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Contributed Paper

Rapid assessment of management options for promoting stock rebuilding in data-poor species under climate change

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Abstract: The development of species recovery plans requires considering likely outcomes of different management interventions, but the complicating effects of climate change are rarely evaluated. We examined how qualitative network models (QNMs) can be deployed to support decision making when data, time, and funding limitations restrict use of more demanding quantitative methods. We used QNMs to evaluate management interventions intended to promote the rebuilding of a collapsed stock of blue king crab *(Paralithodes platypus)* (BKC) around the Pribilof Islands (eastern Bering Sea) to determine how their potential efficacy may change under climate change. Based on stakeholder input and a literature review, we constructed a QNM that described the life cycle of BKC, key ecological interactions, potential climate-change impacts, relative interaction strengths, and uncertainty in terms of interaction strengths and link presence. We performed sensitivity analyses to identify key sources of prediction uncertainty. Under a scenario of no climate change, predicted increases in BKC were reliable only when stock enhancement was implemented in a BKC hatchery-program scenario. However, when climate change was accounted for, the intervention could not counteract its adverse impacts, which had an overall negative effect on BKC. The remaining management scenarios related to changes in fishing effort on BKC predators. For those scenarios, BKC outcomes were unreliable, but climate change further decreased the probability of observing recovery. Including information on relative interaction strengths increased the likelihood of predicting positive outcomes for BKC approximately 5–50% under the management scenarios. The largest gains in prediction precision will be made by reducing uncertainty associated with ecological interactions between adult BKC and red king crab *(Paralithodes camtschaticus)*. Qualitative network models are useful options when data are limited, but they remain underutilized in conservation.

Keywords: conceptual model, loop analysis, ocean acidification, *Paralithodes platypus*, qualitative network models, species recovery

Evaluación Rápida de las Opciones de Manejo para la Promoción de la Recuperación de Especies con Deficiencia de Datos bajo el Cambio Climático

Resumen: El desarrollo de los planes de recuperación de especies requiere de la consideración de los resultados probables de las diferentes intervenciones de manejo, pero los efectos agravantes del cambio climático rara vez

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están incluidos en esta evaluación. Examinamos cómo los modelos cualitativos de redes (QNMs) pueden implementarse para apoyar la toma de decisiones cuando los datos, el tiempo y el financiamiento sufren limitaciones que restringen el uso de métodos cuantitativos más demandantes. Usamos los QNMs para evaluar las intervenciones de manejo con la intención de promover el repoblamiento del colapsado cangrejo rey azul (*Paralithodes platypus*) (BKC) alrededor de las islas Pribilof (oriente del Mar de Bering) y así determinar cómo su eficiencia potencial puede modificarse bajo el cambio climático. Con base en aportaciones de los grupos de interés y una revisión bibliográfica construimos una QNM que describía el ciclo de vida del BKC, sus interacciones ecológicas importantes, impactos potenciales del cambio climático, fortalezas relativas de interacción, y la incertidumbre en relación con las fortalezas de interacción y la presencia de vínculos. Realizamos análisis de sensibilidad para identificar las fuentes clave de incertidumbre en la predicción. Bajo un escenario de ausencia de cambio climático, los incrementos pronosticados en la población de BKC fueron confiables solamente cuando el reforzamiento de la población se realizó en un escenario de programa de cultivo de BKC. Sin embargo, cuando se incluyó el cambio climático, la intervención de conservación no pudo contrarrestar los impactos adversos del cambio climático, lo cual tuvo un efecto negativo generalizado sobre los BKC. Los escenarios de manejo restantes estuvieron relacionados con los cambios en los esfuerzos de pesca sobre los depredadores del BKC. Para los estos últimos escenarios, los resultados de la población de BKC no fueron confiables, pero el cambio climático disminuyó todavía más la probabilidad de observar una recuperación. La inclusión de información sobre las fortalezas relativas de interacción incrementó la posibilidad de predecir los resultados de la población de BKC en ∼ 5 – 50% bajo los escenarios de manejo. Las mayores ganancias en la precisión de la predicción se lograrán reduciendo la incertidumbre asociada con las interacciones ecológicas entre los BKC adultos y el cangrejo rey rojo (*Paralithodes camtschaticus*). Los modelos cualitativos de redes son opciones útiles cuando los datos son limitados, pero permanecen subutilizados en la conservación.

Palabras clave: acidificación oceánica, análisis de ciclos, modelo conceptual, modelos cualitativos de redes, recuperación de especies, *Paralithodes platypus*

摘要: 制定物种恢复计划时需要考虑不同管理干预措施可能产生的结果, 但气候变化在其中的复杂影响仍很少得到评估。我们研究了当数据、时间和资金方面的限制导致严格的定量方法使用受限时, 应如何利用定性网络模型来支持决策。本研究用定性网络模型评估了旨在促进普里比洛夫群岛周围 (白令海东部) 蓝帝王蟹 (*Paralithodes platypus*) 崩溃种群重建的管理干预措施, 以确定这类方法在气候变化背景下的潜在效果。基于利益相关者提供的信息和文献综述, 我们构建了一个定性网络模型, 来描述蓝帝王蟹的生命周期、关键生态互作、潜在的气候变化影响、相关互作强度, 以及互作强度和连接的不确定性, 并通过敏感性分析确定了预测不确定性的主要来源。结果表明, 在不考虑气候变化的情况下, 只有实施蓝帝王蟹孵化项目带来种群增长时, 预测结果才显示出可靠的种群数量上升。但考虑气候变化的情况下, 干预措施并不能抵消气候变化的不利影响, 蓝帝王蟹总体上仍受到负面影响。其余管理情景还与对蓝帝王蟹捕食者的捕捞量变化有关, 虽然它们预测的蓝帝王蟹保护结果并不可靠, 但气候变化还是会进一步降低物种恢复的可能性。加入相关互作强度的信息可以使管理情景下预测蓝帝王蟹有效恢复的可能性增长约 5-50%。减少成年蓝帝王蟹与红帝王蟹 (*Paralithodes camtschaticus*) 之间生态互作的不确定性可以最大程度地提升预测精度。定性网络模型在数据有限的情况下十分有用, 但在保护中尚未得到充分利用。【**翻译: 胡怡思; 审校: 聂永刚**】

关键词: 物种恢复, 海洋酸化, 概念模型, 定性网络模型, 回路分析, 蓝帝王蟹 (*Paralithodes platypus*)

Introduction

Managers are increasingly charged with recovering species of conservation concern that face multiple threats and may require the implementation of several simultaneous interventions. In fished ecosystems, overharvest is a major concern and can result in stock collapse (e.g., Pinsky & Byler 2015). Although reductions in harvest mortality may improve stock status (Lotze et al. 2011), this is not always the case (Hutchings & Reynolds 2004; Worm et al. 2009). At low abundance levels, population dynamics may be dominated by depensatory natural mortality (Keith & Hutchings 2012) or shifts in food-web configuration, climate regime, or habitat quality can potentially hinder stock rebuilding (Hutchings & Reynolds 2004). Management interventions beyond harvest control may therefore be necessary for promoting recovery and require an ecosystem-based approach (Murawski 2010).

However, climate change is important when considering the long-term efficacy of different management interventions (Rahel et al. 2008; Bell et al. 2018). Ocean acidification (OA), warming, and shifts in oxygen levels may directly alter stock productivity by altering physiological rates and intrinsic (nonpredatory) natural mortality and indirectly through ecological pathways that propagate the direct impacts on climate sensitive species (Gilman et al. 2010; Pörtner & Peck 2010). Consequently, shifts in environmental conditions can alter the likelihood that recovery plans are successful (Bell et al. 2018) and may further complicate the ability to anticipate unintended outcomes from possible management interventions (Hulme 2005; Rahel et al. 2008). Modeling tools can help organize our current state of understanding, enable evaluation of risks and uncertainties associated with different potential climate impacts and management interventions, and facilitate transparency in developing conservation strategies (Addison et al. 2013).

Quantitative modeling approaches that address the implications of climate change for management are diverse and vary widely in terms of their capacity to represent ecological detail (Plagányi et al. 2011). Adoption of quantitative models can prove challenging, particularly in data-poor systems because in practice their scope and structure is often determined by data availability (Addison et al. 2013). If the resulting models depart substantially from the conceptual models held by stakeholders and decision makers or omit important social, economic, political or ecological considerations, they are less likely to be incorporated into the decision-making process (Addison et al. 2013). If poorly explained, the models may also be perceived as black boxes, further discouraging their use (Addison et al. 2013).

Alternatively, qualitative methods, such as qualitative network models (QNMs) (also known as loop analysis), can be used to predict management intervention outcomes under climate change (e.g., Harvey et al. 2016; Marzloff et al. 2016). At their core, QNMs formalize conceptual models that resolve the key variables composing the system of interest, and links between variables are specified based on known, assumed, or hypothesized causal relationships (Levins 1998). The mathematical form of the relationships between any pair of variables need not be specified; only the sign of change (i.e., positive, neutral, or negative) that an increase in the level of 1 variable causes in another is specified (Puccia & Levins 1985; Levins 1998). A QNM is well suited to data-limited situations, straightforward to tailor based on the question at hand, and lends itself to visualization, which may improve transparency and permit closer scrutiny by and input from nontechnical audiences (Levins 1998; Harvey et al. 2016). Direct and indirect effects and feedbacks are integrated into model predictions that are qualitative in nature, but nonetheless useful for comparing the potential efficacy, risks, and trade-offs associated with different management interventions (e.g., Raymond et al. 2011; Harvey et al. 2016). The flexibility of QNMs permits representation of systems that span traditionally distinct disciplines (e.g., coupled social-ecological systems; Zador et al. 2017) as well as scenarios that include multiple stressors (e.g., Harvey et al. 2016; Marzloff et al. 2016).

We examined how QNMs can help support structured decision making by comparing possible outcomes of management interventions intended to promote recovery in the Pribilof Islands stock of blue king crab (BKC) (*Paralithodes platypus*) in the eastern Bering Sea. Following the initiation of a commercial BKC fishery in the 1970s, the stock rapidly declined and has remained at low levels since its first closure in 1988 (NPFMC 2018). After reopening the fishery for 1 season in 1998, the fishery has remained closed since 1999, and despite additional gear and effort restrictions aimed at reducing BKC bycatch mortality in other fisheries (details are given in the Supporting Information), the stock has not recovered. The reasons for the lack of recovery since the fishery closures are not fully understood. The decline has been partly attributed to a shift in climate from cooler to warmer conditions and an increase in predators of king crab species (Zheng & Kruse 2000), although high exploitation rates were almost certainly a contributing factor (NPFMC 2011). Other Bering Sea crab stocks also underwent steep declines during the same period in the late 1970s and early 1980s, but all have recovered to some extent since the late 1990s. The Pribilof Islands BKC stock, however, remains at historically low levels.

To date, in addition to closure of the directed fishery, management actions have focused on the reduction of Pribilof Island BKC bycatch in other fisheries. From 2009 to 2016, bycatch in Bering Sea groundfish fisheries averaged 263 crabs per year in an average of 1,100,000 hauls of fixed gear (pot and longline) and 55,000 hauls of trawl gear (NPFMC 2018). Other management interventions may be options for promoting recovery; however, warmer temperatures and lower seawater pH due to anthropogenic climate change are also anticipated in the eastern Bering Sea (Mathis et al. 2015; Hermann et al. 2019), which may also have direct and indirect effects on BKC. We compared the potential efficacy of different management-intervention scenarios on recovering BKC that were identified through engagement with stakeholder groups and evaluated how incorporating future climate change altered scenario outcomes.

Methods

Blue King Crab Conceptual Model

We developed a conceptual model of Pribilof Islands BKC to identify potential new management interventions for stock recovery and possible effects of future climate change (Fig. 1). In addition to performing a detailed literature review, we held workshops in 3 locations (Anchorage and St. Paul Island, Alaska, and Seattle, Washington). Participants included representatives of the Aleut community of St. Paul Island, the municipal government of St. Paul, local fishery associations, and scientists from academia, state, and federal agencies. At each workshop, we led discussions and exercises to cocreate conceptual models of BKC and described important BKC interactions with other benthic community members, interactions within the benthic community, and potential management intervention and climate-change scenarios. We synthesized information gained at these workshops into a composite conceptual model, which was cast as a signed directed graph (digraph), where links (graph

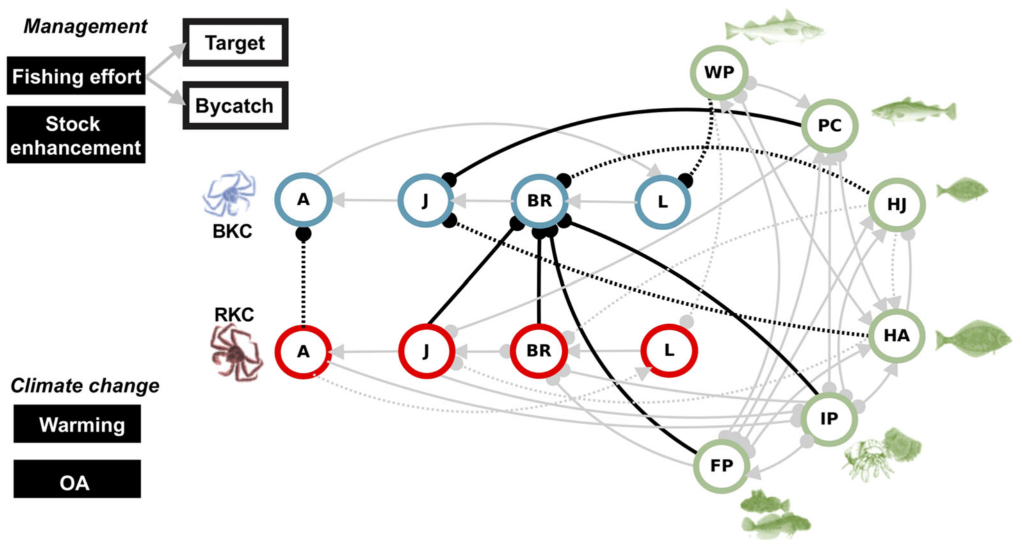

Figure 1. Interaction network for Pribilof Island blue king crab (BKC) (circles, species, life-history stages within a species, or functional group nodes; links terminating with an arrow, positive influence; links terminating with a dot, negative influence; black links, interactions with BKC nodes; gray links, interactions between all other nodes; rectangular nodes with black fill, management action [fishing effort, stock enhancement] or climate-change variables [ocean acidification, (OA); warming, ocean warming]; rectangles with white fill, fishing mortality rates of target and bycatch species; L, larval stage; BR, benthic recruit stage; J, juvenile stage; A, adult stage; RKC, red king crab; WP, walleye pollock; PC, Pacific cod; HJ, Pacific halibut juvenile; HA, Pacific halibut adults; IP, small invertebrate predators; FP, small fish predators). Rectangular nodes are linked to species nodes depending on the climate stressor and management intervention scenario (Table 1). All nodes have a negative self-interaction (not shown).

edges) connect system variables (graph vertices or nodes) and represent the sign of direct effects (Fig. 1). Full details of the species and life-history nodes included in the model and further information on the ecological, climate, and management-related nodes and links are summarized in the Supporting Information.

In addition to representing ecological interactions within the benthic community, the model also reflects the observation that recent BKC abundances are historically low and the belief of stakeholders that even moderate changes in BKC abundances are unlikely to numerically impact their prey or predators. That is, links representing effects of the various BKC life-history stages on other species nodes are not included in the model (Fig. 1). This and other assumptions (Fig. 1 & Supporting Information) can be revised, for instance, if BKC abundances reach ecologically relevant densities in the future; however, such exercises are outside the scope of this study.

We categorized links in the network as certain if they were known to occur with high confidence based on available data or participant knowledge and uncertain if evidence for their existence was limited or ambiguous or opinions were divergent (Supporting Information). For several pairs of links, information was available on their relative strengths from predation, temperature, and OA experiments (Supporting Information). This information was also retained and incorporated into model predictions. Following previous QNMs of ecological systems (e.g., Raymond et al. 2011; Harvey et al. 2016; Marzloff et al. 2016), we included negative self-interactions for all nodes to represent negative density-dependence or stabilizing feedback by variables outside the model (Puccia & Levins 1985). The life-history stages, species, and functional groups included in the final QNM represented our desire to generate a minimal realistic model that retained the essential behavior of the system with minimal complexity (Plagányi et al. 2014).

Qualitative Network Models

The conceptual model, when cast as a signed digraph, corresponds to the community matrix, which encapsulates all the pairwise per capita interactions between species in a system (Puccia & Levins 1985), and QNMs are based on analysis of the community matrix (Dambacher et al. 2002; Melbourne-Thomas et al. 2012). The value of elements composing the community matrix (interaction strength) represents the effect a small change in 1 variable (row) has on the per capita growth rate of another (column). Predicted changes in system equilibrium levels resulting from long-term effects of a press perturbation (defined as a sustained shift in the level of a variable) are obtained from the negative of the inverse community matrix (Puccia & Levins 1985). However, obtaining quantitative estimates of interaction strengths of community matrices for even simple systems can be difficult and labor intensive (Dambacher et al. 2002).

In QNMs, the sign of interactions is specified, but interaction strengths are sampled from uniform probability distributions that reflect vague priors (Melbourne-Thomas et al. 2012). Outcomes of the press perturbation are summarized across a large number of simulated community matrices. The general simulation framework also permits incorporating structural uncertainty (i.e., uncertainty in the presence or absence of links) into outcome predictions (Melbourne-Thomas et al. 2012).

The basic protocol proceeded as follows. First, for a specified model, the presence or absence of uncertain links was determined by drawing from a binomial probability distribution. The probability of drawing a present link was set to 0.5 following previous studies that have used the same approach to represent link uncertainty (Melbourne-Thomas et al. 2012). Next, elements for the corresponding community matrix were assigned values from a uniform probability distribution spanning 0.01–1 or −1 to −0.01, depending on the sign of the link. The realized community matrix was then checked against system stability criteria (Melbourne-Thomas et al. 2012). If stable, the system response to the press perturbation was calculated. If unstable, the matrix was discarded and a new matrix was drawn. For each press scenario, outcome uncertainty was described by summarizing sign responses from 10^4 stable community matrices. Percent-sign agreement was calculated as $100 \times |P - N|/T$, where T is the total number of stable community matrices and P and N are the number of positive and negative outcomes, respectively. Outcomes with 60–80% and >80% sign agreement were considered moderate and high sign agreement, respectively; outcomes <60% were considered inconsistent (e.g., Raymond et al. 2011). In QNMs, the level of sign agreement depends on the countervailing balance of feedback cycles (Dambacher et al. 2002). All else being equal, as the number of feedback cycles conveying positive and negative effects approaches similar values, ambiguity in the sign response increases (Dambacher et al. 2002).

We sought to also incorporate information on relative interaction strengths for several pairs of links (Supporting Information). In the simulation procedure, this was accomplished by drawing interaction strengths from uniform probability distributions as before, but interactions with inequality conditions were checked (all inequality conditions were set with respect to the per capita nature of the interaction strengths). If the conditions were met, the matrix was advanced. If not, interaction strengths were exchanged (i.e., they swapped locations in the community matrix) to comply with the inequality. The community matrix was then advanced to the next step where it was checked against system stability criteria. The method is computationally more efficient than simpler brute-force approaches that reject realized community matrices if inequality conditions are not met (e.g., Baker et al. 2018), but it produces the same results (within Monte Carlo error) (Supporting Information).

Perturbation Scenarios

We evaluated the response of BKC to scenarios that included the individual and simultaneous effects of different management interventions and climate-change impacts (Table 1). To date, BKC management has focused on bycatch reduction by restricting various fisheries in waters surrounding the Pribilof Islands that largely overlay the historical distribution of Pribilof Island BKC (see Supporting Information), but based on input received at the BKC workshops, 5 alternative management-intervention scenarios were identified for the region. First, reinitiate a Pacific cod pot fishery. A pot fishery targeting Pacific cod is resumed and adult red king crab (RKC) *(Paralithodes camtschaticus)* and BKC are bycatch. Second, increase Pacific halibut longline fishing effort. Fishing effort increases in the Pacific halibut longline fishery. Bycatch of other species does not change. Third, reinitiate a RKC pot fishery. A pot fishery targeting RKC adults is permitted, and adult BKC are bycatch. Fourth, reinitiate a groundfish trawl fishery. Trawl fisheries targeting walleye pollock and Pacific cod are permitted in the region. Adult BKC and RKC and adult and juvenile Pacific halibut are bycatch in the fishery. Fifth, enhance the stock. A BKC hatchery program is developed and implemented, and benthic recruits are released in the environment.

Fishery management interventions (1–4) are premised on the observation that species targeted by the fisheries are also predators of BKC (Supporting Information). The scenarios entail increasing fishing effort (intervention 2) or reinitiating fisheries in waters from which they were previously excluded as part of earlier unsuccessful attempts to recover BKC stocks through bycatch reduction (interventions 1, 3, and 4). These scenarios were represented by including the node fishing effort, which was positively linked to 2 other nodes, target and bycatch, which represented the fishing mortality directed at the 2 categories of species specific to each scenario (Table 1). Further, it was assumed that, for a given level of fishing effort, mortality rates would be higher for targeted species relative to bycatch species in these scenarios. That is, it was assumed that fishers and managers would act to minimize bycatch mortality rates relative to the directed fishery by, for instance, avoiding fishing in areas of high bycatch, requiring gear modifications, fishing during seasons when the species overlap may be less or by implementing additional regulatory measures. In practice, we imposed an inequality condition whereby the strength of the interaction between fishing

Table 1. Summary of individual management options intended to promote blue king crab recovery and climate-change scenarios related to ocean warming and acidification.*

Scenario category	*Individual scenarios (pressed node)*	*Linked to*	*Linked to*
Management intervention	trawl (fishing effort)	(+) target	(–) Pacific cod (–) walleye pollock
		(+) bycatch	(–) BKC-A (–) RKC-A (–) Pacific halibut-A
	Pacific cod pot (fishing effort)	(+) target	(–) Pacific cod
		(+) bycatch	(–) BKC-A (–) RKC-A
	Pacific halibut longline (fishing effort)	(+) target	(–) Pacific halibut-A
	red king crab pot (fishing effort)	(+) target (+) bycatch	(–) RKC-A (–) BKC-A
	stock enhancement (stock enhancement)	(+) BKC-BR	
Climate change	ocean acidification (OA)	(–) BKC-BR (–) BKC-L (–) RKC-BR (–) RKC-L (–) Invertebrate predators	
	ocean warming (warming)	(+) RKC-L, (+) RKC-BR (+) RKC-J, (–) BKC-L (–) BKC-BR, (–) BKC-J (–) Pacific cod (–) walleye pollock	

**For each scenario, the sign of the effect (link) of the pressed node on the recipient node is given in parentheses. Abbreviations: BKC, blue king crab; RKC, red king crab; OA, ocean acidification; A, adult; J, juvenile; BR, benthic recruit; L, larval. Citations and rationales for the link signs and details regarding inequality conditions between links related to the OA scenario are provided in the Supporting Information.*

effort and target was greater than the interaction with bycatch. We included scenarios in which fishery interventions were implemented individually and where all fishery interventions were implemented simultaneously (Table 1).

To represent the stock enhancement scenario (5), the node stock enhancement was added to the model and linked positively to BKC benthic recruits. This scenario was also supported by stakeholder participants and reflects recent advances in culture methods for BKC and evidence that stock enhancement may be a viable option based on survival rates in the wild for cultured RKC benthic recruits (see Supporting Information). In the absence of contrary information, it was assumed that depensatory mortality on BKC does not occur. Further, if depensatory mortality does occur in BKC but in life-history stages earlier than benthic recruit, stock enhancement may still be a viable option. The stock-enhancement scenario was evaluated individually and with all fishery management options simultaneously (Table 1).

Climate effects originating from OA and ocean warming were considered in scenarios both individually and together (Table 1). For OA, we assumed the adverse impacts would be stronger on the benthic and juvenile stages of RKC compared with BKC based on the collective findings of experimental studies (Supporting Information). To represent the species-specific inequality in effect strength, the node OA (which represents ocean acidification and the partial pressure of seawater CO_2) was linked negatively to the benthic recruit stages of RKC and BKC, and an inequality condition conveying the stronger negative effect of OA on RKC relative to BKC was applied (Supporting Information). A second inequality condition was also applied to a pair of negative links that extended from OA to the RKC and BKC juvenile nodes (Table 1 & Supporting Information). The OA and warming scenarios were run individually and simultaneously, and additional management intervention scenarios were run that included both climate-change stressors.

All QNM perturbation analyses were performed in R 3.5.1 (R Development Core Team 2018).

Uncertainty Analyses

To evaluate the sensitivity of predicted outcomes to the inclusion of inequality conditions, we repeated the simulation procedure without enforcing the inequality conditions and obtained the difference in the percentage of positive sign outcomes between the runs with and without the inequalities. We identified species with outcomes with similar sensitivities to the inequality conditions across scenarios and identified scenarios that were similar based on the sensitivity of species outcomes. Similarities were based on Euclidean distance, and species and scenarios were grouped using cluster analysis and the unweighted pair-group method with arithmetic averages (Legendre & Legendre 1998).

We evaluated the sensitivity of adult BKC outcomes to the presence or absence of uncertain links (e.g., Raymond et al. 2011). For a given scenario, inequality conditions were enforced and simulated outcomes of adult BKC were sorted according to whether a given uncertain link was present or absent. The difference in the percentage of positive sign outcomes between the 2 groups was then obtained. We identified uncertain links that had a similar effect on the outcome of adult BKC across scenarios and scenarios that were similar based on the sensitivity of adult BKC to the uncertain links. Similarity calculations for scenarios and uncertain links were performed following the same procedure as for the inequality sensitivities. Cluster analyses were performed in R with the statistical library vegan (Oksanen et al. 2018).

Results

Management Scenarios

Overall, sign agreement of adult BKC outcomes to the fishery intervention scenarios was low (Fig. 2), but positive outcomes (moderate sign agreement) were observed for BKC benthic recruit or juvenile stages in scenarios that included Pacific cod pot or RKC pot fisheries (Fig. 2). In contrast, many of the RKC life-history stages decreased (moderate sign agreement) under the fishery-intervention scenarios. The different responses between RKC and BKC life-history stages are related to their different ecological interactions in the model. First, the benthic recruit and juvenile RKC stages are more vulnerable to small fish and invertebrate predators (IP and FP in Fig. 1) than those of BKC, and this was represented in the model with inequality constraints on the corresponding predation interactions. Second, RKC are more aggressive than BKC, and RKC juveniles prey directly on BKC benthic recruits (Fig. 1). In the fishing-intervention scenarios, a trophic cascade arises: the target species are reduced, their prey (FP and IP) increase, which decreases RKC (Fig. 2). The same trophic cascade effects BKC, but ambiguity in the response of BKC is heightened because reductions in RKC also decrease its negative effects on BKC (Fig. 1).

In contrast, under the stock-enhancement scenario, all life-history stages of BKC responded positively (high sign agreement), and no changes were predicted for the remaining species in the system (Fig. 2). However, when stock enhancement was combined with all other fishery interventions, the sign agreement of adult BKC outcomes decreased (low sign agreement [Fig. 2]), indicating a larger number of countervailing feedbacks under that scenario.

Climate Scenarios

Under ocean warming, all life-history stages of BKC decreased and those of RKC increased (moderate to high sign agreement), reflecting the negative and positive direct effects of warming on the 2 species, respectively, combined with the indirect effects of increased predation by RKC on BKC (Fig. 2). The responses of other species were more complex. For instance, the link from ocean warming to Pacific cod and walleye pollock was negative in both instances, but walleye pollock increased (moderate sign agreement), whereas Pacific cod decreased (moderate sign agreement) in response to the warming scenario (Fig. 2). In that case, the net reduction in predation on walleye pollock by Pacific cod and their shared predator Pacific halibut partly contributed toward counteracting the direct adverse effect of warming on walleye pollock.

The OA scenario impacted the food web in a different manner relative to warming (Fig. 2). Sign agreement of BKC life-history stages was low under OA, but unlike the ocean-warming scenario RKC responded negatively with moderate to high sign agreement depending on life-history stage (Fig. 2). This was related to 3 factors. First, OA had a stronger negative effect on RKC relative to BKC juveniles and benthic recruits (Supporting Information). Second, OA adversely affected the small IP group, which are prey to RKC juveniles (Fig. 1); a decrease in IP further decreased RKC. Last, reducing RKC was advantageous for BKC because RKC negatively affects BKC, and thus partly offsets the direct negative effects of OA. In addition, the outcomes for 3 additional species groups (Pacific halibut, walleye pollock, and small IPs) changed direction relative to outcomes under warming, reflecting the different ecological pathways through which OA impacts are transmitted (Fig. 2). When OA and warming were combined, all BKC life-history stages responded negatively (moderate sign agreement) (Fig. 2). For the remaining species, outcomes were generally intermediate to those predicted under the individual scenarios (Fig. 2).

Scenario Combinations

The probability of positive outcomes for BKC life-history stages decreased further when climate change was also considered with the individual fishery interventions; moreover, negative (moderate sign agreement) outcomes were instead predicted (Fig. 2). The positive BKC outcomes observed under the stock-enhancement scenario changed to negative (moderate sign agreement) when

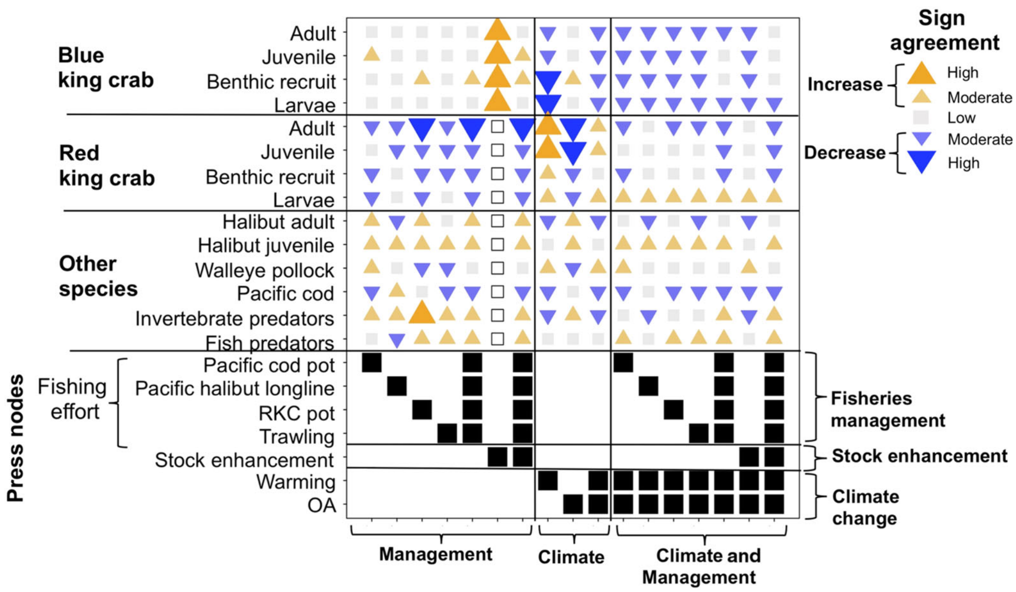

Figure 2. Predicted simulated response of variables in the blue king crab network to management and climate scenarios (white open squares, no predicted change in response of a node to perturbation; black squares, nodes positively pressed in a given scenario).

climate change was also considered. When fishing, stock enhancement, and climate change were combined, outcomes for most BKC life-history stages exhibited low sign agreement (Fig. 2).

Uncertainty Analyses

The sign outcomes of BKC life-history stages were most sensitive to inequality constraints under scenarios that included OA impacts and trawl and RKC fishery management interventions (Fig. 3). For those scenarios, including inequality constraints increased the percentage of positive sign outcomes of BKC life-history stages by approximately 25–50% relative to outcomes without the constraints (Fig. 3). The outcomes of RKC adults and juveniles were moderately sensitive (>15% change), but this was limited to scenarios that included both climate stressors (ocean warming and acidification) and a subset of the individual fishery management interventions (stock enhancement and RKC pot and Pacific halibut longline fisheries) (Fig. 3). Responses of most other remaining species were generally less sensitive (<15% change) to inclusion of the inequalities under the various scenarios (Fig. 3).

For nearly all scenarios that included fisheries interventions, positive sign outcomes for BKC adults were approximately 25–75% higher when a negative interaction between adult RKC and BKC was present (Fig. 4). The second and third most important uncertain links also included RKC life-history stages: a positive link between RKC adults and larvae (representing self-recruitment) and a negative (predation) link between juvenile halibut and benthic recruit RKC (Fig. 4). These links were most influential primarily in scenarios that included RKC pot and trawling interventions (Fig. 4).

Discussion

Our primary result highlights how climate change may alter conclusions regarding the likely efficacy of management interventions intended to promote population rebuilding. Stock enhancement had the highest probability of increasing adult BKC abundance with the least disruption to the system, but climate change decreased the probability substantially. Similarly, the probability of increasing adult BKC abundance decreased under climate change for the fishery-intervention scenarios. These findings demonstrate the importance of accounting for climate change in the assessment of proposed management interventions and the role QNMs can play in predicting potential community outcomes in data-limited settings.

More generally, the results highlight trade-offs among system components under the different management interventions, but also indicate that BKC outcomes are uncertain in the face of climate change. This result in itself is important because recognizing and characterizing uncertainty is critical for transparency and effective decision making (Addison et al. 2013). Qualitative network models and their underpinning conceptual models should be considered working meta-hypotheses of system structure (Puccia & Levins 1985), and to that end, identifying sources of uncertainty can help guide research prioritization and model refinement (Hill et al.

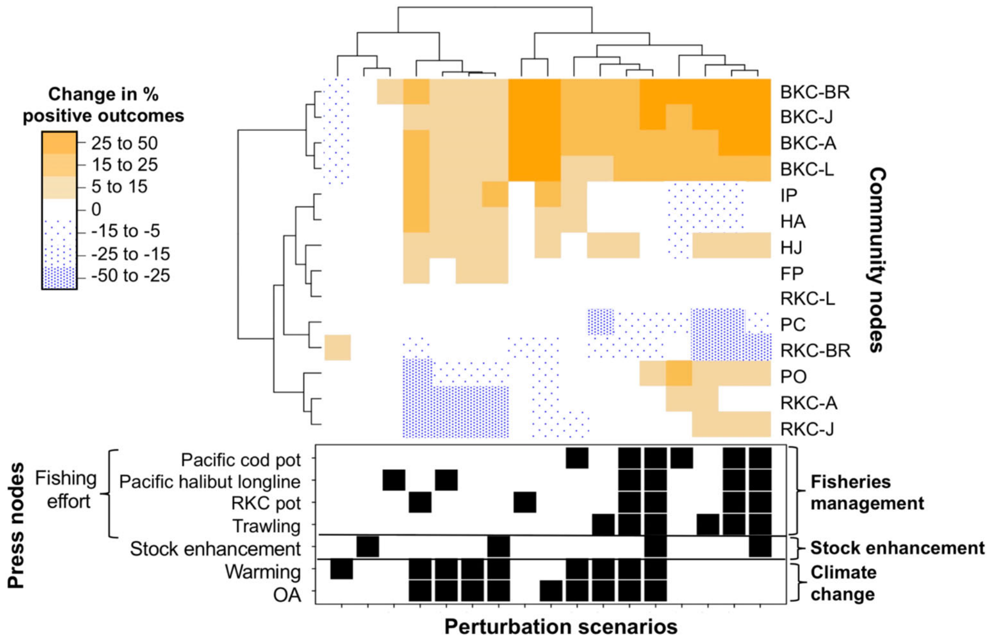

Figure 3. Sensitivity of node outcomes (percentage of positive simulated outcomes) to inclusion of inequality constraints (i.e., outcome with inequalities-outcome without inequalities) under climate and management scenarios (black squares, nodes positively pressed in a given scenario; species codes as in Fig. 1). Scenarios and nodes ordered according to similarity (Euclidean distance) in sensitivity across nodes and scenarios, respectively.

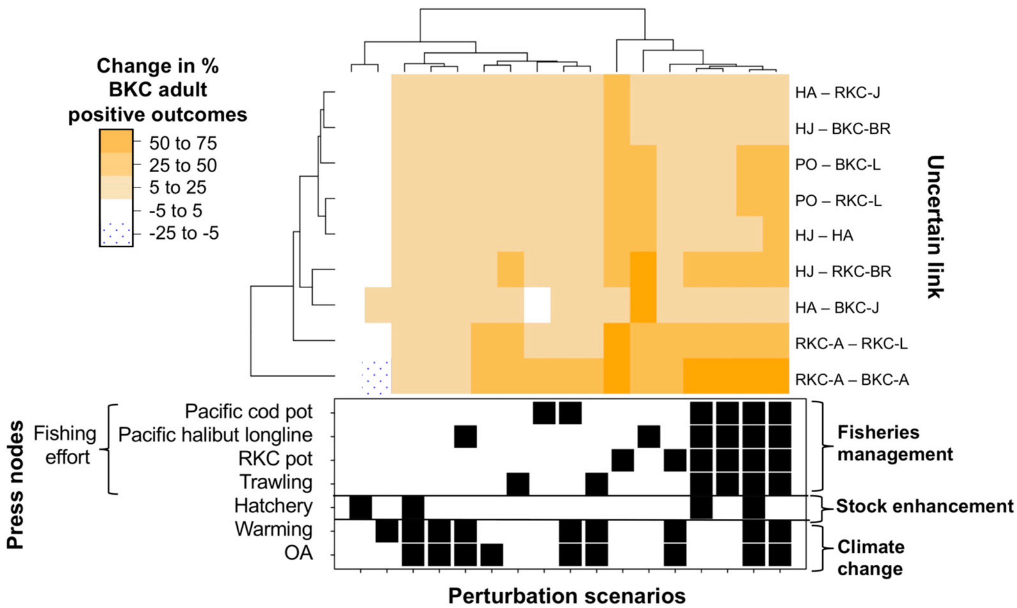

Figure 4. Sensitivity of blue king crab (BKC) adult outcomes (percentage of positive simulated outcomes) to presence or absence of uncertain links (i.e., outcome with a link-outcome without a link) under climate and management scenarios (black squares, nodes positively pressed in a given scenario; species codes, as in Fig. 1.; link signs are given in the Supporting Information). Uncertain links and perturbation scenarios are ordered according to similarity (Euclidean distance) in sensitivity across nodes and uncertain links, respectively.

2007). Overall, when uncertain links were present, the probability of a positive adult BKC response increased, particularly for scenarios that included fisheries management interventions. For many scenarios, 1 specific link (a negative effect by adult RKC on adult BKC) had a disproportionate effect on BKC outcomes, which suggests that obtaining additional information on its plausibility would give the largest gains in prediction precision. Previous researchers hypothesized antagonistic interactions between adult BKC and RKC (NPFMC 2011), but experimental work to date has focused only on interactions between benthic recruit and juvenile stages (Daly & Long 2014; Long et al. 2015). Some evidence opposing the hypothesis has emerged from comparison of BKC and RKC spatial distributions, but those conclusions were based on spatially coarse survey data, which may not be particularly informative (NPFMC 2011). Additional field, laboratory, or survey analyses to test this hypothesis would be desirable.

The incorporation of inequality conditions into probabilistic QNM predictions had a notable influence on the outcomes of all BKC life-history stages to the various fishery management interventions. Although we focused on imposing inequalities between pairs of interactions, the approach could feasibly be extended to accommodate more elaborate sets of inequality constraints. From a Bayesian perspective, the approach amounts to updating the posterior predictive distribution with data in the form of the inequality conditions. The approach therefore follows in the tradition of previous QNM studies that have applied rejection criteria based on the ability of realized matrices to reproduce known aspects of system behavior (Raymond et al. 2011; Melbourne-Thomas et al. 2012). Areas for further work include methods for incorporating expert knowledge in the form of priors on interaction strengths, and approaches suggested for other types of network models (e.g., fuzzy cognitive maps; Baker et al. 2018) may prove useful for QNMs as well.

Like all models, QNMs are based on assumptions that should be considered in their interpretation. For instance, outcomes from press perturbations are based on assumptions that the modeled system be at or near equilibrium conditions and that partial derivatives of system variables are adequately approximated by linear functions near equilibrium conditions (Dambacher et al. 2009). These assumptions are also common to quantitative food-web models, and methods to account for some of these issues are available (Dambacher et al. 2009). Further, assumptions embedded in the intervention scenarios and the ecological system may require further scrutiny. For instance, the stock-enhancement scenario is based on the assumption that BKC benthic recruits are not subject to depensatory mortality and that the release of cultivated benthic recruits will increase densities in the wild. Studies on cultivated RKC suggest that this assumption may be reasonable for BKC (Long et al. 2018), but additional research, including an economic analysis incorporating those results, would be necessary before any attempt at large-scale stock enhancement. Other types of network models are available that differ in regard to their underlying mathematics, representation of feedbacks and uncertainty, and required inputs (e.g., fuzzy cognitive maps and Bayesian belief networks [McCann et al. 2006; Baker et al. 2018]) that could be used alongside QNMs to form an ensemble of models to more fully represent projection uncertainty.

Although we focused solely on ecological interactions in our model, QNMs can also be expanded to represent social, cultural, and economic subsystems that may be needed to represent other factors relevant to management decision making (Harvey et al. 2016). A more holistic understanding of the social and ecological dynamics of the Pribilof Islands marine ecosystem is required to rigorously assess trade-offs in BKC management, but doing so is beyond the scope of this work. As understanding of climate impacts on the EBS ecosystem improves, the climate scenarios can easily be updated and the analysis rerun. If distinct climate impacts scenarios are developed, they could also be crossed with different management interventions to identify actions that produce outcomes robust to future climate uncertainty (Plagányi et al. 2011). In our experience, assembling the conceptual model (or multiple models) underpinning network analyses is the single largest time investment. Subsequent analyses are rapid with the aid of available software. Identifying possible management outcomes under climate change remains a major challenge, but QNMs hold considerable promise as tools for organizing system knowledge, setting research priorities, and supporting decision making.

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Supporting Information

Additional details on BKC management and the conceptual model (Appendix S1), model link descriptions (Appendix S2 and Appendix S3), summary of the model inequality conditions (Appendix S4), and comparison of model predictions based on different simulation protocols (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author. The BKC signed digraph and R scripts for performing perturbations with the inequality conditions are available from Figshare at https://doi.org/10.6084/m9.figshare.8009621.v1 (Reum JCP. 2019. Qualitative Network Model with Interaction Inequality Conditions).

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