



Original Article

Evaluating trophic and non-trophic effects of shellfish aquaculture in a coastal estuarine foodweb

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Ferriss, B. E., Reum, J. C. P., McDonald, P. S., Farrell, D. M., and Harvey, C. J. Evaluating trophic and non-trophic effects of shellfish aquaculture in a coastal estuarine foodweb. – ICES Journal of Marine Science, 73: 429–440.

Received 9 July 2015; revised 28 August 2015; accepted 8 September 2015; advance access publication 13 October 2015.

Expansion of the shellfish aquaculture industry has the potential to affect the structure and dynamics of coastal estuarine foodwebs. To better understand foodweb trade-offs, we incorporated both trophic and non-trophic interactions (e.g. habitat facilitation and predator refuge) into a foodweb model of central Puget Sound to predict the effects of an increase in geoduck (*Panopea generosa*) aquaculture. At a basin scale, the foodweb can support at least 120% increased geoduck aquaculture, above current production levels (landings of 10 546 kg in 2012), with only minor changes in individual species' biomass and/or metrics of ecosystem resilience. The non-trophic effects of increased geoduck aquaculture, related to the influence of anti-predator structure, had a stronger influence on the foodweb than the trophic role of cultured geoducks as filter-feeders and prey to other species. Increased geoduck culture caused substantial increases in biomass densities of surfperch, nearshore demersal fish, and small crabs, and decreases in seabirds, flatfish, and certain invertebrates (e.g. predatory gastropods and small crustaceans). This study identifies species that should be a priority for additional empirical research and monitoring related to bivalve aquaculture interactions, including demersal fish, small crustaceans, and seabirds. It also provides insights into the benefits and challenges of incorporating habitat-related data into a foodweb model. Understanding these relationships can inform management decisions by clarifying trade-offs in ecosystem functions and services in Puget Sound and facilitates estimation of direct and cumulative effects of bivalve aquaculture at a foodweb scale.

Keywords: aquaculture, foodweb, model, non-trophic, shellfish.

Introduction

Bivalve aquaculture is a rapidly growing, global industry that occurs primarily in coastal waters and depends on functioning, productive ecosystems. Interactions between cultured bivalves and the environment can vary with species, grow-out method, harvest and maintenance disturbance regimes, and scale of development (Simenstad and Fresh, 1995; Dumbauld *et al.*, 2009). In regions with both high bivalve densities and water retention times, bivalves may locally deplete phytoplankton (Asmus and Asmus, 1991; Banas *et al.*, 2007), potentially reducing symptoms of eutrophication (Zhou *et al.*, 2006). However, bivalve aquaculture may also alter the

composition of benthic communities (Simenstad and Fresh, 1995; Dubois *et al.*, 2007; Dumbauld *et al.*, 2009; Cheney *et al.*, 2012) and influence the abundance and distribution of higher trophic level animals such as seabirds (Connolly and Colwell, 2005; Zydulis *et al.*, 2009; Faulkner, 2013). Understanding these interactions is important to sustainably manage industry expansion and is critical for supporting ecosystem approaches to aquaculture development (NRC, 2010; Cranford *et al.*, 2012).

Foodweb models, such as Ecopath with Ecosim (EwE; Polovina, 1984; Christensen and Walters, 2004), are useful tools for addressing resource management issues in an ecosystem context. To date,

applications of EwE to bivalve aquaculture have been restricted to modelling trophic relationships, through their role as filter-feeders and prey to other species (Jiang and Gibbs, 2005; Leloup et al., 2008; Byron et al., 2011b). However, bivalve aquaculture may also have important non-trophic effects. Changes in pelagic–benthic coupling, competition for space, prey concentration, predator refuge, and altered habitat structure (either biogenic structure or gear structure) may change the behavior of species and influence interspecific interactions [see review by Dumbauld et al. (2009) and NRC (2010)]. These non-trophic effects of aquaculture are widely documented, but often difficult to incorporate into traditional foodweb models.

Mediation functions are a tool within Ecosim that simulates the influence of a third (mediating) variable on predator–prey interactions, following Wootton's (1994) definition of an interaction modification. Mediation functions can be used to describe non-trophic interactions between species or species and habitats within a foodweb modelling framework (Ainsworth et al., 2008; Ma et al., 2010; Espinosa-Romero et al., 2011; Plummer et al., 2013). For example, mediation functions can be applied to systems in which shellfish farms modify the vulnerability of prey to predators through facilitation (e.g. concentrating prey thereby increasing predation) or protection (e.g. refuge that decreases predation). The mediation effect is the enhancement or dampening caused by the shellfish farm on predator–prey interactions (Christensen et al., 2000). The widespread use of mediation functions is limited by the dearth of knowledge of their functional shape and the strength of the mediating relationships (Harvey, 2014), which typically require regionally specific, empirical data to parameterize. McDonald et al.'s (2015) study on the interaction of geoduck aquaculture and the surrounding community provides us with the data needed to overcome these limitations.

Currently, geoduck (*Panopea generosa*) is the most valuable shellfish cultivated in intertidal Washington State. Recent reported landings have approached 589 670 kg with an estimated value of \$18 500 000 USD (2010 aquaculture landings estimates, Washington Department of Fish and Wildlife). As suspension-feeders, geoducks have a direct trophic effect on phytoplankton, but non-trophic effects resulting from the cultivation process may also influence community members (McDonald et al., 2012, 2015; Price et al., 2012). Geoduck aquaculture production occurs on a 5–7 year cycle. In the early phase of the cycle, a common practice is to protect newly outplanted juvenile geoduck (i.e. seed) from predators by placing them inside vertically oriented sections of polyvinyl chloride (PVC) tube (10–15 cm diameter) inserted into the tideflat; the tubes are then covered with netting to eliminate predator access (McDonald et al., 2015). Initial stocking density is typically 20–30 clams m⁻² (VanBlaricom et al., 2015). These anti-predator structures are removed after ~2 years once the clams have reached a size refuge from most predators (McDonald et al., 2015). Market-sized geoducks are eventually harvested individually by hand in the sixth or seventh year in a process of liquefaction, whereby a harvester uses a hose to inject large volumes of low-pressure water into sediments around the clam to loosen and extract it (VanBlaricom et al., 2015). McDonald et al. (2015) and VanBlaricom et al. (2015) showed, respectively, that anti-predator structure and disturbance resulting from harvest of cultured geoducks can suppress some benthic species while promoting others, and thus culture practices likely have important mediation effects. These empirical data can enable evaluation of geoduck aquaculture expansion on the foodweb and assessment of the relative

importance of trophic vs. non-trophic interactions on the community in a single modelling framework.

In the present study, we revised and expanded a previously published EwE model of the central Basin of Puget Sound (Harvey et al., 2012b) to help evaluate the ecological effects of geoduck aquaculture expansion. Central Puget Sound is the largest of four sub-basins that compose Puget Sound, a major fjordal system located in the northwest USA (Figure 1). Currently, central Puget Sound supports significantly less geoduck harvest relative to other major shellfish-producing regions in Washington State, but the potential to develop geoduck culture further exists. In this study, we examined the effects of geoduck aquaculture on the central Puget Sound ecosystem. Specifically, we sought to explore the influence of trophic and non-trophic interactions on biomass predictions in a foodweb model and identify community and ecosystem responses to increased geoduck farming. We first modified an existing, dynamic, mass-balanced foodweb model of central Puget Sound to include cultured shellfish functional groups and added mediation functions that captured the non-trophic effects of geoduck culture on the surrounding foodweb. We subsequently calculated the trophic and non-trophic effects of expanded geoduck aquaculture on community structure under varying scenarios of expansion.

Material and methods

Model development

We modified a recently parameterized EwE model of central Puget Sound (Harvey et al., 2012b) to incorporate ecological relationships between geoduck aquaculture and the larger foodweb. The central Puget Sound model domain drains a total area of 35 500 km², encompassing all marine habitat between Tacoma Narrows (47.2681°N, 122.5506°W) in the south and Whidbey Island (47.9013°N, –122.3778°W) in the north (Figure 1). Central Puget Sound includes intertidal habitats dominated by sand, gravel, and occasional eelgrass or algal habitats and mud-bottomed subtidal habitats that exceed depths of 250 m in some areas (Figure 1). In addition, the region includes large bays, many pocket estuaries, and receives freshwater inputs from moderately sized rivers (Cedar River, White River, and Green River; Figure 1).

As a general overview, we first revised the EwE model to include additional taxonomic detail regarding nearshore biota relevant to intertidal bivalve aquaculture. Next, we incorporated mediation functions into the model that corresponded to the non-trophic effects of geoduck culture on other species. The functions were directly informed by field experiments and observations (McDonald et al., 2015) and corresponded to mediation effects that reduced the vulnerability of certain species to predation (i.e. predator refuge) or increased the search rate of predators (i.e. habitat exclusion). Finally, we ran scenarios in Ecosim, simulating increased geoduck aquaculture.

The Ecopath model (Polovina, 1984; Christensen and Pauly, 1992) balances biomass gains and losses for each functional group using the following expression:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i = BA_i + Y_i + \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} \quad (1)$$

where the biomass (B), production to biomass ratio (P/B), and ecological efficiency (EE) (the fraction of production used in the system) of prey group i are balanced with the biomass accumulation (BA) and mortalities due to fisheries (Y), and predation by all

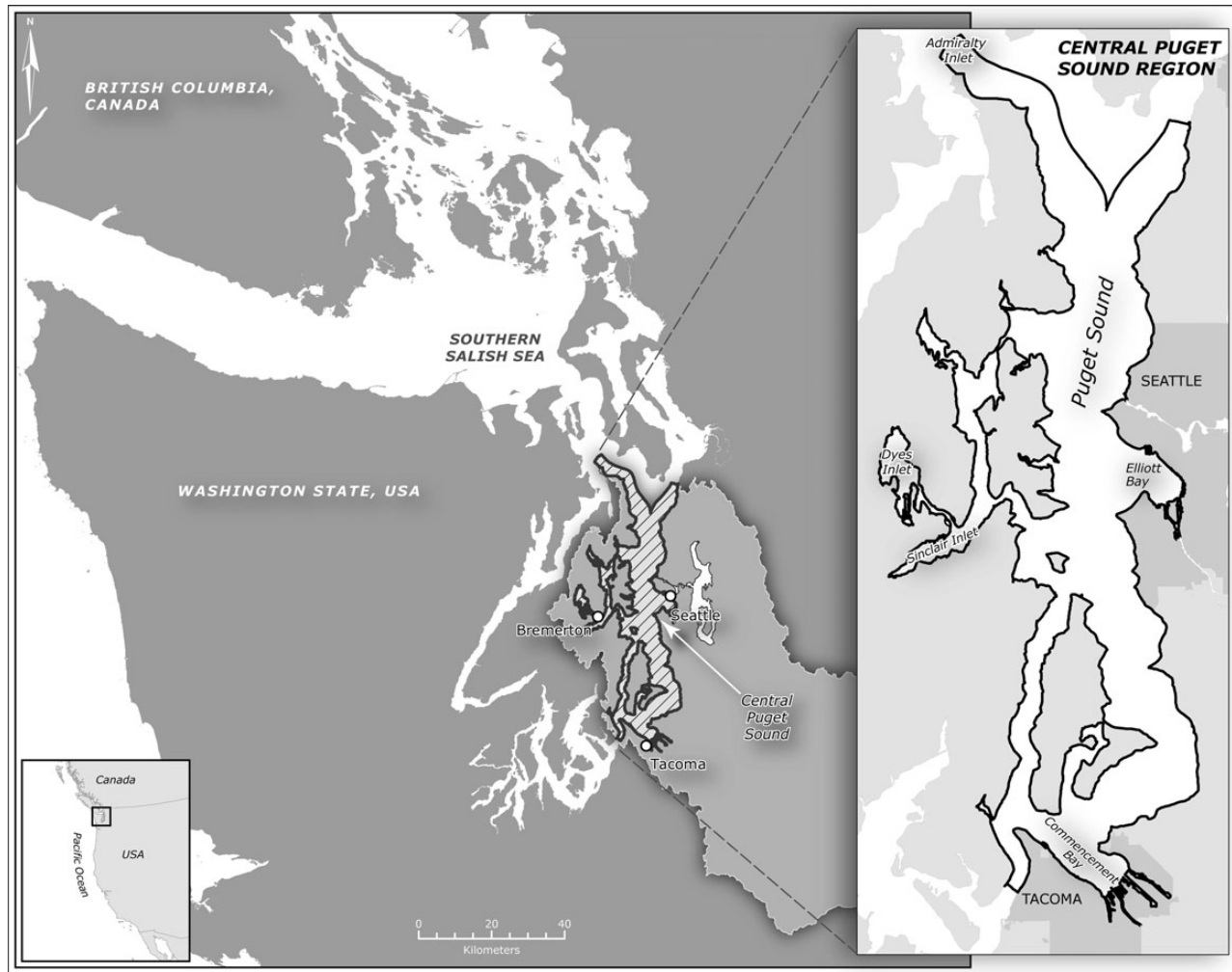


Figure 1. Map of the central Puget Sound, the spatial domain for the EwE model, and the rest of the southern Salish Sea, as well as catchment areas (lightly shaded) that feed directly into central Puget Sound. Inset shows Puget Sound in more detail (Harvey et al., 2012b).

groups j . Predation mortality is calculated using the biomass of all predator groups j , the consumption to biomass ratio (Q/B) of all predator groups, and the fraction of group i in the diet of each group j (DC). Ecopath uses matrix inversion to calculate one parameter (often B or EE) for each group based on inputs of the other parameters such as diet, production, consumption, and mortality rates.

Ecosim adds a temporal dynamic to the foodweb model, allowing the biomass of functional groups to change due to trophic dynamics, harvest, other mortality, immigration, and emigration. A set of differential equations are solved in Ecosim, based on the form:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \quad (2)$$

where $dB_i \cdot dt^{-1}$ represents the growth rate of group i . Biomass increases with net growth efficiency (g_i), total consumption of group i (Q_{ji}), and immigration (I_i). Biomass decreases with predation mortality (Q_{ij}) by all predators on group i , non-predation mortality (M_i), fishing mortality (F_i), and emigration (e_i).

We revised the central Puget Sound model to include additional detail in nearshore functional groups and cultured geoduck groups

(Table 1 and Supplementary Tables S1 and S2). Specifically, we added migratory shorebirds (e.g. dunlins *Calidris alpina*), great blue herons (*Ardea herodias*), small brachyuran crabs, and red rock crab (*Cancer productus*). We also divided the existing infaunal bivalve group into two groups: large- and small-bodied bivalves. Large-bodied bivalves consisted principally of species of interest to recreational and commercial harvesters (e.g. butter clam *Saxidomus gigantean*, horse clam *Tresus capax*, and heart cockle *Clinocardium nuttallii*). Small-bodied bivalves included those not targeted by commercial or recreational harvest (e.g. purple Transennella *Transennella tantilla* and amethyst gem clam *Gemma gemma*).

We added cultured geoducks as a multistanza group, to separate the stages in which anti-predator structure is present (years 1–2), anti-predator structure is absent (years 3–5), and harvest occurs (years 6–7). We calculated the central Puget Sound standing stock biomass based on the 2012 aquaculture landings estimate of 10 546 kg (Washington Department of Fish and Wildlife) and an average geoduck weight of 0.7 kg at harvest. We assumed an estimated natural mortality rate of 50% from outplanting to harvest, with half the mortality occurring in the first 2 years (B. Phipps and J. Gibbons, pers. comm.). We used the von Bertalanffy growth equation to calculate individual growth (maximum length = 158 mm,

Table 1. Functional groups in the EwE model with major representatives.

Functional group	Common name	Scientific classification
Harbour seals	Harbour seal	<i>Phoca vitulina</i>
Sea lions	California sea lion	<i>Zalophus californianus</i>
	Steller sea lion	<i>Eumetopias jubatus</i>
Gulls	Various gulls	<i>Larus</i> spp.
Resident diving birds	Various cormorants	<i>Phalacrocorax</i> spp.
	Pigeon guillemot	<i>Cephus columba</i>
Migratory diving birds	Western grebe	<i>Aechmophorus occidentalis</i>
	Various loons	<i>Gavia</i> spp.
	Common murre	<i>Uria aalga</i>
Nearshore diving birds	Various scoters	<i>Melanitta</i> spp.
	Various goldeneyes	<i>Bucephala</i> spp.
Herbivorous birds	Dabbling ducks	<i>Anas</i> spp.
	Various geese	<i>Branta</i> spp.
Migratory shorebirds	Dunlins	<i>Calidris alpina</i>
Great blue herons	Great blue herons	<i>Ardea herodias</i>
Raptors	Bald eagle	<i>Haliaeetus leucocephalus</i>
Wild salmon	Chum salmon	<i>Oncorhynchus keta</i>
	Chinook salmon	<i>O. tshawytscha</i>
	Coho salmon	<i>O. kisutch</i>
Hatchery salmon	Chum salmon	<i>O. keta</i>
	Chinook salmon	<i>O. tshawytscha</i>
	Coho salmon	<i>O. kisutch</i>
Pink salmon	Pink salmon	<i>O. gorbuscha</i>
Pacific herring	Pacific herring	<i>Clupea pallasii</i>
Forage fish	Surf smelt	<i>Hypomesus pretiosus</i>
	Pacific sand lance	<i>Ammodytes hexapterus</i>
Surfperches	Shiner perch	<i>Cymatogaster aggregata</i>
	Striped seaperch	<i>Embiotoca lateralis</i>
Spiny dogfish	Spiny dogfish	<i>Squalus acanthias</i>
Skates	Longnose skate	<i>Raja rhina</i>
	Big skate	<i>R. binoculata</i>
Ratfish	Whitespotted ratfish	<i>Hydrolagus colliei</i>
Pacific hake	Pacific hake	<i>Merluccius productus</i>
Pacific cod	Pacific cod	<i>Gadus macrocephalus</i>
Walleye pollock	Walleye pollock	<i>Theragra chalcogramma</i>
Lingcod	Lingcod	<i>Ophiodon elongatus</i>
Rockfish	Copper rockfish	<i>Sebastes caurinus</i>
	Quillback rockfish	<i>S. maliger</i>
Piscivorous flatfish	Pacific sanddab	<i>Citharichthys sordidus</i>
Small-mouthed flatfish	English sole	<i>Parophrys vetulus</i>
	Rock sole	<i>Lepidopsetta bilineata</i>
Demersal fish	Various poachers	Family Agonidae
	Various eelpouts	<i>Lycodes</i> spp.
	Various small sculpins	Family Cottidae
Squid	Opalescent (market) squid	<i>Loligo opalescens</i>
Octopus	Red octopus	<i>Octopus rubescens</i>
	Giant Pacific octopus	<i>Enteroctopus dofleini</i>
Shrimp	Pandalid shrimp	Family Pandalidae
	Sand shrimp	<i>Crangon</i> spp.
Cancer crabs	Dungeness crab	<i>Cancer magister</i>
Red rock crab	Red rock crab	<i>Cancer productus</i>
Sea stars	Sunflower star	<i>Pycnopodia helianthoides</i>
	Pink sea star	<i>Pisaster brevispinis</i>
Sea urchins	Green sea urchin	<i>Strongylocentrotus droebachiensis</i>
	Red sea urchin	<i>S. franciscanus</i>
Other grazers	Various snails	Class Gastropoda
	Various chitons	Class Polyplacophora
Small crustaceans	Various amphipods	Suborders Gammaridea, Corophiidea
	Various mysids	Family Mysidae

Continued

Table 1. Continued

Functional group	Common name	Scientific classification
Small crabs	Various crabs	Infraorders Brachyura, Anomura
Large sea cucumbers	California sea cucumber	<i>Parastichopus californicus</i>
Predatory gastropods	Moon snail	<i>Euspira lewisii</i>
	Hairy triton	<i>Fusitriton oregonensis</i>
Mussels	Blue mussel	<i>Mytilus edulis</i>
Barnacles	Various barnacles	Suborder Balanomorpha
Geoducks	Geoduck	<i>Panopea abrupta</i>
Cultured geoduck	Geoduck	<i>Panopea generosa</i>
Large infaunal bivalves	Butter clam	<i>Saxidomus gigantea</i>
	Horse clam	<i>Tresus capax</i>
	Native littleneck clam	<i>Leukoma staminea</i>
	Manila clam	<i>Venerupis philippinarum</i>
Small infaunal bivalves	Purple Transennella	<i>Transennella tantilla</i>
	Amethyst gemclam	<i>Gemma gemma</i>
	Charlotte macoma	<i>Macoma carlottensis</i>
	Baltic macoma	<i>Macoma balthica</i>
Soft infauna	Polychaetes	Class Polychaeta
Deposit feeders	Brittlestars	<i>Amphiodia urtica</i>
	Various sea cucumbers	Class Holothuroidea
Suspension-feeders	Various sponges	Phylum Porifera
	Various bryozoans	Phylum Bryozoa
	Sea pen	<i>Ptilosarcus gurneyi</i>
Tunicates	Various sea squirts	Class Ascidiacea
Bacteria	Various bacteria	
Microzooplankton	Various microzooplankton	
Copepods	Various copepods	Order Calanoida
Euphausiids	Pacific krill	<i>Euphausia pacifica</i>
Small gelatinous zooplankton	Various small jellyfish, ctenophores, and other soft plankton	
Jellyfish	Lion's mane jelly	<i>Cyanea capillata</i>
	Moon jelly	<i>Aurelia labiata</i>
	Fried egg jelly	<i>Phacellophora camtschatica</i>
Macrozooplankton	Various planktonic shrimp, amphipods, and larval crustaceans	
Phytoplankton	Various diatoms, dinoflagellates and phytoflagellates	
Benthic microalgae	Various benthic diatoms	
Benthic macroalgae	Various understory algal species	
Overstory kelp	Bull kelp	<i>Nereocystis luetkeanus</i>
Eelgrass	Native eelgrass	<i>Zostera marina</i>
Detritus	Not available	
Plant/algal material	Not available	
Salmon carcasses	Not available	<i>Oncorhynchus</i> spp.

length at maturity = 75 mm, $k = 0.19$; Bradbury and Tagart, 2000; Calderon-Aguilera et al., 2010), and logistic growth to estimate the number of geoducks over time. We assumed von Bertalanffy growth to keep consistent with the Ecpath biomass calculations for multistanza groups. To determine density ($t \text{ km}^{-2}$), we divided these biomass estimates by the product of total area in central Puget Sound (757.08 km^2 ; Harvey et al., 2012b) and the proportion

of that area in the 0- to 10-m depth range (0.137 km²; Harvey *et al.*, 2012b). The resulting densities are 5.288 t km⁻² (years 1–2), 9.689 t km⁻² (years 3–5), and 5.025 t km⁻² (years 6–7). The density would be largely underestimated in planted areas and overestimated in unplanted areas. This is consistent with how other Ecopath population densities are estimated.

Mediation

Mediation functions are a tool within Ecosim that can simulate the influence of a functional group or species on the strength of predator–prey interactions between a different pair of species. The consumption rate (Q) of prey (i) by predator (j) is defined in Ecosim as

$$Q = \left(\frac{a_{ij}}{A_{ij}} \right) \cdot \frac{v_{ij} \cdot B_i}{(2V_{ij} + (a_{ij}/A_{ij}) \cdot P_j)} \cdot P_j \quad (3)$$

where a_{ij} is the rate of effective search for i by j , A_{ij} is the search area in which j forages for i , v_{ij} is the flow rate of biomass (B_i) between pools that are vulnerable or invulnerable to predation, and P_j is the abundance of j in A_{ij} . A mediation function influences a_{ij} , A_{ij} , and (or) v_{ij} according to a user-defined function. An increased v_{ij} makes i subject to greater top-down control and increasing a_{ij} makes j a more efficient consumer of i . Input mediation multipliers range from 0 to 1, and are rescaled by Ecosim to equal one when the biomass of the mediating group is at its initial baseline density.

We included two sets of mediation functions: non-aquaculture-related interactions previously published for the central Puget Sound model (Harvey *et al.*, 2012a; Plummer *et al.*, 2013; Harvey, 2014), and those based on an empirical study of the effects of geoduck culture on macrobenthic communities in South Puget Sound (summarized in Table 2; McDonald *et al.*, 2015). Following Plummer *et al.* (2013), we allowed increasing eelgrass biomass to positively mediate v_{ij} values for the prey of juvenile salmon (i.e. greater top-down control as eelgrass aggregates prey), negatively mediate v_{ij} values for juvenile salmon and young of the year crab (i.e. more bottom-up control as eelgrass increases and provides refuge from nearshore predators), and positively mediate the a_{ij} value for juvenile Pacific herring *Clupea pallasii* (greater juvenile herring productivity as eelgrass increases and provides spawning substrate). Harvey *et al.* (2012a) described a behavioral mediation effect where resident and overwintering bald eagles *Haliaeetus leucocephalus* (the mediating groups) harass nearshore diving and herbivorous seabirds, which causes them to expend more energy to avoid eagle predation while foraging. That is, the variables A_{ij} (of the nearshore diving and herbivorous seabirds) and v_{ij} (of their prey), which relate foraging ability, were modelled as a decreasing function of increasing eagle biomass.

The geoduck aquaculture mediation functions are primarily based on observed numerical responses of benthic invertebrates to anti-predator structure (partially buried PVC tubes with net covers) placed on plots with outplanted geoducks over their first 2 years (Table 2). Functional groups thought to gain refuge from the anti-predator structure, and that exhibited higher biomass densities inside geoduck plots with the anti-predator structure, had mediation functions wherein vulnerability to predation (v_{ij}) decreased as a function of increasing geoduck culture (Table 2). If a prey and its predator species both had higher biomass densities inside geoduck anti-predator structure, we added two separate positive and negative mediation functions on the predation vulnerability

of the prey species, as we could not determine how the predator–prey dynamics would play out (e.g. demersal fish prey upon surfperch and both groups had higher biomasses inside geoduck farms; Table 2). For groups that showed lower biomass densities inside geoduck plots and that were thought to be excluded (e.g. flatfish and predatory gastropods, Table 2), their search rates (a_{ij}) were set to decrease as a function of increasing cultured geoduck biomass (Table 2). That is, they became less efficient at finding prey. These geoduck mediation effects were only applied to predator–prey functional groups found in intertidal habitats where geoduck farms are likely to be sited.

McDonald *et al.* (2015) found an anti-predatory structure on geoduck plots to have an exclusionary effect on flatfish and predatory gastropods (moon snail *Lunatia lewisii*), and an attraction effect on demersal fish (e.g. gunnels and shiner perch), small crabs, sea stars, and red rock crabs (Table 2). The small crustaceans and large infaunal bivalve groups were unique in that they had relationships to multiple geoduck stanzas (i.e. the youngest geoduck stanza associated with the anti-predator structure and the oldest stanza subject to harvest). Small crustacean biomass densities (based on *Corophium* amphipods) decreased in geoduck plots with the anti-predator structure, and were assumed to be excluded from the plots (their search rate a_{ij} decreased; Table 2). During the geoduck harvest stage, small crustacean biomass densities increased, and predator refuge was assumed (their vulnerability v_{ij} decreased; Table 2). Large infaunal bivalve biomass (based on the heart cockle) increased in geoduck anti-predator structure (predator refuge; their vulnerability v_{ij} decreased) and decreased during the final, harvest stage of cultured geoducks (habitat exclusion; their search rate a_{ij} decreased; Table 2).

In the absence of empirical data on the shape and strength of these functions, we set the shape of all mediation functions to a hyperbolic function, as this is the most conservative approach (Harvey, 2014), defined as

$$\frac{M_{\min} + (M_{\max} - M_{\min})}{1 + k \cdot B} \quad (4)$$

where the endpoints are defined by M_{\max} (Ecosim: Y_{zero}) and M_{\min} (Ecosim: Y_{end}), and the curve has a gradient of k (Ecosim: Y_{base}). The values for each parameter were set to 2, 0, and 1, respectively, for all functional groups except small crustaceans. The small crustacean group is composed of mysid shrimps, cumaceans, benthic amphipods (suborders Gammaridea and Corophiidae), and benthic isopods. Because benthic amphipods are directly targeted by a cultured geoduck mediation effect (Table 2), but make up only one-third of the small crustacean group as defined by Harvey *et al.* (2012a), we made the functional curve for this mediation effect more conservative while keeping the same hyperbolic trend by setting k to 1.5.

Analysis

Our analysis consisted of two phases. First, we estimated the ecological carrying capacity for cultured geoducks in central Puget Sound and assessed the presence of ecological thresholds related to increasing geoduck aquaculture. Second, we identified trophic and non-trophic effects of geoduck culture on individual functional groups.

Ecological carrying capacity is the biomass of cultured geoducks that can be supported by the existing levels of phytoplankton production [as defined by Harvey *et al.* (2012a)], before the foodweb

Table 2. Mediation effects specific to geoduck culture in Puget Sound (McDonald et al., 2015) and added to the central Puget Sound EwE model.

Species/group (McDonald et al., 2015)	EwE group	Mediation parameter
Starry flounder (<i>Platichthys stellatus</i>) Sand sole (<i>Psettichthys melanostictus</i>)	Small mouth flatfish (–)	– <i>a</i> surfperch, small mouth flatfish ⁽¹⁾ – <i>a</i> shrimp, small mouth flatfish ⁽¹⁾ – <i>a</i> YOY crab, small mouth flatfish ⁽¹⁾ – <i>a</i> other grazers, small mouth flatfish ⁽¹⁾ – <i>a</i> small crabs, small mouth flatfish ⁽¹⁾ – <i>a</i> small mouth flatfish, barnacles ⁽¹⁾ – <i>a</i> soft infauna, small mouth flatfish ⁽¹⁾
Speckled sanddab (<i>Citharichthys stigmaeus</i>)	Piscivorous flatfish (–)	– <i>a</i> deposit feeders, small mouth flatfish ⁽¹⁾ – <i>a</i> surfperch, piscivorous flatfish ⁽¹⁾ – <i>a</i> demersal fish, piscivorous flatfish ⁽¹⁾ – <i>a</i> shrimp, piscivorous flatfish ⁽¹⁾ – <i>a</i> other grazers, piscivorous flatfish ⁽¹⁾ – <i>a</i> small crabs, piscivorous flatfish ⁽¹⁾ – <i>a</i> barnacles, piscivorous flatfish ⁽¹⁾ + <i>a</i> soft infauna, piscivorous flatfish ⁽¹⁾
Saddleback gunnel (<i>Pholis ornate</i>) Pinpoint gunnel (<i>Apodichthys flavidus</i>) Crescent gunnel (<i>Pholis laeta</i>) Bay pipefish (<i>Syngnathus leptorhynchus</i>) Snake prickleback (<i>Lumpenus sagittal</i>) Tubesnout (<i>Aulorhynchus flavidus</i>)	Demersal fish (+)	– <i>v</i> demersal fish, sea lions ⁽¹⁾ – <i>v</i> demersal fish, gulls ⁽¹⁾ – <i>v</i> demersal fish, resident birds ⁽¹⁾ – <i>v</i> demersal fish, migratory birds ⁽¹⁾ – <i>v</i> demersal fish, great blue herons ⁽¹⁾ – <i>v</i> demersal fish, migratory eagles ⁽¹⁾ – <i>v</i> demersal fish, resident eagles ⁽¹⁾ – <i>v</i> demersal fish, juvenile wild salmon ⁽¹⁾ – <i>v</i> demersal fish, juvenile hatchery salmon ⁽¹⁾ – <i>v</i> demersal fish, piscivorous flatfish ⁽¹⁾
Shiner surfperch (<i>Cymatogaster aggregate</i>)	Surfperch (+)	– <i>v</i> surfperch, resident birds ⁽¹⁾ – <i>v</i> surfperch, migratory birds ⁽¹⁾ – <i>v</i> surfperch, great blue herons ⁽¹⁾ – <i>v</i> surfperch, migratory eagles ⁽¹⁾ – <i>v</i> surfperch, resident eagles ⁽¹⁾ – <i>v</i> surfperch, juvenile wild salmon ⁽¹⁾ – <i>v</i> surfperch, juvenile hatchery salmon ⁽¹⁾ – <i>v</i> surfperch, piscivorous flatfish ⁽¹⁾ – <i>v</i> surfperch, small mouth flatfish ⁽¹⁾ – <i>v</i> surfperch, demersal fish ⁽¹⁾ + <i>v</i> surfperch, demersal fish ⁽¹⁾ – <i>v</i> surfperch, YOY crab ⁽¹⁾
Red rock crabs (<i>Cancer productus</i>)	Red rock crabs (+)	– <i>v</i> red rock crabs, gulls ⁽¹⁾ – <i>v</i> red rock crabs, resident birds ⁽¹⁾ – <i>v</i> red rock crabs, demersal fish ⁽¹⁾ + <i>v</i> red rock crabs, demersal fish ⁽¹⁾ – <i>v</i> red rock crabs, octopus ⁽¹⁾ – <i>v</i> red rock crabs, sea stars ⁽¹⁾ + <i>v</i> red rock crabs, sea stars ⁽¹⁾
Small crabs (Infraorder Brachyuran)	Small crabs (+)	– <i>v</i> small crabs, forage fish ⁽¹⁾ – <i>v</i> small crabs, surfperch ⁽¹⁾ + <i>v</i> small crabs, surfperch ⁽¹⁾ – <i>v</i> small crabs, demersal fish ⁽¹⁾ + <i>v</i> small crabs, demersal fish ⁽¹⁾ – <i>v</i> small crabs, sea stars ⁽¹⁾ + <i>v</i> small crabs, sea stars ⁽¹⁾
Pacific moon snails (<i>Euspira lewisii</i>)	Predatory gastropods (–)	– <i>a</i> urchins, predatory gastropods ⁽¹⁾ – <i>a</i> other grazers, predatory gastropods ⁽¹⁾ – <i>a</i> mussels, predatory gastropods ⁽¹⁾ – <i>a</i> barnacles, predatory gastropods ⁽¹⁾ – <i>a</i> large infaunal bivalves, predatory gastropods ⁽³⁾ – <i>v</i> small infaunal bivalves, predatory gastropods ⁽³⁾ + <i>v</i> small infaunal bivalves, predatory gastropods ⁽³⁾ – <i>a</i> suspension-feeders, predatory gastropods ⁽¹⁾ – <i>a</i> tunicates, predatory gastropods ⁽¹⁾

Continued

Table 2. Continued

Species/group (McDonald et al., 2015)	EwE group	Mediation parameter		
Heart cockles (<i>Clinocardium nuttallii</i>)	Large infaunal bivalves (+ ⁽¹⁾ /− ⁽³⁾)	− $v_{\text{large infaunal bivalves, gulls}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, gulls}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, nearshore birds}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, nearshore birds}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, migratory shorebirds}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, migratory shorebirds}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, surfperch}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, surfperch}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, piscivorous flatfish}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, piscivorous flatfish}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, small mouth flatfish}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, small mouth flatfish}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, demersal fish}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, demersal fish}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, octopus}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, octopus}}$ ⁽³⁾		
		− $v_{\text{large infaunal bivalves, YOY crab}}$ ⁽¹⁾		
		+ $v_{\text{large infaunal bivalves, YOY crab}}$ ⁽³⁾		
		Heart cockles (<i>Clinocardium nuttallii</i>)	Large infaunal bivalves (+ ⁽¹⁾ /− ⁽³⁾)	− $v_{\text{large infaunal bivalves, red rock crab}}$ ⁽¹⁾
				+ $v_{\text{large infaunal bivalves, red rock crab}}$ ⁽³⁾
− $v_{\text{large infaunal bivalves, sea stars}}$ ⁽¹⁾				
+ $v_{\text{large infaunal bivalves, sea stars}}$ ⁽³⁾				
− $v_{\text{large infaunal bivalves, small crabs}}$ ⁽¹⁾				
+ $v_{\text{large infaunal bivalves, small crabs}}$ ⁽³⁾				
− $v_{\text{large infaunal bivalves, small crabs}}$ ⁽³⁾				
+ $v_{\text{large infaunal bivalves, small crabs}}$ ⁽³⁾				
− $v_{\text{large infaunal bivalves, predatory gastropods}}$ ⁽¹⁾				
+ $v_{\text{large infaunal bivalves, predatory gastropods}}$ ⁽³⁾				
Corophium amphipods	Small crustaceans (− ⁽¹⁾ /+ ⁽³⁾)	− $a_{\text{bacteria, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{bacteria, small crustaceans}}$ ⁽³⁾		
		+ $a_{\text{phytoplankton, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{phytoplankton, small crustaceans}}$ ⁽³⁾		
		+ $a_{\text{benthic microalgae, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{benthic microalgae, small crustaceans}}$ ⁽³⁾		
		+ $a_{\text{benthic macroalgae, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{benthic macroalgae, small crustaceans}}$ ⁽³⁾		
		+ $a_{\text{eelgrass, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{eelgrass, small crustaceans}}$ ⁽³⁾		
		+ $a_{\text{algal/plant matter, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{algal/plant matter, small crustaceans}}$ ⁽³⁾		
		+ $a_{\text{detritus, small crustaceans}}$ ⁽¹⁾		
		+ $v_{\text{detritus, small crustaceans}}$ ⁽³⁾		

Sign (+ or −) in the EwE Group column indicates the effect of geoduck culture on the functional group, as observed by McDonald et al. (2015). The superscript numbers 1 and 3 associated with the mediation parameter indicate whether the mediation function is based on the effect of anti-predation structure in the first stanza of culture (years 1 and 2) or due to harvest disturbance in the third stanza (years 6 or 7). Mediation parameters correspond to an increase (+) or decrease (−) in the vulnerability (v_{ij}) of the prey (i) or search rate (a_{ij}) on the predator (j).

becomes unbalanced. The foodweb was deemed “unbalanced” when the ecotrophic efficiency of phytoplankton exceeded 1 [as calculated by the mass–balance algorithm described in Equation (1)], and occurs when phytoplankton grazing mortality exceeds total productivity (Jiang and Gibbs, 2005; Byron et al., 2011a). We calculated ecological carrying capacity by incrementally increasing the cultured geoduck biomass and associated landings until reaching the ecological carrying capacity threshold. We increased the cultured geoduck biomass and landings proportional to the base model values.

We calculated changes in ecosystem attributes by using four established indices: the Ecosystem Reorganization Index, the Shannon Diversity Index, Mean Trophic Level (MTL), and Mixed Trophic Impact (Libralato et al., 2006; Samhouri et al., 2010). These attributes describe the capacity of an ecosystem to absorb perturbations while retaining essential structure

and function and quantify the ecosystem impact of individual functional groups. The Ecosystem Reorganization Index approximates ecosystem resilience (Folke et al., 2004) by measuring the extent to which perturbations cause changes in the relative biomass of individual functional groups ($B_{t,i}$; Samhouri et al., 2009):

$$R = - \left[\sum_i \left| \frac{B_{t_2,i} - B_{t_1,i}}{\sum_i B_{t_1,i}} \right| - \left| \frac{\sum_i B_{t_2,i} - \sum_i B_{t_1,i}}{\sum_i B_{t_1,i}} \right| \right] \cdot 100 \quad (5)$$

A value of R farther from 0 indicates lower resilience, implying that the aggregate biomass and the individual functional groups respond differently in magnitude and direction to a pressure. This is a relative index, with 0 as the lower bound (unstressed) and an unlimited upper bound (stressed) dependent on changes

Table 3. Ecosystem attributes measured in response to increased geoduck biomass in the central Puget Sound foodweb.

Attributes	Per cent increase in geoduck biomass (t km^{-2})							Unstressed state
	20	70	80	90	100	110	120	
Ecosystem Reorganization Index	0.65	2.34	2.68	3.01	3.34	3.65	3.97	Close to 0
Shannon Diversity Index	3.23	3.23	3.23	3.23	3.23	3.23	3.23	High
Change in MTL relative to base	0.02	0.05	0.05	0.06	0.06	0.06	0.06	High MTL

Attributes reflect system conditions at the end of 50-year simulations.

in biomass. We used the Shannon Diversity Index and a biomass-weighted MTL of the foodweb as additional indicators of how changes in cultured geoduck biomass might affect overall foodweb structure. Lower species diversity generally indicates a more stressed ecosystem as species dominance increases and functional redundancy decreases (Odum, 1985). Lower MTL indicates shorter food chains and a more stressed foodweb due to reduced energy flow at higher trophic levels and/or greater sensitivity of predators to stress (Odum, 1985). The Mixed Trophic Impact (m_{ij}) quantifies the direct and indirect impacts of (impacting) group i on (impacted) group j across all trophic pathways that link the two groups, as calculated in Ecopath with Ecosim software. The index does not include connections via mediation functions and thus does not represent non-trophic interactions. We calculated the cumulative Mixed Trophic Impact (ε_i) to determine the net influence of each functional group on the foodweb following Libralato *et al.* (2006):

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2} \quad (6)$$

We evaluated the trophic and non-trophic effects of adding cultured geoduck to central Puget Sound by creating three versions of the model: (i) current (low) level of cultured geoducks (base model), (ii) 120% cultured geoduck biomass but no geoduck mediation functions (i.e. trophic effects only); and (iii) 120% cultured geoduck biomass with geoduck mediation functions (i.e. trophic and non-trophic effects). To perturb the foodweb, we forced an increase in cultured geoduck biomass and associated landings by 120% over 50 years. A 120% increase represented a realistic level of increase in geoduck aquaculture and was a large enough perturbation to allow us to examine changes across multiple trophic levels, habitats, and life histories (e.g. birds, pelagic fish, demersal fish, and invertebrates). We compared functional group biomass predictions from the base model (low cultured geoduck biomass) with those from the model with 120% cultured geoduck biomass and no geoduck mediation effects (trophic effects only), as well as the model with 120% cultured geoduck biomass with geoduck mediation functions (trophic and non-trophic effects) to determine the ecological impacts of expanding geoduck aquaculture. We calculated the per cent change in the relative biomass of each functional group in year 50. We then ran the 50-year simulations with individual mediation functions turned off to determine their specific effects on the target functional group as well as their impact on other trophically linked functional groups in the foodweb. Finally, we ran simulations with only individual mediation functions turned on for demersal fish and small crustaceans to determine their influence throughout the foodweb. These functional groups are important prey for a large portion of the foodweb and are likely to have disproportionate effects on foodweb dynamics.

Results

A 120% increase in cultured geoduck biomass had a limited impact on phytoplankton biomass and measures of ecological resilience. The current cultured geoduck standing stock is $\sim 0.1\%$ of the estimated ecological carrying capacity in central Puget Sound (5928 t km^{-2}). At this threshold, the ecotrophic efficiency of phytoplankton exceeded a value of 1, due to grazing mortality exceeding total phytoplankton productivity. As cultured geoduck biomass approached 120% of its initial level, the Ecosystem Reorganization Index diverged from 0 by a small amount indicating a slight reduction in stability, the MTL slightly increased, indicating increased stability, and the Shannon Diversity Index remained constant (Table 3). The Mixed Trophic Impact was very low for cultured geoduck (ranking in the bottom 10 of all 79 functional groups; Supplementary Table S3).

The addition of cultured geoducks into the central Puget Sound foodweb without any mediation functions had very little impact on the simulated biomasses of other functional groups (Supplementary Table S4). That is, after increasing the geoduck biomass by 120% over 50 years, the direct trophic effect of geoduck as a grazer on phytoplankton and as prey resource to other species was nearly negligible. The biomass densities of two geoduck predator groups, sea stars and age 4+ Dungeness crabs (*Cancer magister*), increased by 2% whereas all other functional groups varied by $< 1\%$ (Supplementary Table S4). The low Mixed Trophic Impact values for cultured geoduck further support these results (Supplementary Table S3).

In contrast, the addition of cultured geoduck mediation functions had a notable impact on the foodweb (Figure 2 and Supplementary Table S4). The biomass of functional groups that were linked to geoduck culture through mediation functions changed considerably, with the biomass densities of some groups increasing and decreasing by over 20% (e.g. surfperch, small crabs, predatory gastropods, and small mouth flatfish; Figure 2). In addition, changes in the biomass of functional groups directly linked to geoduck culture, propagated through the foodweb, contributing to additional changes to biomass in other groups (Figure 2 and Supplementary Table S4).

In total, the biomasses of 9 of the 10 functional groups with cultured geoduck mediation functions changed substantially and were among the top 20 groups demonstrating the greatest change in biomass (Figure 2). Red rock crab was the one exception, which showed $< 1\%$ change in biomass and had a negative trend despite a positive mediation function (Supplementary Table S4). Small crab biomass increased as a direct effect of their targeted mediation function and decreased without it (Figure 2).

Geoduck mediation functions linked to demersal fish and small crustaceans had substantial effects on the foodweb (Figure 3), supported by the high cumulative Mixed Trophic Impact values for demersal fish and small crustaceans (ranked 11th and 25th of 79 functional groups; Supplementary Table S3). For example, the cultured geoduck–demersal fish mediation function resulted in decreases in herons (-23%) and resident birds (-17%), and

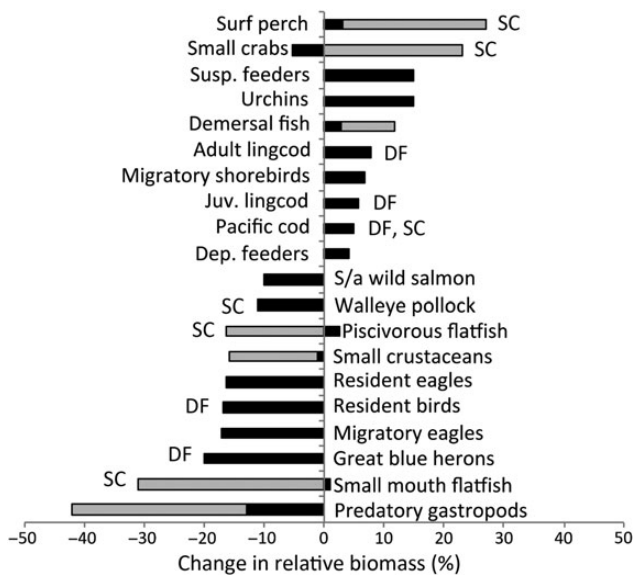


Figure 2. Functional groups with the greatest change in relative biomass between initial conditions and a simulated 120% increase in geoduck biomass over 50 years. Changes in biomass resulting from targeted mediation effects (grey) or trophic connections to groups targeted by mediation effects (black) are indicated. For all but “small crabs”, effects are additive. The labels DF (demersal fish) and SC (small crustaceans) denote if those groups are one of their top three prey (as defined by Ecosim). Relative changes in biomass for all foodweb members are in Supplementary Table S2.

increases in Pacific cod (*Gadus macrocephalus*; +7%) and harbour seals (*Phoca vitulina*; +7%; Figure 3). The cultured geoduck–small crustacean mediation functions resulted in reductions in the biomasses of juvenile wild salmon (−7%) and juvenile hatchery salmon (−4%).

Discussion

Foodweb models focused on evaluating the ecological effects of aquaculture have largely neglected non-trophic effects. Our analysis demonstrates the importance of including non-trophic interactions when evaluating the ecological effects of shellfish aquaculture. Accounting for trophic and non-trophic interactions, we demonstrate that the central Puget Sound foodweb can support an increase in geoduck aquaculture with limited changes in individual species’ biomass and ecosystem resilience at a basin scale. We also identified several functional groups that may be substantially affected by increased geoduck culture. In contrast, models with only trophic effects of cultured geoduck predicted negligible changes in biomass for functional groups due to geoduck aquaculture.

Habitat modification and facilitation are the predominant ecological effects of geoduck aquaculture in a highly productive system such as central Puget Sound. The trophic impacts of cultured geoducks as both grazer and prey were not influential at the system level. Cultured geoducks did not substantially reduce the availability of phytoplankton for other species, as demonstrated by the small impact on ecological carrying capacity. In addition, geoduck predators (moon snails, starfish, flatfish, red rock crab, and seabirds) are all generalists to varying degrees and showed a limited change in biomass in response to increased geoduck aquaculture. The impact of anti-predator structure (PVC tubes and nets) placed on

geoduck plots, however, had a larger influence on the surrounding foodweb by providing predation refuge or by changing foraging opportunities. In turn, these effects propagated throughout the foodweb. The ecological effects of aquaculture structure and habitat modification have been observed for other bivalve species in a range of systems [reviewed in Coen *et al.* (2011)]. Pacific oyster on-bottom culture may reduce eelgrass densities, blade size, and growth rates (Dumbauld *et al.*, 2009; Tallis *et al.*, 2009) and mudflat graveling for clam cultivation may alter benthic community composition (Thom *et al.*, 1994; Simenstad and Fresh, 1995). We suggest that efforts to understand the ecological effects of shellfish aquaculture in productive systems should go beyond modelling the direct trophic effects of bivalves and incorporate non-trophic information when possible. In addition, empirical research is required to determine the functional form and strength of these non-trophic interactions to better determine their influence on the surrounding community (Harvey, 2014).

Functional groups sensitive to changes in increased geoduck aquaculture represent various habitats, trophic levels, and life histories, and are candidate indicators for environmental impacts of increased bivalve aquaculture (e.g. Samhouri *et al.*, 2009). Notably, these species were only sensitive to changes in cultured geoduck with the inclusion of non-trophic mediation effects. Some of these groups (birds, salmon, and benthic fish) are already represented in existing and suggested indicator lists of ecosystem health for Puget Sound (Kershner *et al.*, 2011; Puget Sound Partnership, 2013; Harvey *et al.*, 2014), partly due to the existence of ongoing monitoring programmes. Other species sensitive to geoduck culture (nearshore demersal fish, small crustaceans, and flatfish) are less consistently sampled in the region, but may also prove informative as indicators. Our indicators of ecosystem structure and function (MTL, Shannon Biodiversity Index, Ecosystem Reorganization Index, and Mixed Trophic Impact) did not show conclusive trends, implying that the effects of geoduck culture may be more influential at the species vs. the system level. Additional diet, life history, and aquaculture interaction data for nearshore, demersal fish, small crustaceans, and various bird groups would improve our model and further refine the list of candidate ecosystem indicators for geoduck aquaculture.

The demersal fish and small crustacean functional groups were sensitive to increased cultured geoduck biomass and subsequently influenced biomass changes throughout the foodweb. Their substantial bottom-up influence is due to the aggregation of multiple key prey species into single functional groups, and their multiple trophic connections across the foodweb. The demersal fish community (e.g. poachers, eelpouts, and sculpins) is one of the most diverse and abundant in Puget Sound; however, relatively little is known of their biomass, diet, and life history (Reum and Essington, 2008; Harvey *et al.*, 2012b). In the model, the demersal fish benefit from predator refuge provided by the anti-predation structure on geoduck farms, allowing their population to increase while other predator populations (e.g. seabirds) decreased due to the lack of prey availability. Small crustaceans are one of the most important functional groups in the system, supporting the most bird groups, fish groups, and certain invertebrates (e.g. shrimp, octopuses, age 0+ *Cancer* crabs, and sea stars; Harvey *et al.*, 2012b). This group is one of the seven functional groups that comprise 68% of the total biomass in the foodweb (Harvey *et al.*, 2012b). The small crustaceans experienced a net decrease in biomass as cultured geoduck biomass increased, due to a negative interaction with anti-predation structure associated with cultured geoducks (although they

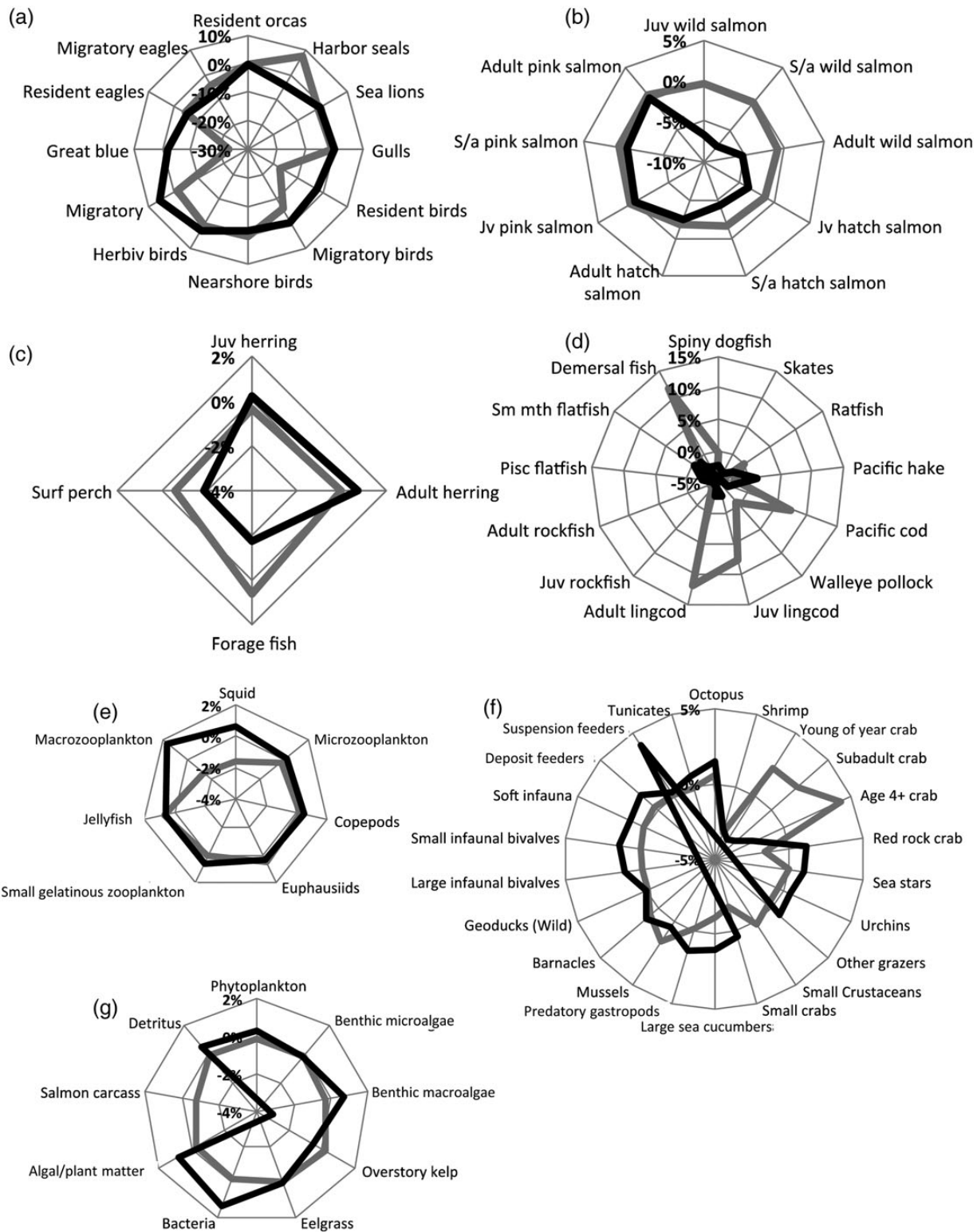


Figure 3. Per cent change in relative biomass due to the addition of individual geoduck mediation effects (see Table 2 for details) on demersal fish (grey lines) and small crustaceans (black). Foodweb groups are divided according to: (a) marine mammals and birds, (b) salmon, (c) pelagic vertebrates, (d) benthic vertebrates, (e) pelagic invertebrates, (f) benthic invertebrates, and (g) primary producers, microbial, and detrital groups.

responded positively to the harvest stage) and potentially due to an increase in predation (e.g. by surfperch and small crabs). Obtaining additional biomass, diet, and life history data and creating species-

specific functional groups for demersal fish and small crustaceans would clarify the trophic linkages responding directly to changes in cultured geoduck biomass.

The substantial decrease of most bird groups in the model is important to note, as these are important ecologically, culturally, and socio-economically. A decrease in eagle populations as cultured geoducks increase should benefit other bird groups through release from predation (Harvey *et al.*, 2012b). The biomass of other birds decrease, however, implying bottom-up control in that they have reduced access to key prey (e.g. demersal fish and small crustaceans) due to the predator refuge provided by anti-predator nets on geoduck farms. Migratory shore birds (biomass increase) do not primarily prey upon demersal fish and small crustaceans, and are likely benefiting from a release of eagle predation while not suffering prey depletion. Limited empirical studies have shown both negative and positive interactions between bivalve aquaculture and marine birds (Kelly *et al.*, 1996; Connolly and Colwell, 2005; Zydalis *et al.*, 2009; Coen *et al.*, 2011) in other systems, suggesting that some interactions are likely. Further empirical study is required to understand the relationship between shellfish aquaculture and birds, and validate these results.

Mediation functions in Ecosim are an important tool for incorporating non-trophic interactions into foodweb models, and can help improve their utility in supporting ecosystem approaches to aquaculture. Although mediation functions can help incorporate habitat-specific patterns in the model, they are not equivalent to spatially explicit models (e.g. Atlantis or Ecospace; Fulton *et al.*, 2004a, b; Walters *et al.*, 2010) and are unable to address such issues as the spatial scale of influence of geoduck farms and local community effects. For instance, shifts in the biomass of the subtidal walleye pollock (*Gadus chalcogrammus*) and Pacific cod in response to increased cultured geoduck are most likely due to the model assumptions that demersal fish and small crustaceans are basin-wide, continuous populations. Spatial resolution can enhance model performance (Fulton *et al.*, 2003, 2004c; Gruss *et al.*, 2014), but may also increase uncertainty in model predictions due to limited habitat data. The incorporation of mediation functions into spatial versions of EwE (i.e. Ecospace) offers a promising area of future research as it could enable evaluation of spatially explicit aquaculture development scenarios.

Acknowledgements

Financial support was provided to BEF through a Washington State contract to Washington Sea Grant. Thanks to Joth Davis, Jim Gibbons, Tom Good, Kristin Marshall, Brian Phipps, Jameal Samhoury, and Phil Levin for helping inform the model, analysis, and improving the manuscript. We also thank participants in an August 2014 workshop on shellfish aquaculture in Washington State, which was facilitated by Washington Sea Grant and supported by funds made available by Washington State.

Supplementary data

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

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Handling editor: Jason Link