prey 2, which competed with but grew more slowly than the prey 1 population and which provided less per capita trophic support to the predator population, persisted (albeit at low,

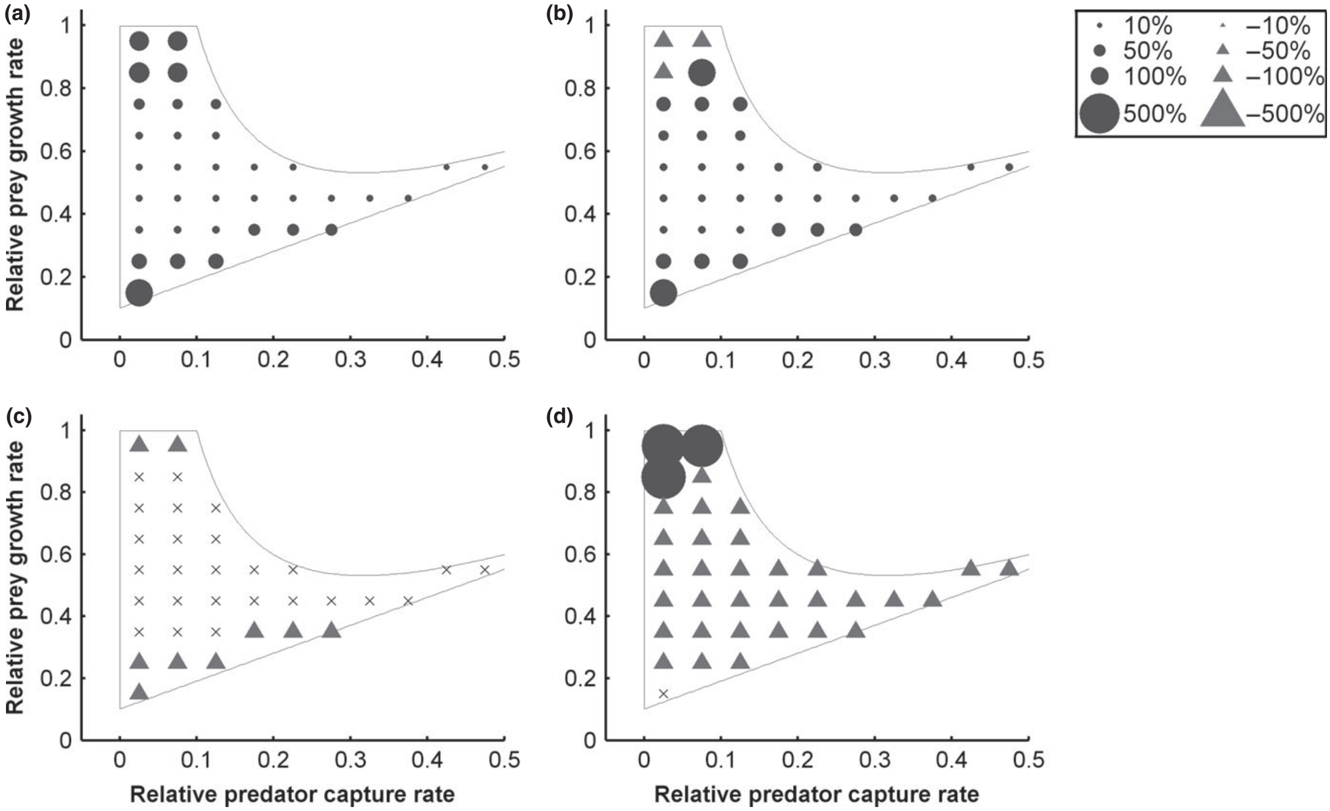

Figure 1 The value of coordinated management, measured as the percentage change over uncoordinated management, in each of 35 3-species/3-sector ecosystems (heuristic model). Relative prey growth and predator capture rates describe R_2 and C_2, respectively, given $R_1 = C_1 = 1$. (a) The value of coordination to the joint social value of the ecosystem (${}_H\Pi$; 13–232%). The value of coordination to private sectors, ${}_H\Pi_q$: prey 1 [−100–240%, (b)], prey 2 [−100% or 0%, (c)], and predator [−100–610%, (d)]. The legend applies to all panels. Zero change in value is indicated with an 'X'.

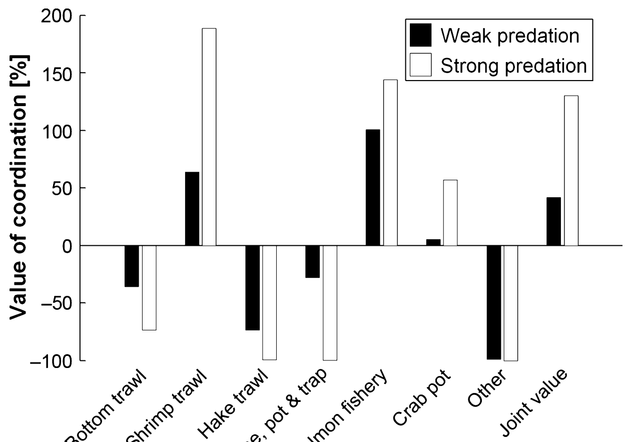

Figure 2 The value of coordination to individual fishery sectors (${}_E\Pi_q$) and the joint social value (${}_E\Pi$) in the Northern California Current Marine Ecosystem (Ecosim model), given weak and strong predation interactions.

typically unprofitable levels) under uncoordinated management in 31/35 ecosystems, but was invariably driven extinct under coordinated management to maximise the total profits in the ecosystem (Fig. 4c).

The Ecosim model predicted similarly mixed effects of coordinated fishery management on key conservation indicator groups in the NCCME (Fig. 5). Biomass of high trophic-level species declined the most dramatically (52–66%), mainly due to increased fishing pressure on salmon, a high-value high-trophic level fishery species. Coordinated fishery management increased the biomass of low trophic level groups (i.e. forage fish) – in large part due to increased fishing pressure on hake, a major predator of forage fish, to reduce hake populations and provide more forage fish prey for salmon to support the salmon fishery. The increase in prey under coordination also improved biomass of predatory marine mammal and seabird species. However, coordination generated a dramatic increase in fishery discards (by-catch), mainly due to increased bottom, hake and shrimp trawling effort.

DISCUSSION

By using the Nash equilibrium to identify optimal uncoordinated management among interacting sectors, we have isolated ecological and economic responses to coordinated management *per se*, eliminating the confounding effects of non-optimal reference scenarios. Through two case studies, we found that the benefits of coordination depend on the ecology of the interacting species, being greatest when the community is close to a coexistence boundary or when interaction strengths are large. Furthermore, we found that coordination can have substantial and sometimes unexpected ecological effects, including strategic simplification of the food web and both positive and negative impacts on non-target species. Although coordination always increased the total economic benefits across all sectors combined, there was always at least one sector that suffered losses (sometimes substantial) in profit or revenue.

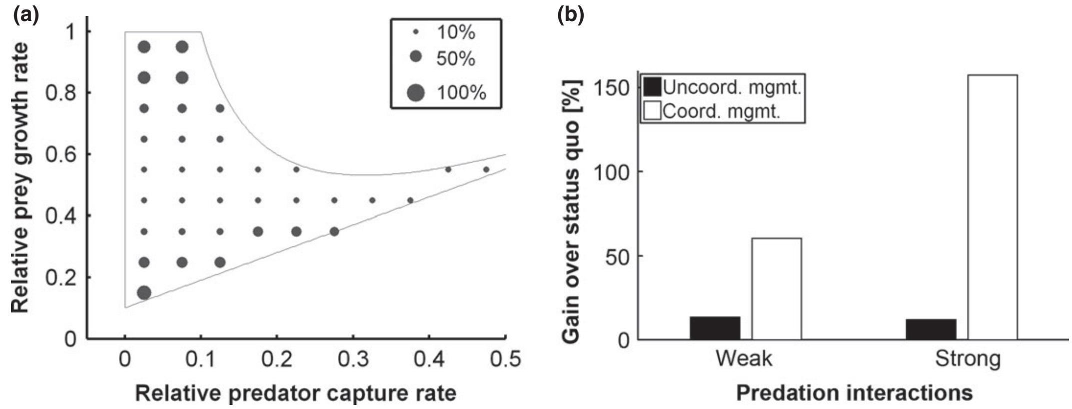

Figure 3 Gains in joint social value from coordinated and uncoordinated management over reference management strategies. (a) Gain from coordination in particular relative to the total increase achieved when management is converted from open access to coordinated management, in each of 35 3-species ecosystems (heuristic model). (b) Total gains from uncoordinated and coordinated fishery management over outcomes from status quo fishery effort conditions in the Northern California Current Marine Ecosystem (Ecosim model), given weak and strong predation interactions.

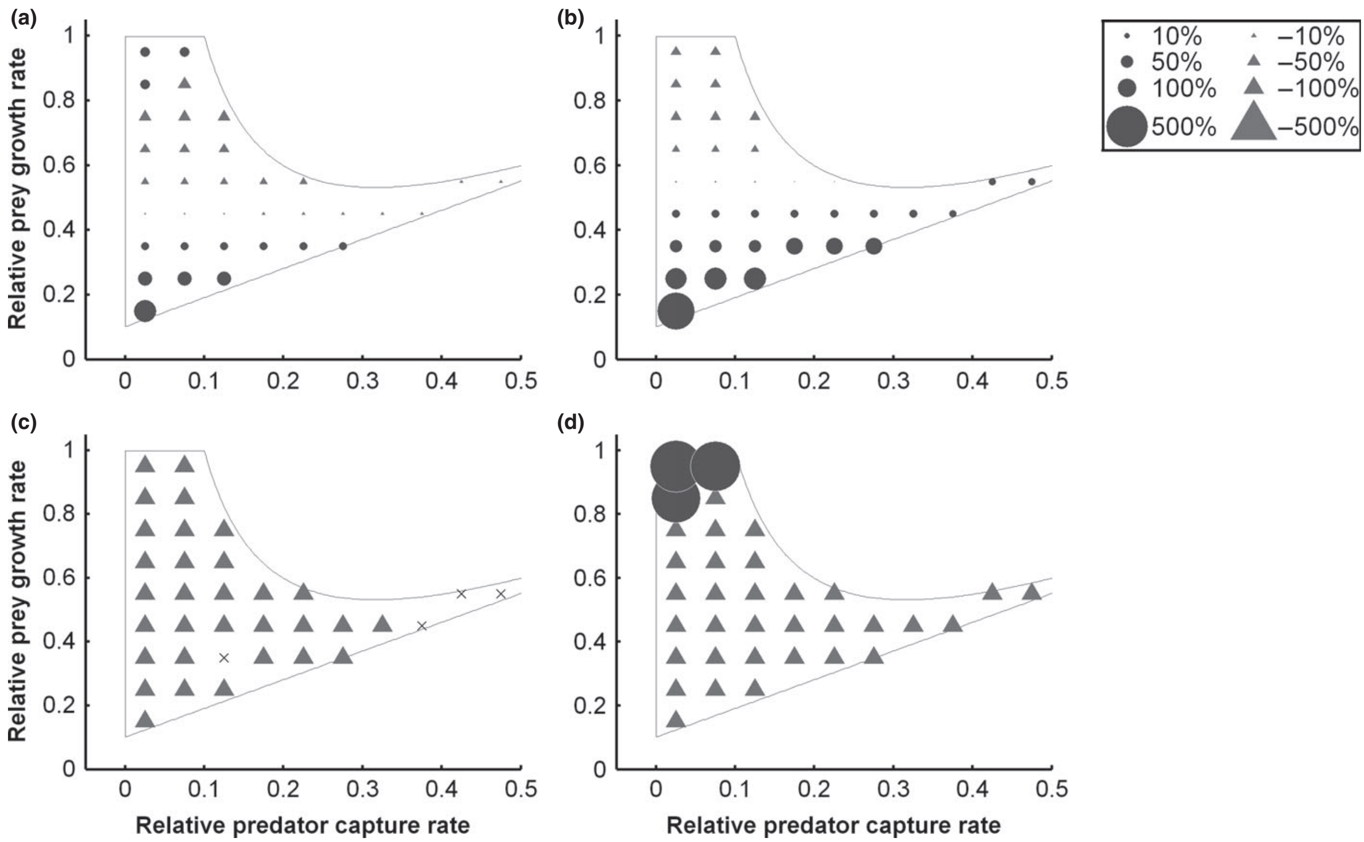

Figure 4 Conservation effect of coordinated management on species biomass in each of 35 3-species ecosystems (heuristic model). Percentage changes in cumulative (a), prey 1 (b), prey 2 (c), and predator (d) biomass. The legend applies to all panels. Zero change in value is indicated with an 'X'.

The greatest gains from coordination occurred when management could most easily affect species' population levels and maximise particular sector payoffs. In the heuristic model harvest effort directly mediated the natural growth rates of the prey species (i.e. F reduced R for each species), and relative levels of growth determined species coexistence and thus strongly influenced ecosystem-level population dynamics. Consequently, gains from coordination were greatest when coexistence among all three species was already marginal and it was relatively easy for coordinated management to 'push' the system to a state of species exclusion that maximised the joint social value of the ecosystem via increased productivity of the remaining species. Similar ecosystem shifts have been observed when overfishing combines with marginal climate conditions to drive declines of one species and increases in another (Litzow & Ciannelli 2007). These dynamics explain why the value of coordination was greatest in ecosystems with high or low R_2 values. In the Ecosim model, gains from coordination

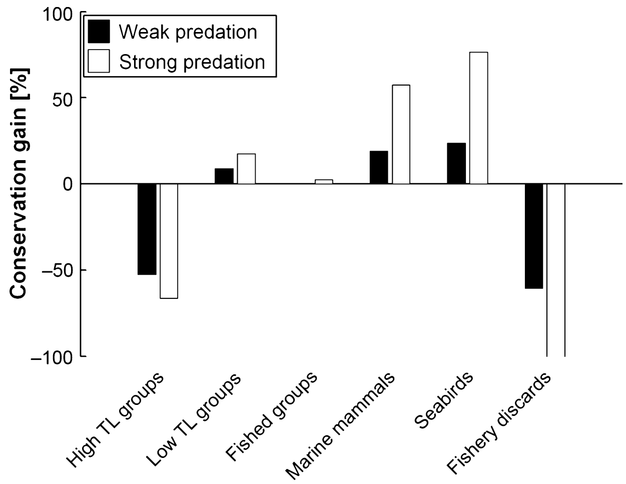

Figure 5 Gains in key conservation indicators due to coordinated management of fisheries in the Northern California Current Marine Ecosystem (Ecosim model), given weak and strong predation interactions. Positive percentages reflect increases in biomass in the wild, or decreases in fishery discards biomass (under strong predation, discards increased 235% [white bar cut]).

also were greatest when species interactions were most easily affected by management, in this case, under strong predation interaction parameter settings. Furthermore, the maximum value of coordination (130%) did not exceed that in the heuristic model (232%), which is unsurprising given that trophic coupling declines with ecosystem complexity as direct effects of consumption and productivity are spread throughout the food web (Polis & Strong 1996; Micheli 1999). Collectively these results suggest that coordinated management may be most beneficial in ecosystems having strong interspecific interactions among species near the margins of coexistence. Consequently, a variety of ecosystems having trophic cascades driven by bottom-up and/or top-down ecological forcing (e.g. terrestrial forest, freshwater stream and lake, and marine continental shelf, open ocean and benthic ecosystems) may be amenable to coordinated management (Estes & Duggins 1995; Pace *et al.* 1999; Shurin *et al.* 2002; Lafferty 2004; Casini *et al.* 2008; Baum & Worm 2009; Lindegren *et al.* 2011). However, for large ecosystems with weak or uncertain trophic coupling (e.g. NW Atlantic shelf; Link 2002), the value of coordination should not be discounted without formal analysis, because in general the joint social value under uncoordinated management declines with increasing number of sectors in the ecosystem (because costs of not coordinating are dissipated; Snidal 1985). This, in part, explains why the Ecosim model, with 7 interacting sectors, still revealed considerable value from coordination even with weak predation interactions. In the extreme, if an ecosystem's resources are divided among an unlimited number of sectors, the Nash equilibrium would be expected to degrade to the 'tragedy of the commons' where the resources are invariably squandered to a fraction of the value attainable through coordinated management (Cornes & Sandler 1983).

In both models, and across all ecosystems evaluated, coordinated management never produced a 'win-win' solution, even though society as a whole always gained. This contrasts with the classic game theoretic Prisoner's Dilemma (Poundstone 1992). The classical Prisoner's Dilemma represents a perfectly symmetrical system where there is no difference between the sectors, their options, and the payoffs from those options. In our models species have different demographic traits and asymmetric interactions (e.g. between predator and prey), and prices vary among species the sectors target. Such asymmetry in the ecosystem results in coordination being characterised by different actions among the sectors – not all of whom directly benefit – for maximising the joint social value (Snidal 1985; Wang *et al.* 2010). In economic terms, coordination is generally not Pareto-improving (i.e. harmful to no one) when sectors are asymmetrical (Hutton *et al.* 2001; Erdlenbruch *et al.* 2008). Accordingly, asymmetry in our models led coordinated management to focus on particular high-growth species (e.g. prey 1 over prey 2) and high-value sectors (e.g. shrimp, salmon) to the detriment of others. Similarly, in the context of land-use acquisition, coordination produces win-lose outcomes when sectors are constrained to asymmetrical decision-making rules (Bode *et al.* 2011). Hence, asymmetry has important implications for the political viability of coordinated natural resource management in ecosystems. Ecosystem-based approaches to management can fail due to political stalemates among sectors who derive different private benefits from coordination (Hoel 1998; Granek *et al.* 2010). This challenge to EBM, and the observation here that sector losses in private payoffs due to coordination are common and sometimes large (100%), highlights the importance in quantifying coordination's expected impacts on private payoffs prior to its implementation. Successful coordinated management may require reconciling the increase in joint social value with grievances by sectors expected to experience decreased private payoffs; e.g. with transfer payments or other ways of sharing the overall gains among the sectors (Sumaila 2005).

Asymmetry in natural ecosystems also means that some sectors may gain substantially from coordinated management (e.g. 101% for the salmon fishery, given weak predation interactions) even when the societal gains are only modest (42%; Fig. 2). Further, the more prosperous sectors under uncoordinated management typically benefited the most from coordination (Fig. S2). Consequently, such sectors may selfishly and effectively advocate for coordination – individually, cooperatively or potentially in collusion – even though from a societal perspective the cost of retrofitting management may not be worthwhile (Schattschneider 1960; Cowen & Sutter 1999; Baumgartner *et al.* 2009; Bode *et al.* 2011). This discrepancy between private and public values of coordination, and its association with sector prosperity that could be used for pro-coordination lobbying, emphasises the importance of quantifying EBM policies *a priori* to their potential implementation, and of transparency in the political processes shaping these policies, to ensure that they are chosen appropriately and designed optimally.

Many natural resource management scenarios today are uncoordinated and sub-optimal in other ways (e.g. poorly enforced, or with too many participants in each sector); making them more ecosystem-based would involve fixing these factors and implementing coordination. Our consideration of two such reference management strategies – open access and status quo – revealed that coordination can be a major contributor to the overall gains from an ecosystem-based transformation. In the Ecosim model in particular, strategic uncoordinated management did little to elevate the joint social value over the status quo. By comparison, coordination substantially increased the value of the ecosystem, contributing up to an order of magnitude more than uncoordinated management did over status quo. These results provide quantitative support for previous assertions that coordinated management is one of the key, defining process of EBM that generates its success over non-EBM approaches (Slocombe 1993, 1998; Rosenberg & McLeod 2005; McLeod & Leslie 2009).

We focused on economic payoffs to sectors from resource extraction, while conceding that a comprehensive calculation of joint social value would include non-market resources such as ecological properties and conservation. Market and non-market resources can in theory be integrated into our analytical framework. However, formulating payoffs from intrinsic values of non-market factors is challenging (White *et al.* 2012), as is modelling how non-market-based sectors interact with and affect market-based sector payoffs (e.g. how conservation interests interact with extraction industry interests to affect environmental regulations). In the absence of an explicit characterisation of these complex dynamics, an evaluation of the effects of coordinated management among market-based sectors on non-market ecosystem conditions can provide an initial understanding of the impact of an economically focused EBM policy on the ecological properties and intrinsic value of an ecosystem. In this study, we evaluated non-market conservation indicators that were not an explicit part of the uncoordinated and coordinated management objective functions, and showed mixed effects from coordination. In the heuristic model the most striking effect was a loss in species diversity (richness), despite an average increase in total species biomass across the evaluated ecosystems. In the Ecosim model, coordination did not compromise diversity but did severely impact several high biomass predatory fish species due to increased fishing pressure. Also, increased trawling substantially increased fishery discards, a major cause of conservation concern. Nonetheless, marine mammal and seabird species thrived under coordinated management due to their increased trophic support from more forage fish in the ecosystem. In this case economic and conservation interests were aligned in protecting low trophic level species to increase growth of predator species populations higher up the food chain (Smith *et al.* 2011). Overall, the results indicate that coordinated natural resource extraction actions can generate strong ecological impacts that both compromise and enhance conservation. Importantly, if these conservation values were explicitly included in the objective functions, we could have obtained very different results. Future research is needed that explicitly considers how conservation regulations (e.g. minimum allowable biomass levels) affect the efficacy of coordinated management, and that more directly incorporates the payoffs and actions of conservation sectors into the optimisation framework.

Our case study models were deterministic (i.e. they did not include stochasticity), and we focused on maximising equilibrium payoffs (sustainable annual sector profit and revenue), rather than some (discounted) present value of payoffs generated along a transient trajectory starting from a particular initial condition. In that setting, our evaluation of equilibrium static controls (i.e. constant harvest levels) captures expected sector decisions. Further, our focus on strategic sectoral games at equilibrium aligns with a key assumption of the Nash equilibrium: sectors know, or can learn, how to optimally respond to the ecosystem and each others' actions (Myerson 1999). Alternatively, consideration of temporally variable ecosystem dynamics (e.g. driven by El Niño Southern Oscillation) and/or management objectives (e.g. rebuilding of a collapsed stock) would require optimisation over a temporally dynamic game. In theory our general analytical framework is just as applicable to these more complex dynamics, although in practice deriving the solutions for estimating effects of coordination is more challenging (Levhari & Mirman 1980). However, notwithstanding the Nash equilibrium's limited ability to precisely predict dynamic human behaviours and ecosystem conditions (but see Goldburg 1994), its simplicity and explicitness maintain its utility for analysing social institutions (e.g. renewable natural resource management) and evaluating proposals for institutional reform (e.g. ecosystem-based management) across a diversity of systems (Myerson 1999). In the context of this perspective, integration of the tractable and explicit Nash equilibrium into our analytical framework generates approximate but quantitative and thus testable conclusions on the effects of coordination in different case study ecosystem scenarios.

Overall, this study suggests that coordinated management is a critical component of EBM's ability to substantially enhance an ecosystem's value to society. However, our results also temper societal expectations that coordination is a panacea that will always vastly improve joint social value at no cost. Our case studies also revealed interesting interactions between ecology and coordinated management, although the generality of those patterns remains to be seen. Application of our framework to other case studies with different dynamics, inclusion of more sectors, consideration of transaction costs of coordination and uncertainty in socioeconomic factors affecting sector decisions, and contrasts with empirical studies, will help identify ecosystem and socioeconomic conditions under which coordination is of critical importance for achieving management objectives.

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AUTHORSHIP

CW and CC formulated the basic theory and constructed the analytical framework. CW and BK conducted the heuristic case study analysis. CB and CW conducted the Northern California Current Marine Ecosystem case study analysis. CW wrote the first draft of the manuscript, and all four authors contributed substantially to revisions.

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