ICES Journal of Marine Science Advance Access published July 11, 2015

ICES Journal of Marine Science

ICES CIEM International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science; doi:10.1093/icesjms/fsv119

Qualitative network models in support of ecosystem approaches to bivalve aquaculture

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Reum, J. C. P., McDonald, P. S., Ferriss, B. E., Farrell, D. M., Harvey, C. J., and Levin, P. S. Qualitative network models in support of ecosystem approaches to bivalve aquaculture. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsv119.

Received 8 May 2015; revised 10 June 2015; accepted 12 June 2015.

Predicting the effects of aquaculture development for coastal ecosystems remains challenging, particularly for data-limited systems, and tools that account for complex ecological interactions are needed to support ecosystem approaches to aquaculture. Here, we used qualitative network models (QNMs) to examine the potential community effects of increasing bivalve aquaculture in South Puget Sound, a large estuarine system in Washington, United States. QNMs are formalized conceptual models that require only a qualitative understanding of how variables composing a system interact (that is, the sign of interactions: +, −, and 0) and are therefore well-suited to data-limited systems. Specifically, we examined community-wide responses to scenarios in which bivalve cultivation effort increased for three different bivalve species (Manila clam *Venerupis philippinarum*, Pacific oyster *Crassostrea gigas*, and geoduck *Panopea generosa*). Further, we evaluated community-wide responses to the removal of benthic bivalve predators, a future increase in nutrient loadings, and combinations of these scenarios acting simultaneously. The scenarios enabled identification of potential trade-offs between increased aquaculture and shifts in the abundance of community members and assessment of the possible effects of different management actions. We also analysed the QNM to identify key interactions that influence the sign outcome of community responses to press perturbations, highlighting potential points for management intervention and linkages deserving of more focused quantitative study. QNMs are mathematically robust and highly flexible, but remain underutilized. We suggest that they may serve as valuable tools for supporting ecosystem approaches to aquaculture.

Keywords: community interaction, ecosystem-based management, foodweb, geoduck, loop analysis, oyster, Puget Sound.

Introduction

Bivalve aquaculture production has increased rapidly worldwide and supplies both protein to meet growing human demands and jobs and income that benefit coastal economies. In the United States alone, bivalve aquaculture production has doubled since the 1980s (NRC, 2010). In some regions, bivalve aquaculture has taken place for decades, but the industry is evolving in terms of hatchery rearing technology, growout methods, and the variety of cultivated species. As the industry expands, the conversion of coastal habitat to shellfish farms has raised concerns about the cumulative ecological effects, both positive and negative, of aquaculture on coastal ecosystems (NRC, 2010; Cranford *et al.*, 2012). However, uncertainty over the potential effects remains high in many systems, hindering efforts to implement ecosystem approaches to aquaculture that integrate the ecological, social, and economic context within which aquaculture operates (Soto *et al.*, 2008; Cranford *et al.*, 2012).

Depending on the scale of operation, aquaculture may affect the structure and function of ecological communities to varying degrees (Coen *et al.*, 2011). As suspension feeders, bivalves may reduce water turbidity and phytoplankton concentrations, potentially increasing water clarity, lowering the risk of hypoxic conditions, and improving growth conditions for submerged aquatic vegetation (Newell, 2004). Ultimately, the potential for top-down control on phytoplankton is determined by attributes of individual systems, with the possibility for control generally increasing as water residency and phytoplankton turnover times lengthen and bivalve clearance times shorten (Dame and Prins, 1997; Dame, 2011). Aquaculture may also alter benthic habitat through the addition of structure associated with growout, direct modification of the substrate (e.g. graveling mudflats for clam cultivation), or though changes to the natural disturbance regime due to outplanting, harvest, and maintenance operations (Simenstad and Fresh, 1995; Forrest *et al.*, 2009; Coen *et al.*, 2011). At the same time, cultured bivalves and the epifauna they support may provide food and shelter to predators (e.g. Lopez-Jamar *et al.*, 1984; Caldow *et al.*, 2003; Inglis and Gust, 2003). The net effects of aquaculture may promote some species while suppressing others, resulting in shifts in community structure and foodweb relationships (Dumbauld *et al.*, 2009; Forrest *et al.*, 2009; Coen *et al.*, 2011).

Reviews examining the direct effects of aquaculture on individual species and functional groups are available (e.g. Kaiser *et al.*, 1998; Prins *et al.*, 1998; Newell, 2004; Dumbauld *et al.*, 2009; Forrest *et al.*, 2009; Coen *et al.*, 2011; Dame, 2011), but shellfish farms are embedded within complex ecological communities, and modelling methods are needed that can integrate indirect effects and feedbacks into system-wide predictions (NRC 2010; Cranford *et al.*, 2012). Quantitative foodweb models can play important roles in this regard, and help facilitate ecosystem approaches to aquaculture by enabling a more holistic perspective on management decisions. For instance, quantitative foodweb models can identify possible trophic cascades or changes to energy pathways that might alter the productivity of higher trophic levels (Jiang and Gibbs, 2005; Byron *et al.*, 2011). More generally, quantitative foodweb models offer a framework for organizing system knowledge, simulating potential outcomes of management actions, and identifying key information gaps that might direct future research and monitoring (Plaganyi and Butterworth, 2004). However, despite their potential value, the application of quantitative foodweb models to aquaculture remains challenging (McKindsey *et al.*, 2006). A central issue is that the models typically require extensive site-specific parameterization and forcing data, which precludes broad scale adoption and use in data-poor systems (Plaganyi and Butterworth, 2004; Cranford *et al.*, 2012). Finally, conveying uncertainty in quantitative model predictions due to both parameter and structural uncertainty can be difficult (McKindsey *et al.*, 2006; Hill *et al.*, 2007; Link *et al.*, 2012).

Qualitative network models (QNMs) offer an alternative or complementary method that is particularly suited for modelling data-limited systems (Puccia and Levins, 1985). QNMs require only a qualitative understanding of the relationships linking species and variables within a system, that is, whether the sign of pairwise interactions of variables are +, −, or 0. The approach was first developed by Levins (1974) and Puccia and Levins (1985) to facilitate the analysis of feedbacks in network models. The approach permits the rapid assembly of hypotheses of system structure and accounts for direct, indirect, and feedback effects in qualitative predictions. Like quantitative ecosystem models, QNMs offer a framework for organizing system knowledge, and their flexibility makes them particularly useful in supporting the conceptual synthesis of diverse information sources (Plagányi *et al.*, 2011). In QNMs, the predicted responses of community members to perturbations are qualitative and therefore imprecise. However, QNMs deemphasize precise measurements of model parameters, which in practice can be difficult to obtain for natural communities, and instead focus effort on describing general relationships among variables which is typically more feasible for complex ecosystems (Levins, 1998; Dambacher *et al.*, 2009).

In addition to elucidating potential community-wide responses to aquaculture, QNMs can also help to identify the effects of environmental conditions or management actions for cultured species. Changes in processes that affect food supply (e.g. phytoplankton production) and natural mortality (e.g. through predation or disease) are some of the key issues that influence production (Spencer, 2008). The models thus enable exploration of a potentially diverse range of scenarios: any variable(s) within the defined aquaculture–environment system can be perturbed and the response of the community examined. Although QNMs are valuable for organizing system knowledge and predicting the effects of management interventions or environmental change in data-poor systems, they remain underutilized in general (Dambacher *et al.*, 2009; Melbourne-Thomas *et al.*, 2012).

Here, we use QNMs to investigate aquaculture–environment interactions in South Puget Sound, an important shellfish-growing estuary in Washington, United States. Although shellfish aquaculture has taken place in the region for more than a century, interest in further expansion and development of the industry is high. Moreover, the potential ecological effects of current practices are only partially understood, and possible future responses have yet to be examined. Specifically, we developed a QNM and analysed three different types of scenarios to help demonstrate the versatility of the approach for evaluating a range of issues relevant to aquaculture. First, we examined potential community-wide responses to scenarios of increased aquaculture. In doing so, we sought to identify potential trade-offs between bivalve species and the abundances of other community members. Second, we examined the effects of reducing benthic bivalve predators in the system as a potential management option for increasing bivalve abundances. Finally, we simulated the effects of future environmental change (increased nutrient loadings) on both cultured bivalves and the community. We focused specifically on nutrient loadings because nitrogen concentrations are predicted to increase in this region over the next several decades due to growing human populations in the surrounding watersheds and shifts in marine circulation patterns related to climate change (Ahmed *et al.*, 2014; Roberts *et al.*, 2014).

Material and methods

Study site

South Puget Sound is a large (449 km^2; 37 m mean depth) sub-basin of Puget Sound, located in the Northeast Pacific and ∼15% of the sub-basin is tidelands by area (Burns, 1985). South Puget Sound supports a diverse ecological community that includes marine mammals, migratory waterfowl, species of management and conversation concern (e.g. the eelgrass *Zostera marina*, Chinook salmon *Oncorhynchus tshawytscha*) as well as commercial, tribal, and recreational capture fisheries [e.g. Chinook salmon, Dungeness crab *Cancer* (*Metacarcinus*) *magister*]. Cultivation of non-native Pacific oyster *Crassostrea gigas* began in the 1920s after collapse of native Olympia oyster *Ostrea lurida* populations. Manila clam *Venerupis philippinarum*, which may have been accidentally introduced with Pacific oysters brought from Japan, became a focus of cultivation efforts in the 1940s. Commercial culture of geoduck *Panopea generosa* developed in the early 1990s to augment lucrative wild harvest in subtidal areas, and has since increased dramatically. Recent reported shellfish aquaculture landings have approached 1 500 000 kg yr^{-1} and consist of Pacific oyster (55%), Manila clam (23%), and geoduck (16%), with remaining landings (10%) composed of assorted non-native bivalves (blue mussel *Mytilus* spp., European oyster *Ostrea edulis*, Eastern oyster *Crassostrea virginica*, Kumamoto oyster *Crassostrea sikamea*) and native Olympia oyster (aquaculture harvest statistics for 2010, Washington Department of Fish and Wildlife).

Qualitative Network Models

QNMs are a special type of graph known as a digraph and consists of variables and linkages or, equivalently, nodes and edges (Puccia and Levins, 1985). The linkages in the graph correspond to a matrix of interactions that, in ecology, typically represent trophic interactions. However, linkages can also represent other ecological interactions such as competition and facilitation or interactions between species or any other type of variable (e.g. abiotic, social, and economic). The analysis of QNMs draws upon graph theory and matrix algebra and is based specifically on analysis of the community matrix (Levins, 1974; Puccia and Levins, 1985).

A central premise of the approach is that the *per capita* change in a species or the level of some non-species variable can be described as a continuous function of the other variables in the system. The dynamics of n interacting variables can be represented as a set of ordinary differential equations, where for each variable x ($i = 1, 2, \ldots, n$):

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f_i(x_1, x_2, \ldots, x_n;\ c_1, c_2, \ldots, c_n)$$

That is, the growth rate of variable x_i is a function of the levels of some or all variables in the system, and usually itself, and a set of growth parameters c. For species variables, their c parameters may correspond to birth, death, or immigration rates. The interaction coefficient a_{ij} measures the direct effect of a small change in the level of variable j on the growth rate of variable i, and is defined as the partial derivative of f_i with respect to x_i (Bender *et al.*, 1984):

$$a_{ij} = \frac{\partial f_i}{\partial x_j}$$

Although the effects of x_j on x_i may not necessarily be linear, the approach assumes that the dynamics of each variable can be adequately approximated by a linearization near equilibrium levels (Stone and Roberts, 1991). The $i \times j$ matrix containing the a_{ij} elements is the community interaction matrix **A**. The negative inverse of **A** can be used to estimate the long-term effects of a press perturbation, which is defined as a sustained shift in the magnitude of a growth parameter of a species (Bender *et al.*, 1984). However, for natural ecosystems, precise quantitative specification of **A** is rarely possible (Levins, 1998).

Instead, under a qualitative approach, only the signs of the a_{ij} terms are needed. In traditional "loop analysis", sign specification of **A** alone can provide qualitative predictions of press perturbation impacts (Puccia and Levins 1985), but even in relatively simple systems, multiple feedbacks can result in qualitative predictions with high sign indeterminacy (Dambacher *et al.*, 2003). Using a probabilistic framework, both parameter uncertainty (i.e. the magnitude of a_{ij}) and potential structural uncertainty (i.e. the presence or absence of links) can be incorporated into predictions of community outcomes to a given press perturbation and the level of sign determinacy directly estimated (Raymond *et al.*, 2011; Melbourne-Thomas *et al.*, 2012). As used in the context of QNMs, structural uncertainty refers to instances when it is unclear if a linkage exists, but if it does occur its sign is known (Raymond *et al.*, 2011). The procedure employs a simulation approach that proceeds as follows: (i) a simulated community interaction matrix (**A***) is generated by retaining all certain linkages and the inclusion of uncertain linkages is determined by sampling from a binomial distribution; (ii) interaction coefficients (a_{ij}) for all links are then sampled from a uniform distribution spanning two orders of magnitude (0.01–1.0); (iii) the simulated community interaction matrix (**A***) is tested against stability criteria (Melbourne-Thomas *et al.*, 2012), and if stable the inverse of the negative community matrix is calculated to obtain the predicted response of the community to a given press perturbation. The procedure is repeated many times (10^4) to obtain distributions of the community outcomes due to a given press perturbation. Further extensions of the simulation approach exist that permit additional filtering of **A*** to only those matrices that also predict community responses in agreement with experimental or observational evidence (Raymond *et al.*, 2011; Melbourne-Thomas *et al.*, 2012).

The South Puget Sound Model

For South Puget Sound, we sought to build a qualitative model of aquaculture embedded with an ecological community. To do so, we performed a literature review of relevant ecological studies conducted in South Puget Sound and other estuaries in the NE Pacific, and consulted shellfish growers and researchers to identify key cultured bivalves species (Pacific oyster, Manila clam, and geoduck), their main predators and competitors, and other species or functional groups that, in turn, influence their respective dynamics. Because we sought to evaluate the potential effects of increased nutrient loadings and bivalve predator control, we also included additional nodes and linkages in the QNM to allow simulation of these perturbation scenarios. Interactions thought to influence the dynamics of variables within the system were identified, some of which were considered uncertain, reflecting uncertainty in model structure. An overview of the model is depicted in Figure 1 and further details of the nodes included in the model, along with descriptions of the interactions corresponding to each link and the level of certainty of the interaction, are provided in Supplementary data, Table S1.

To reduce the number of nodes, functionally similar species were grouped under a single node (Puccia and Levins, 1985). For instance, the nodes "small fish", "zooplankton" and "phytoplankton" represent taxonomically diverse groups, but we assumed that the ecological function of species within each node were similar. In addition, we grouped small-bodied benthic invertebrates into one of two classes: those that associate with structurally complex habitats (e.g. biogenic structure such as eelgrass meadows and oyster beds, as well as growout gear associated with Pacific oyster and geoduck cultivation) and those that prefer mud or unstructured habitat (e.g. Ferraro and Cole, 2007). The former and latter were referred to as "structure invertebrates" and "non-structure invertebrates", respectively. Although benthic invertebrate community structure may differ among types of complex habitats in South Puget Sound, we made the simplifying assumption that these species

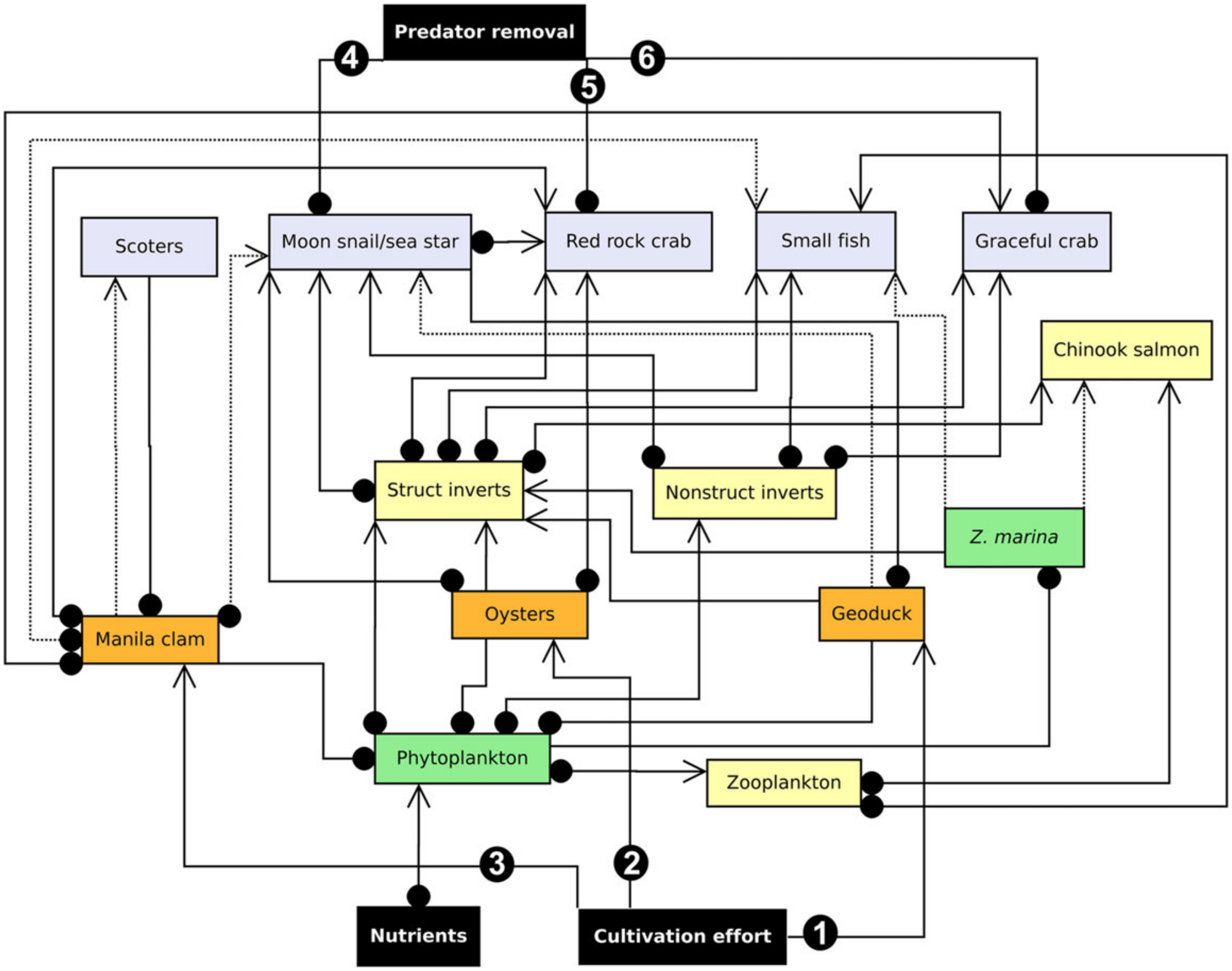

Figure 1. Qualitative interaction network of bivalve aquaculture in South Puget Sound, Washington. Links that terminate with an arrowhead indicate a positive effect; those that terminate with a filled circle indicate a negative effect. Links with both an arrow and a filled circle indicate a predator–prey relationship. All community members have a limiting self-interaction (negative), but for clarity these are not shown. Dashed links indicate linkages that are uncertain. Detailed descriptions of the relationships (unnumbered) between nodes are provided in Supplementary data, Table S1). Links labelled 1–6 are included in the model based on the scenario under consideration (see Table 1). Node colour codes: green: primary producers; orange: bivalves; yellow: other community members; black: nodes pressed in the various model scenarios. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

play similar functional roles and could be utilized by similar predator assemblages in the absence of detailed information on invertebrate community structure across habitat types. The model is therefore "minimal realistic" in that we sought to include enough detail to capture the interplay of direct and indirect interactions that influence aquaculture and community-wide dynamics but also minimize the number of variables in the model to aid interpretability and reduce prediction uncertainty (Fulton *et al.*, 2003).

Perturbation scenarios

We considered three main types of perturbation scenarios: (i) increase in bivalve aquaculture, (ii) decrease in bivalve predation rates through predator removal, and (iii) increase in nutrient loads. To implement the scenarios, the nodes "Cultivation effort" and "Predator removal" were added to the community QNM (Figure 1) and linkages extending from these nodes to community member nodes were added depending on the specific perturbation scenario (Table 1).

For example, to evaluate potential community-wide responses to increased geoduck cultivation, a positive link was added to the model, extending from "Cultivation effort" to "Geoduck" (the linkage labelled "1" in Figure 1). The node "Cultivation effort" corresponds to the effort placed by growers into expanding the area over which bivalve cultivation occurs. The remaining labelled linkages (2 through 6) were excluded from the model. The "Cultivation effort" node was then pressed in the simulation, and the response of the community was calculated. Similarly, community responses to increases in Pacific oyster or Manila clam culture were simulated by adding linkages labelled 2 or 3, respectively, to the model, and excluding all other labelled linkages, and pressing "Cultivation effort" (Table 1).

In South Puget Sound, anti-predator exclusion technologies (e.g. mesh netting, bag-on-rack or bag-on-bottom methods, protective polyvinyl chloride tube sections) are already used extensively on Pacific oyster, Manila clam, and geoduck plots (Toba *et al.*, 1992; Simenstad and Fresh, 1995; McDonald *et al.*, 2015); however,

Table 1. Summary of model scenarios evaluated for the South Puget Sound QNM.

		Links added					
Scenario code	**Press variable(s)**	**Geoduck**	**Pacific oysters**	**Manila clam**	**Moon snail/sea star**	**Red rock crab**	**Graceful crab**
A1	CE	1 (+)					
A2	CE		2 (+)				
A3	CE			3 (+)			
A4	CE	1 (+)	2 (+)	3 (+)			
B1	PR				4 (−)		
B2	PR					5 (−)	
B3	PR						6 (−)
B4	PR				4 (−)	5 (−)	6 (−)
C1	NU						
D1	CE, PR	1 (+)	2 (+)	3 (+)	4 (−)	5 (−)	6 (−)
D2	CE, NU	1 (+)	2 (+)	3 (+)			
D3	PR, NU				4 (−)	5 (−)	6 (−)
D4	CE, PR, NU	1 (+)	2 (+)	3 (+)	4 (−)	5 (−)	6 (−)

For each scenario, the pressed node is indicated.
Link numbers correspond to labelled links in Figure 1 and the sign of the relationship between the pressed node and community members is denoted. Pressed nodes: CE, cultivation effort; PR, predator removal; NU, nutrients.

predation loss remains an issue. As an added measure, predators could be culled. In practice, this might be achieved through the manual removal of predators on culture plots or initiation of a targeted fishery on predators. To evaluate the effects of removing predators on the community, we added the node "Predator removal", which corresponds to the level of effort applied to bivalve predator removal. We specifically examined the community-wide effects of removing common benthic invertebrate predators that were represented by three different nodes in the model: red rock crab *Cancer productus*, graceful crab *Cancer gracilis*, and the moon snail/sea star complex (Figure 1), which is characterized by moon snails (*Euspira lewisii*) and sea stars (sunflower sea star *Pycnopodia helianthoides*, pink sea star *Pisaster brevispinus*, ochre sea star *Pisaster ochraceus*, mottled sea star *Evasterias troscheli*). Negative linkages extending from "Predator removal" to each benthic predator node were added to the model, to simulate reductions in predator densities (Table 1).

Finally, we considered a scenario in which nutrient loadings increase. In South Puget Sound, nitrogen levels are likely to increase over the next several decades as human populations in the surrounding watersheds grow. In addition, circulation patterns on the Washington coast may shift in response to anthropogenic climate change, resulting in the delivery of additional marine-derived nitrogen relative to present day conditions (Ahmed *et al.*, 2014; Roberts *et al.*, 2014). We evaluated the effects of a potential future increase in nutrient loadings on the community by pressing the node "Nutrients" (Figure 1, Table 1).

In addition to the three main types of perturbation scenarios, we also examined community-wide outcomes when scenarios were combined (Table 1). Specifically, we sought to identify how scenario combinations might reinforce or counteract the predicted outcome of community members relative to the individual scenarios.

Linkage influence

Finally, we identified linkages that strongly influenced the sign outcome of community members. We used a statistical approach wherein the simulated responses of community members were treated as response variables and the simulated interaction strengths corresponding to each linkage were treated as predictor variables. The approach is similar to methods described by Melbourne-Thomas *et al.* (2012). However, unlike that study, we used Multivariate Adaptive Regression Splines (MARS) instead of Generalized Boosted Regression (GBR) models. While the predictive ability of GBR models is comparable or slightly better than MARS, they are computationally more demanding, particularly when many predictor variables are considered in the model building process. Because we sought to identify important linkages for all 14 community members in the South Puget Sound model, we deemed this distinction important. Further, while both approaches are able to fit non-linear response functions and higher order interaction terms, the MARS algorithm permits variable selection based on deviance reduction criteria, which is not possible with GBR. Given the large number of potential predictor variables (61 linkages in total), identifying those that explained a certain minimum level of variance was useful for focusing attention on the most important predictors.

To simplify evaluation of linkage influence, we assumed that all uncertain linkages in the model were certain (Raymond *et al.*, 2011). That is, linkages noted as uncertain were all retained in each model simulation. We simulated 1500 stable networks and calculated the sign response of community members to a press scenario in which predator removal, nutrient loadings, and cultivation effort were all increased simultaneously (Scenario D4, Table 1). For each community member the qualitative outcome (+, −) was treated as a binomial response variable. All MARS models were fit following Leathwick *et al.* (2005) and allowing first and second order interaction terms; variables that explained 0.01 or more of the residual squared error in the response variable were retained. For all fitted models, the percentage of explained deviance associated with each retained predictor (i.e. the predictor's relative importance) was calculated (Milborrow, 2014). Finally, cluster analyses were performed on the relative importance values to identify linkages that influenced similar community members and community members influenced by similar linkages; dendrograms were calculated based on the Bray–Curtis dissimilarity coefficient and the complete linkage clustering method (Legendre and Legendre, 1998). All statistical analyses were performed using the statistical software package "R" version 3.0.3 (R Development Core Team, 2014); MARS models were estimated using the library "earth" version 4.0.0 (Milborrow, 2014) and dendrograms were calculated using the library "vegan" version 2.0-10 (Oksanen *et al.*, 2013).

Results

Cultivation effort

Increased cultivation effort, when applied to individual bivalve species (Scenarios A1 through A3), resulted in positive responses to the bivalve species directly affected. Sign determinacy, which corresponds to the level of consistency in the simulated sign responses, was >70% in all scenarios (Figure 2). For most other community members, sign determinacy was lower (<70%) but some trends were apparent. Phytoplankton responded negatively and the eelgrass *Z. marina* responded positively across scenarios, and the bivalve predator red rock crab increased as well (Figure 2). Consistent trends in other community members towards negative (zooplankton, non-structure invertebrates) and positive responses (nutrients) were also observed (Figure 2).

In contrast, when cultivation effort was applied to all three bivalve species simultaneously (Scenario A4), each bivalve species responded positively but sign determinacy decreased relative to the individual press scenarios for Manila clam and Pacific oyster (Figure 2). Additionally, the sign responses for nutrients, phytoplankton, zooplankton, non-structure invertebrates, *Z. marina*, and red rock crab were similar to those under the individual scenarios, but for these community members sign determinacy generally increased, exceeding 70% (Figure 2).

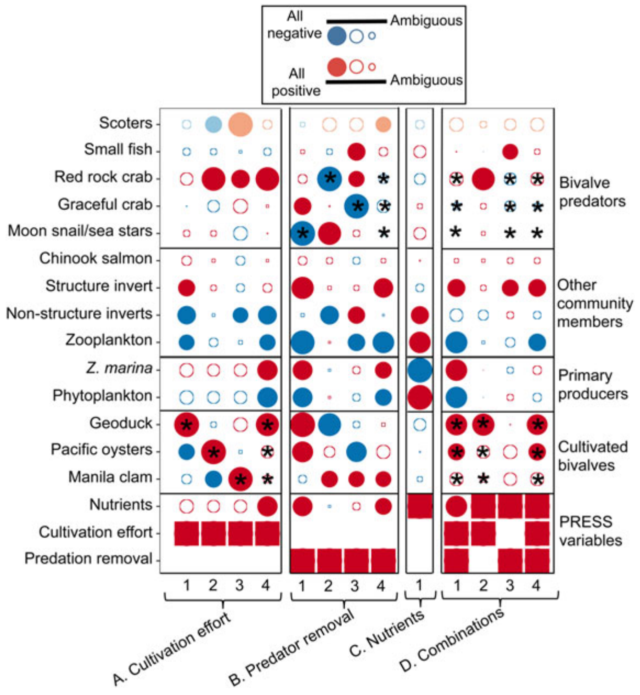

Figure 2. Simulated community responses to increased bivalve cultivation effort, benthic predator removals, and nutrients inputs in South Puget Sound, Washington. Scenario letter and number codes correspond to scenario descriptions provided in Table 1. Nodes pressed in each scenario are indicated by a solid square. The relative size of the circle symbols scale with the level of consistency of the simulated sign response of community members. For added reference, closed circles indicate sign consistency >70%; open circles, ≤70%. Red and blue symbol colours correspond to net positive and negative responses, respectively. Light red and light blue symbols indicate instances were >25% of the simulated responses were 0 (symbol scale is based on the non-zero predicted sign responses). For each scenario, community members that were directly linked to the pressed variable(s) are noted by an asterisk overlaid on their respective responses.

Predator removal

In the individual predator removal scenarios (B1 to B3), each targeted predator decreased (Figure 2). The responses of cultured bivalves, however, to the different predator removal scenarios were variable. Removal of moon snail/sea stars (B1) resulted in increases in geoduck and Pacific oyster, while removal of red rock crab (B2) increased Manila clam but decreased geoduck. Removal of graceful crab (B3) also increased Manila clam, but Pacific oyster decreased. Responses of the remaining community members also differed as well between scenarios, with no consistent trends in sign responses among primary producers, bivalve predators, or other community members (Figure 2).

In the scenario in which all three predators were removed simultaneously (scenario B4), the sign responses of the predators were negative, sign determinacy was low, and among the cultured bivalves, only Manila clam showed a positive response with high sign determinacy (Figure 2). Primary producers, nutrients, and zooplankton responded in the same manner as when cultivation effort was increased on all three species simultaneously (Figure 2).

Nutrients

For primary producers, increased nutrients resulted in a positive response in phytoplankton and negative response in *Z. marina* (Scenario C1), which was the opposite of the pattern observed in the cultivation effort and predator control scenarios (Figure 2). Further, increased nutrients resulted in a predicted increase in phytoplankton and non-structure invertebrates (Figure 2). Responses for all the remaining community members, including the bivalves and bivalve predators, had low sign determinacy (Figure 2).

Scenario combinations

In Scenario D1, cultivation effort and predator removals for all three bivalves were pressed. Overall, the sign response of all bivalves, primary producers, nutrients, and zooplankton were similar to both separate scenarios (A4 and B4), though variation in sign determinacy was apparent for a few community members (e.g. red rock crab, structure invertebrates, Pacific oyster, manila clam; Figure 2).

With increased nutrients and cultivation effort (Scenario D2), most community members exhibited responses with low sign determinacy; only geoduck, and red rock crab (both positive responses) showed high sign determinacy. Similarly, sign determinacy was predominately low for community members when nutrients and predator removal were increased (D3). In that case, positive responses in small fish and structure invertebrates had high sign determinacy.

Finally, simultaneous increases in cultivation effort, predator removal, and nutrients (Scenario D4) resulted in positive responses in all three bivalves, though sign determinacy was high for only two of the three (geoduck and Pacific oyster; Figure 2). As for the remaining community members, only two exhibited responses with high sign determinacy (structure invertebrates, and zooplankton), which responded positively and negatively, respectively (Figure 2).

Linkage influence

On average, the fitted MARS models explained 22% of the deviance in the sign response of each community member under Scenario D4 (increased nutrients, culture effort, and predator removal; Table 2).

Table 2. Influence of model linkages on the predicted sign outcome of South Puget Sound community members under Scenario D4 as estimated using MARS models. For each community member, the percentage of simulated responses that were negative is presented along with the deviance explained by the MARS model. In addition, the number of retained predictors corresponding to linkages directly connected to the pressed nodes are presented (a total of three linkages extended from cultivation effort and predator removal; one from nutrients) along with the number of linkages from between community members (61 were available).

Species	% Negative response	Deviance explained (%)	Cultivation effort	Predator removal	Nutrients	Other linkages	Total number of linkages
Chinook salmon	40	10	2	1		4	7
Geoduck	11	36	1	2		2	5
Graceful crab	75	28		2		5	7
Manila clam	24	20	2	1		2	5
Moon snail/sea stars	31	33	1	2		7	10
Non-struct inverts	66	16	2	2	1	1	6
Oysters	21	29	2	2		3	7
Phytoplankton	59	23	2	1	1	3	7
Red rock crab	28	28	2	1		4	7
Scoters	24	20	2	1		2	5
Small fish	28	15	2	1	1	4	8
Structure inverts	21	12	1	1		4	6
Z. marina	41	23	2	1	1	3	7
Zooplankton	79	13				3	3

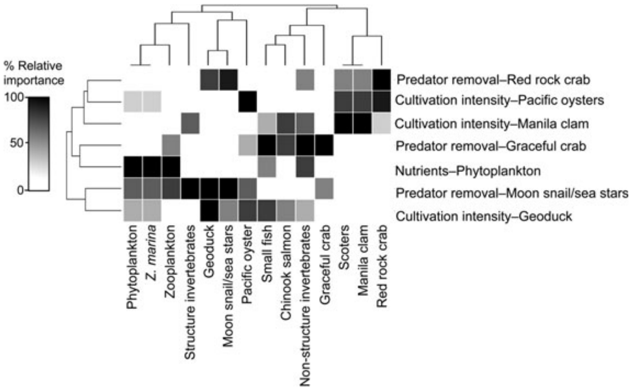

Figure 3. Relative importance of interaction strengths between community members and the nodes "cultivation effort", "predator removals", and "nutrients" as predictors of the sign response of community members (based on press Scenario D4). For each community member (labeled on the *x*-axis), the relative importance of the seven linkages is indicated according to the colour scale. Community members are ordered based on similarity in the relative importance of linkages and linkages are ordered according to their importance to different community members. The *y*-axis notation on the right-hand side of the heat map refers to linkages "from" one model variable (the first in each pair) "to" another (the second in each pair).

The range in explained deviance among community members ranged from 10 to 36% and the number of predictors in the final MARS models ranged from 3 to 10 (Table 2). For nearly all community members, linkages directly extending from the variables "cultivation effort" and "predator removal" were identified as important predictors, while the linkage extending from "nutrients" was identified as an important predictor for only five community members (non-structure invertebrates, phytoplankton, small fish, and *Z. marina*; Table 2). The number of predictors corresponding to linkages between community members in the final models varied widely from 0 (zooplankton) to 7 (moon snails/sea star; Table 2).

An overview of the relative importance of linkages extending from pressed variables as predictors of the sign response of community members is depicted in Figure 3. Clusters of community members had sign responses that were influenced by similar sets of linkages. For instance, the sign responses of phytoplankton, *Z. marina*, and zooplankton and scoters, Manila clam, and red rock crab were dependent on similar sets of linkages, respectively (Figure 3). In general, the "Predator removal-Moon snails/sea star" linkage had the highest average relative importance (77%) for the largest number of community members (eight community members; Figure 3). In contrast, the "Cultivation effort-Pacific oyster" linkage has the lowest average relative importance (61%) for the fewest species (six community members; Figure 3).

The fitted MARS models can be examined in further detail to better understand the relationship between interaction strengths and the sign response of community members. For illustrative purposes, we focused on the response of one community member, Manila clam, which showed the lowest sign determinacy among the three cultured bivalve species (Table 2). The fitted MARS model for Manila clam included five linkages that explained 20% of the deviance in the sign response. Three linkages were included in the model as univariate spline functions (Figure 4a–c) and the remaining two linkages were included in interactions (with two of the three other variables) and were modelled as bivariate spline functions (Figure 4d and e).

As expected, an increase in interaction strength between cultivation effort and Manila clam resulted in a higher probability of observing a positive response in Manila clam (Figure 4a). Similarly, the probability of a positive response increased as expected with reductions in red rock crab predation on Manila clam (Figure 4c). Interestingly, the response of Manila clam was also associated with the interaction between cultivation effort and Pacific oyster; an increase in the interaction strength corresponded to a decrease in the probability of a positive Manila clam response (Figure 4b).

The remaining variables in the MARS model were included in interaction terms and were therefore depicted using surface plots (Figure 4d and e). In these figures, the probability of observing a positive response in Manila clam is depicted as a function of the two variables included in the interaction term. Overall, the

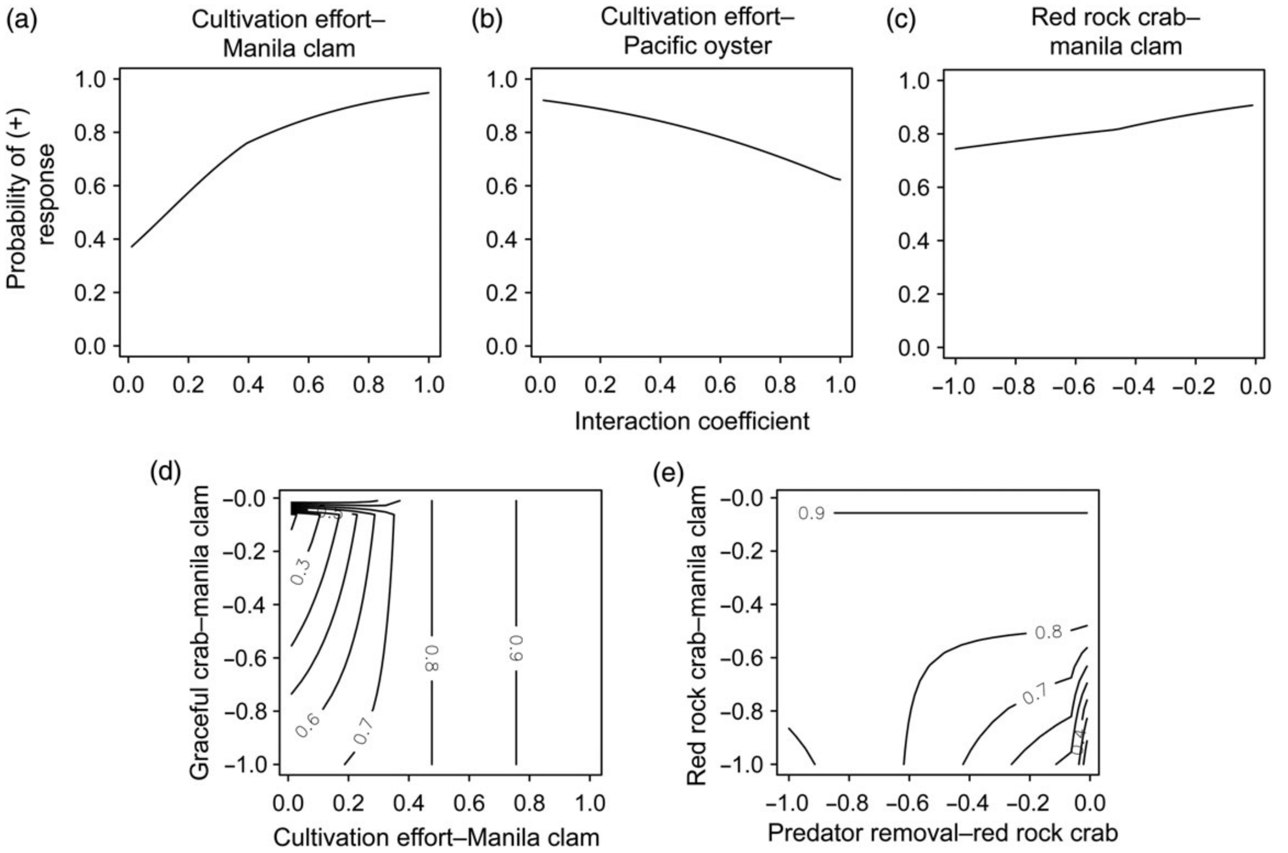

Figure 4. Partial dependency plots indicating the functional relationship between the magnitude of interaction coefficients (corresponding to linkages in the South Puget Sound QNM) and the probability of a positive sign response in Manila clam under Scenario D4 (simultaneous increases in predator control, cultivation effort, and nutrients) based on the fitted MARS model. (a – c) Linkages that were included as first-order predictors in the model. (d and e) Interaction terms in the model; the probability of observing a positive response is a function of two linkages and is depicted as a response surface contour plot.

probability of a positive Manila clam response increased with reductions in graceful crab predation on Manila clam (i.e. reduced negative interaction) and increased with the strength of interaction between cultivation effort and Manila clam (Figure 4d). In the second surface plot, weakened predation by red rock crab on Manila clam and stronger removal of red rock crab corresponded to higher probabilities of a positive response by Manila clam (Figure 4e).

Discussion

Ecosystem approaches to aquaculture require an understanding of the potential ecological outcomes associated with expansion or change in aquaculture practices, and QNMs can play an important role in this capacity. As we show for South Puget Sound, specifying network structure alone may enable qualitative prediction and help identify potential counterintuitive outcomes or trade-offs associated with different development and management scenarios. In the individual bivalve cultivation effort scenarios, for instance, trade-offs between different bivalve species were predicted: cultivation effort applied to geoducks increased geoducks, but led to decreases in Pacific oyster. Similarly, cultivation effort applied only to Pacific oyster increased Pacific oyster, but led to a decrease in Manila clam. Such patterns are likely due in part to indirect pathways involving the predator red rock crab, wherein an increase in one bivalve results in higher abundances of red rock crab, which increases predation on other bivalve prey. Trade-offs were also evident in removal scenarios of individual predators which had opposing effects on different bivalve species: removal of red rock crab decreased geoduck and increased Manila clam, while removal of graceful crab decreased Pacific oyster and increased Manila clam. While these scenarios highlight potential species trade-offs they also imply economic trade-offs: geoduck and Pacific oyster are ∼460% and 40% more valuable than Manila clam per pound, respectively. Because QNMs integrate direct effects, indirect effects, and feedbacks they can help identify trade-offs arising from complex ecological interactions that might otherwise be difficult to anticipate (Levins, 1998).

A key benefit of QNMs is that they can help screen management actions that may yield ambiguous or problematic outcomes (Dambacher *et al.*, 2009; Carey *et al.*, 2014). For example, increased cultivation effort did not always ensure increased bivalve production. In scenarios where cultivation effort was applied to only one species of bivalve, the species responded positively and with high sign determinacy. However, under the multispecies press scenario, sign determinacy of the response of two of the three bivalves decreased (Pacific oyster and Manila clam) relative to the individual species press scenarios. Combining cultivation effort with predator removals or increased nutrients also increased ambiguity in the response of some bivalves. Reductions in sign determinacy are due to increases in the number of countervailing feedbacks; that is, the number of pathways conveying negative effects increase relative to the number conveying positive effects (Dambacher *et al.*, 2003). Sign determinacy could be improved with quantitative information on interaction strengths, but this may be impractical to obtain (Puccia and Levins, 1985, Dambacher *et al.*, 2003). From a precautionary perspective, analysing a variety of development and management scenarios can offer insight into conditions that lead to increased outcome uncertainty and where action should proceed with caution.

In instances where sign responses are ambiguous, the simulated results from QNMs can be analysed using statistical methods like MARS to identify linkages that have the largest influence on sign outcomes (Melbourne-Thomas *et al.*, 2012). By distinguishing key linkages, research attention can be focused and potential points for management intervention identified. For Manila clam, under the scenario of a simultaneous press on nutrients, cultivation effort, and predator removals, a subset of linkages in the network strongly influenced its sign response. In addition to the effect of cultivation effort on Manila clam, the strength of linkages associated with pathways that influence predation on Manila clam (by way of red rock crab) were identified as important. If quantification of these interactions were possible, doing so would improve sign determinacy of the Manila clam response. However, in the absence of quantification, the shapes of the spline functions suggest potential routes managers or growers could take to improve the likelihood of a positive response. For instance, increasing cultivation effort on Manila clam relative to Pacific oyster and/or pursuing actions that reduce predation of red rock crab on manila clam might increase the odds of a positive response. The community-wide effects of modifying interaction strengths through management intervention could be explored further through additional qualitative scenarios (Dambacher and Ramos-Jiliberto, 2007). As we show for South Puget Sound, linkage influence can easily be evaluated for all community members, and linkages that determine the sign responses of many species may be promising targets for more detailed quantitative study.

The ability to rapidly assess many scenarios using QNMs can also help to identify sets of management actions that might push the system towards a desired management goal. For instance, all scenarios that included increased cultivation effort predicted (with various levels of sign determinacy) negative responses for nutrients, zooplankton, non-structure invertebrates, and phytoplankton and positive responses for red rock crab and *Z. marina*. Similarity in the sign response of these community members across scenarios is partially because the three bivalve species all play the same functional role as filter feeders in the foodweb. If a management goal is, for example, to increase *Z. marina*, the analysis suggests that multiple management options are available. Additional feasibility criteria (e.g. expense, legality, and public support) could then be applied to further narrow the list of possible management actions.

The scenarios we examined for South Puget Sound aquaculture reflect a small subset of potential applications and the models could easily be tailored to address other aquaculture management issues including pest eradication, invasive species, disease, and climate variability. In addition, changes in policy that influence aquaculture permitting practices could also be evaluated using the QNM. For instance, we assumed that aquaculture would not expand into eelgrass habitats in South Puget Sound, in accordance with current regulations. A policy change allowing such expansion could be simulated by adding negative linkages to *Z. marina* from the bivalve species that are cultivated at the same tidal depths *Z. marina* occurs (e.g. Pacific oyster and geoduck). In the new network, an increase in either bivalve species would have a negative effect on *Z. marina* (Tallis *et al.*, 2009; Ruesink and Rowell, 2012; Wagner *et al.*, 2012). More generally, the web could be expanded further to include social and economic variables (e.g. demand, profit, jobs, recreational opportunities, and scenic quality) to examine social-ecological trade-offs in support of more holistic management efforts (Soto *et al.*, 2008; Dambacher *et al.*, 2009; Cranford *et al.*, 2012).

Like other modelling approaches, QNMs have important limitations. First, a key assumption underpinning the method is that system variables are at or near equilibrium or closely tracking moving equilibrium conditions (Puccia and Levins, 1985). In marine ecosystems, frequent disturbances (e.g. climate variability, pollution, and fishing) may make this assumption unrealistic (Dambacher *et al.*, 2009). However, the assumption is also routinely used in quantitative community and foodweb models (Bender *et al.*, 1984; Yodzis, 1998) and if the system exhibits sustained bounded motion, the issue can be addressed by considering predicted responses within the context of an appropriately long-time scale (Puccia and Levins, 1985, Dambacher *et al.*, 2009). Second, the model assumes that the partial derivatives of system variables are adequately approximated by linear functions near equilibrium conditions. Strong non-linearity may result in the system transitioning across a threshold, whereby links may be created, broken, or reverse in sign. Such thresholds would require the consideration of multiple networks corresponding to different states of the system (Dambacher and Ramos-Jiliberto, 2007). Finally, like all ecosystem models, we made simplifying assumptions regarding how species were aggregated. In general, we sought to aggregate sets of species into variables that were likely to possess similar linkages and therefore respond similarly to system perturbations (Puccia and Levins, 1985). The necessity of lumping variables in speciose ecosystems and the associated caveats of doing so are understood well in both qualitative and quantitative ecosystem modelling arenas (Fulton *et al.*, 2003; Metcalf *et al.*, 2008) and the final model reflected our effort to simplify the system to improve interpretability while also maintaining its essential structure.

In general, field studies on the effects of aquaculture have tended to focus on responses of individual functional or taxonomic groups to changes in culture density or spatial extent (reviewed in Dumbauld *et al.*, 2009; Coen *et al.*, 2011). Models are a practical necessity for developing an integrated understanding of the system-wide effects of aquaculture and can help formalize hypotheses of system structure that can be tested and refined through targeted monitoring (Puccia and Levins, 1985; Melbourne-Thomas *et al.*, 2012). As we demonstrate here, QNMs offer a promising method for synthesizing diverse information sources into a formal conceptual model and are helpful for understanding and predicting the potential effects of aquaculture. Qualitative models can offer a complementary method to quantitative approaches (e.g. Metcalf, 2010; Ortiz *et al.*, 2013) and may be the most feasible option in data-limited systems, requiring as a minimum only basic knowledge of the natural history of key species composing a system (Levins, 1998). QNMs provide imprecise predictions, but this can be viewed as advantageous because emphasis is moved away from the precise measurement of parameters (which may be costly, difficult, or impossible to do) and towards understanding the main processes and community interactions that influence the dynamics of the complete system (Puccia and Levins, 1985; Dambacher *et al.*, 2009). QNMs are flexible, highly robust, and effective frameworks for organizing diverse types of information, and should be of considerable value to resource managers and growers alike.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Acknowledgements

We thank B. Dumbauld, J. Ruesink, J. Samhouri, L. Conway-Cranos, E. Graham, and two anonymous reviewers for helpful comments and conversation on earlier versions of this manuscript. We also thank participants from our August 2014 workshop facilitated by Washington Sea Grant on the ecology and economics of shellfish aquaculture in Washington State for comments and feedback on elements of this work.

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Handling editor: Marta Coll