Effects of climate change on coastal ecosystem food webs: Implications for aquaculture

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ABSTRACT

Coastal ecosystems provide important ecosystem services for millions of people. Climate change is modifying coastal ecosystem food web structure and function and threatens these essential ecosystem services. We used a combination of two new and one existing ecosystem food web models and altered scenarios that are possible with climate change to quantify the impacts of climate change on ecosystem stability in three coastal bays in Maine, United States. We also examined the impact of climate change on bivalve fisheries and aquaculture. Our modeled scenarios explicitly considered the predicted effects of future climatic change and human intervention and included: 1) the influence of increased terrestrial dissolved organic carbon loading on phytoplankton biomass; 2) benthic community change driven by synergisms between climate change, historical overfishing, and increased species invasion; and 3) altered trophic level energy transfer driven by ocean warming and acidification. The effects of climate change strongly negatively influenced ecosystem energy flow and ecosystem stability and negatively affected modeled bivalve carrying capacity in each of our models along the Maine coast of the eastern United States. Our results suggest that the interconnected nature of ecosystem food webs make them extremely vulnerable to synergistic effects of climate change. To better inform fisheries and aquaculture management, the effects of climate change must be explicitly incorporated.

1. Introduction

Increasingly, the value of ecosystem structure and function is communicated through the concept of ecosystem services: that ecosystems provide fundamental life enhancing services for humans (Schröter et al., 2017). Globally, coastal ecosystem food webs provide a variety of ecosystem services such as the provisioning of food and fiber, and cultural, regulating, and supporting services for millions of people (Himes-Cornell et al., 2018; Mehvar et al., 2018). Climate change is destabilizing ecosystem food webs and threatening these services (Schröter et al., 2005; Mooney et al., 2009). Given the abundance of people that rely on coastal ecosystems, and for securing future food security and well-being, the effects of climate change on coastal ecosystems are of particular interest and importance (Scavia et al., 2002; Martínez et al., 2007; Doney et al., 2012). Thus, investigating the effects of climate change on coastal ecosystems is central to understanding how these climatic changes alter food web dynamics and coastal ecosystem services (Richardson and Schoeman, 2004; Harley et al., 2006).

One of the globally most important coastal ecosystem services is food provisioning provided by ecosystem structure and function. With a long tradition of relying on fisheries, coastal communities along the eastern US coast in Maine have adapted to changing natural resource availability (Overholtz, 2002; Johnson et al., 2012). For example, following the collapse of the groundfish fishery and cannery towns up and down the coast, recent focus has been on lobster fishing and developing operations for bivalve and seaweed aquaculture (Moser et al., 2008; Pinsky and Fogarty, 2012; Kim et al., 2017).

Climate change has had demonstrably negative effects on coastal ecosystem food webs and important commercial fisheries (Essington et al., 2006; Brander, 2007; D'Antoni, 2009). Ocean warming in the Gulf

of Maine is thought to be a main contributor to both range loss and range expansion of commercial fisheries and mobile species sensitive to ocean warming (Drinkwater, 2005; Nye et al., 2009; Pershing et al., 2015). Other effects include increased terrestrial dissolved organic carbon (DOC) loading into nearshore ecosystems, altering primary productivity (Balch et al., 2016); increased acidification and ocean warming, affecting shell-forming species (Ullah et al., 2018); and synergistic effects of invasive species, overfishing, and climate change (Harris and Tyrrell, 2001). Synergisms between these ecosystem stressors may contribute to ecosystem food web destabilization and increased vulnerability by altering ecosystem energy flow and material cycling.

One way for coastal ecosystems to provide ecosystem services is through aquaculture. Aquaculture increases food security by expanding production beyond global capture fisheries (Davis et al., 2016). Future seafood demand from shifting diets and growing populations will continue to be met from aquaculture as global capture fishery production has peaked (FAO, 2018). Beyond increasing food security, aquaculture can improve rural livelihoods through increasing employment and income (Olaganathan and Mun, 2017).

Bivalve aquaculture, in particular, can be an efficient and sustainable way to produce protein and in Maine, bivalve aquaculture is becoming increasingly common (Gentry et al., 2017). In 2017 alone, Maine's aquaculture sector produced millions of kg of bivalves and generated nearly $75 million in direct economic impacts. Beyond economic effects, bivalve aquaculture may decrease vulnerability to climate change by using infrastructure that is generally resilient to land-based extreme weather, providing marine-based livelihood potential, and producing food more efficiently (less land and freshwater needed) than land-based agriculture (Filgueira et al., 2016). The multi-institutional and community partner driven Sustainable Ecological Aquaculture Network (SEANET) was created to better understand the social, environmental, and economic potential of building a sustainable aquaculture industry along the coast of Maine (umaine.edu/aquaculture/seanet). By leveraging existing know-how, infrastructure, and coastal natural resources, the development of the aquaculture industry should increase ecosystem provisioning dependability and decrease vulnerability to the effects of climate change.

The goal of this paper was to investigate the potential for aquaculture development along the coast of Maine and how climate change might influence such development. We used a combination of Ecopath food web models (Christensen et al., 2008; www.ecopath.org), to investigate the potential for aquaculture development along the coast of Maine in three different bays. We also used aquaculture as a study context to simulate the effects of climate change on ecosystem energy flow and coastal food web dynamics. With our three ecosystem Ecopath food web models we asked: What are the bivalve carrying capacities in each region? Beyond the comparison of bivalve carrying capacity in each region, we used the primary literature to develop scenarios representing different effects of climate change. With our scenarios representing differing effects of climate change, we ask: How do effects of climate change influence bivalve aquaculture carrying capacities and What particular effects of climate change have a larger magnitude effect on bivalve carrying capacity?

The objectives of this study were to: 1) construct two new ecosystem food web models for two bay ecosystems using data collected from the SEANET along the coast of Maine; 2) use one existing ecosystem food web model (for a total of three bay ecosystem models) to conduct a cross regional analysis of aquaculture carrying capacity along a latitudinal gradient in southern, Midcoast and northern Maine; 3) develop scenarios to model the effects of climate change in each food web; and 4) quantify the effects of climate change on shellfish carrying capacity in three bays along the Maine coastline. For the purposes of this study, we selected three relatively data-rich bays along the Maine coastline: Saco, Penobscot, and Cobscook Bays. The three bays represented differing geomorphological and tidal conditions, hydrological regimes, and food web dynamics.

2. Methods

2.1. Study systems

Our study bays represent the geomorphological range found along the Maine coastline. The bays represent the diversity of bay ecosystems along the coast of Maine and serve as case studies for how different bays and their aquaculture potential may be affected by climate change. From Saco Bay in southern Maine to Cobscook Bay in northern Maine, there is a marked transition from sandy, salt-marsh systems to rocky, rockweed-dominated systems. From the south to north there is a decreasing gradient of freshwater input and an increase in primary producer diversity, driven by the shift in bay geomorphology and the ratio of river discharge to estuary size. We investigated the potential of bivalve aquaculture development in these three distinct systems, while explicitly considering the effects of climate change on bivalve carrying capacities. Here, we defined bivalve carrying capacity as the maximum bivalve biomass that could be supported by existing and available energy in each of the ecosystem food web models. Since we used ecosystem models to estimate aquaculture carrying capacity based on available energy within each system, we did not distinguish between wild bivalve fisheries and bivalve aquaculture production.

Saco Bay is a small, 57 km^2, sandy bay site in southern Maine located ~20 km south of Portland, Maine mainly focused on eastern oyster aquaculture (Fig. 1). The Saco River is a large source of freshwater input into the bay—Saco Bay represents the system in this study with the largest freshwater input. Penobscot Bay is a large (650 km^2) rocky bay site in Midcoast Maine and it contains a number of working waterfront towns with historical importance and is mainly focused on eastern oyster aquaculture. Penobscot Bay receives an intermediate amount of freshwater inputs mainly from the Penobscot River. Cobscook Bay is a medium (105 km^2) rocky bay in northern Maine located in the most northeastern portion of the state (Fig. 1). Cobscook Bay has the smallest volume of freshwater input, largest tidal range, and most convoluted shoreline. Bivalve aquaculture in Cobscook Bay is small and focused on blue mussel production. Each bay experiences similar temperature and precipitation conditions, mean annual air temperature of 18 °C in the summer and −6 °C in the winter and roughly 100 cm per year (Runkle et al., 2017; Maine DEP). In the following sections, we describe Penobscot Bay and Cobscook Bay food web characteristics in more detail. More information about Saco Bay is described in Smith et al. (2016).

2.2. Penobscot Bay food web characteristics

Midcoast Maine represents a transition along the gradient of sandy beaches of southern Maine to the rocky shores of northern Maine. Shoreline heterogeneity supports a diverse population of primary producers, which fuels Penobscot Bay and its upper trophic levels. Besides phytoplankton, species more dominant in southern Maine, such as eelgrass and *Spartina*, are found alongside brown algae, which is more dominant in northern Maine. From a biomass perspective, fucoids and *Spartina* are more massive than eelgrass. A large biomass of zooplankton supports a large population of macroinvertebrates including periwinkle and green crab via various trophic connections (zooplankton – fish – green crabs; barnacle larvae – periwinkle). Harbor seals *Phoca vitulina* and double-crested cormorants *Phalacrocorax auritus* drive top-down controls and feed on a relatively small population of pelagic and groundfish species (Table 1, Supplemental Table 1; Fig. 2).

2.3. Cobscook Bay food web characteristics

The convoluted rocky shoreline of northern Maine supports a wide array of primary producers, which fuels Cobscook Bay and its upper trophic levels. Besides phytoplankton, species more dominant in southern Maine, such as eelgrass and *Spartina*, are found alongside
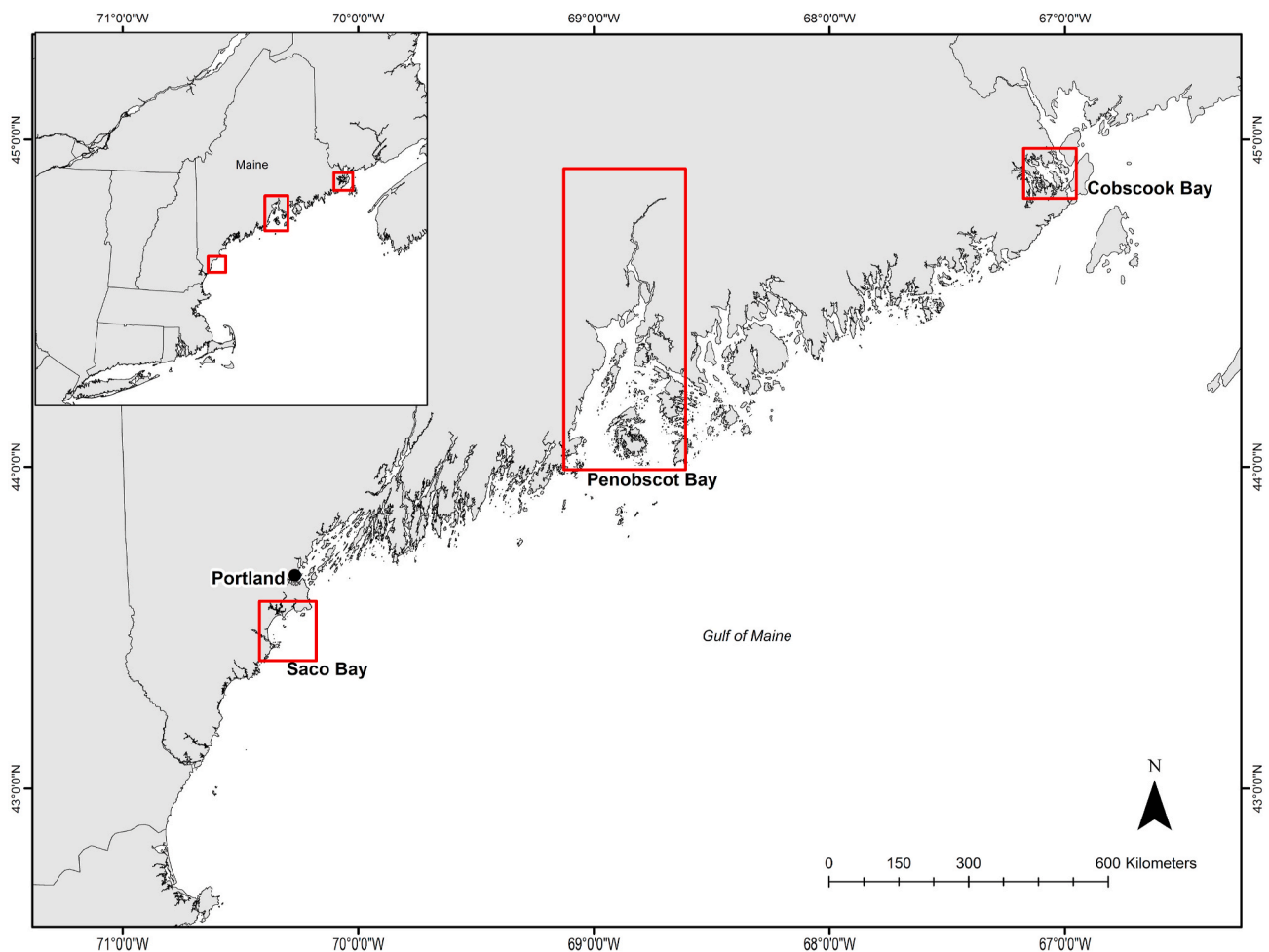
Fig. 1. Map of study bays along the coast of Maine, from Saco Bay in Southern Maine, Penobscot Bay in Midcoast Maine, and Cobscook Bay in Northern Maine. Our study systems were representative of biogeomorphic changes along the coastline.

brown algae, which is more dominant in northern Maine. From a biomass perspective, fucoids, the microphytobenthos, and red/green algae are more massive than eelgrass. As with Penobscot Bay, a large biomass of zooplankton supports a large population of macro-invertebrates including periwinkle and green crab via various trophic connections (zooplankton – fish – green crabs; barnacle larvae – periwinkle). Bald eagle (*Haliaeetus leucocephalus)* drive top-down controls and feed on a relatively small population of pelagic and groundfish species (Table 2, Supplemental Table 2; Fig. 2).

2.4. Modeling approach

We used Ecopath, a static mass balanced ecosystem modeling approach to simulate the marine ecosystem food web and the carrying capacity of commercially important bivalves for Saco, Penobscot, and Cobscook Bays in Maine (Christensen et al., 2008). We used Ecopath for this investigation for several reasons: 1) Ecopath is widely used to model potential for aquaculture and bivalve carrying capacities; 2) Ecopath offers an intermediate blend of complexity and accessibility, which may enhance participation between model users and stakeholders (Byron et al., 2015); and 3) the ability to reconstruct Ecopath models with altered input values to simulate potential effects from climate change scenarios. A straightforward user interface and an intuitive conceptual approach contribute to Ecopath's accessibility and widespread use in the literature to model ecosystem energy flow in a variety of contexts.

Ecopath is an extensively used ecosystem modeling software that explicitly considers the flow of energy through ecosystem trophic levels

(Christensen and Walters, 2004; Ullah et al., 2012; Coll et al., 2015; Colléter et al., 2015). Ecopath explicitly considers the ecosystem level and uses biomass transfer as a proxy for energy transfer between model components. Ecopath is often used in a management context (Christensen and Pauly, 1998; Pauly et al., 2000) and has been used to characterize diverse ecosystem types including estuaries (Monaco and Ulanowicz, 1997; Byron et al. 2011a, Heymans et al., 2016).

Although Ecopath provides an accessible, relevant, and practical manner to investigate our research questions, there are a few limitations to the approach. First, while we developed scenarios that were designed to simulate the predicted effects of climate change, it is not possible to investigate every climate change outcome permutation or feedback. Secondly, it is difficult to explicitly incorporate non-linearity into our model interventions. Necessarily this approach removes complexity for the sake of parsimony. Finally, Ecopath is a static mass balance model meant to provide a snapshot of the system at a moment in time, though our assumption is some of the model simulations represent ecological conditions that will happen in the future as a result of climate change. Despite these limitations, explicitly acknowledging these limitations better informs the ecological interpretation of the model outcomes. Simulating the effects of climate change on bivalve carrying capacities represents a tangible and informative exercise that can better inform future management strategies while considering uncertainties.

2.5. Model parameterization

Ecopath models are parameterized by assembling data that satisfy

Table 1

Penobscot Bay ecological food web model input parameters. Trophic level and ecotrophic efficiency are values solved by Ecopath. Biomass, Production/biomass (P/B), and Consumption/biomass (C/B) are values derived from the literature and references are noted within table. P/B and C/B represent turnover rates per year and biomass is in kg km^{-2}.

Group	Trophic level	Biomass (kg km^{-2})	Production/biomass (y^{-1})	Consumption/biomass (y^{-1})	Ecotrophic efficiency
Phoca vitulina[a]	4.156	97	0.120	1.000	0.000
Phalacrocorax auritus[b]	4.010	1.1	0.040	36	0.000
Osmerus mordax[c]	3.380	37.63	0.380	2.900	0.831
Alosa Pseudoharengus[c]	3.330	430.0	0.910	8.620	0.950
Merluccius bilinearis[c]	3.165	817.7	0.240	4.260	0.147
Pseudopleuronectes americanus[c]	3.070	42.69	0.540	3.800	0.000
Clupea harengus[c]	3.030	554.4	0.600	10.000	0.111
Alosa aestivalis[c]	2.63	36.78	0.600	5.200	0.179
Carcinus maenas[d]	2.688	1215	3.000	10.900	0.000
Bivalves[de]	2.320	2364	1.000	4.000	0.988
Littorina littorea[f]	2.470	8741	1.270	6.370	0.000
Other macrobenthos[g]	2.500	50,000	134.6	845.4	0.046
Zooplankton[h]	2.200	21,970	69.000	150.00	0.509
Pandalus borealis[c]	2.940	500	2.700	15.700	0.859
Phytoplankton[i]	1.000	12,000	282.0		0.857
Spartina[j]	1.000	37,960	2.000		0.692
Zostera marina[k]	1.000	922	5.000		0.575
Fucoids[e]	1.000	100,000	81.6		0.028
Bacteria[l]	2.000	7450	500.0	1500	0.276
Detritus	1.000	200,000			0.000

[a] Waring et al., 2015
[b] Blackwell et al., 1997
[c] NOAA National Marine Fisheries Survey, DMR ME-NH Inshore Trawl Survey
[d] Thompson 2017, SeaLifeBase
[e] ME DMR
[f] Baeta et al., 2011
[g] determined from model prebalancing
[h] Lasley-Rasher unpublished data.
[i] SEANET buoy data
[j] Dame and Kenny 1986
[k] Alexandre et al., 2005
[l] Li et al 2011, Bratbak and Dundas 1984

the following equations: production = predation + catches + net migration + accumulated biomass + other mortality; and consumption = production + respiration + unassimilated food (Christensen et al., 2008). At the very least, Ecopath models are built using three main parameters: biomass (B), production/biomass (P/B), and consumption/biomass (C/B). Ecopath models also require diet matrices, assimilation efficiency, and any potential catch by fleets. We parameterized our new ecosystem food web models by collecting B, P/B, and C/B from various sources including the primary literature, FishBase, and government reports for Penobscot Bay (Table 1, Supplemental Table 1) and Cobscook Bay (Table 2, Supplemental Table 2). Ecopath calculates energy transfer between different groups in the food web that are based on relationships between different groups, which can be found in a diet matrix.

Together, the three parameters were used to calculate ecotrophic efficiency—a relative measure between 0 and 1 of the amount of production that is used by a species group within the food web (Table 1, Table 2). For example, if the ecotrophic efficiency of bivalves is over 1.0, the ecological interpretation is that there are too many bivalves in the ecosystem to be supported by existing energy or production in the system. For the purposes of this study and the scenarios described below, when ecotrophic efficiency of any food web group exceeded 1.0, we determined that the food web became destabilized or unbalanced (see Byron et al., 2011a, b). In other words, the biomass at which ecotrophic efficiency reaches 1.0 is what we defined as the bivalve carrying capacity.

After model parameterization—but before running the model—we used prebalancing diagnostic approaches [i.e. Link 2010] to assess whether the input data met basic assumptions of an ecosystem food web. That is, across trophic levels, we expected lower trophic levels to be more abundant compared to higher trophic level organisms (e.g.

checking that there is a higher biomass of lower trophic levels such as phytoplankton to support higher trophic level consumers). In the instances where trophic principles of an ecosystem food web were not met, we revised model parameters to better reflect trophic energetic relationships. For a more thorough description of these prebalancing techniques for Ecopath see Link (2010); Byron et al. (2011a, b); and Heymans et al. (2016). For this study, we used the built in prebalancing routine now found in Ecopath.

New models for Penobscot Bay and Cobscook Bay were constructed and parameterized for this study (Tables 1 and 2). We used a mix of the primary literature, government reports for both Penobscot Bay (Table 1, Supplemental Table 1) and Cobscook Bay (Table 2, Supplemental Table 2) and a variety of sampled and unpublished datasets from the State of Maine Department of Maine Resources (DMR) Maine – New Hampshire Inshore Trawl Survey and sampling efforts from NOAA's National Marine Fisheries Service in Penobscot Bay. Saco Bay was based on existing models (Smith et al 2016) and updated using phytoplankton data from SEANET (https://umaine.edu/aquaculture/seanet/). We have included our updated version of the Saco Bay model as supplemental information (Supplemental Tables 3 and 4). More information about Saco Bay model parameterization is described in Smith et al. (2016).

2.6. Scenario construction

Following the construction of the two new balanced food web models, we developed three main scenarios with sub scenarios and reconstructed the models to simulate different effects of climate change on food web dynamics and bivalve carrying capacity in the three bays (Table 3). Our scenarios were informed by the primary literature and focused on broad ecosystem-level and interacting effects of climate change. Our first scenario explored the impact of increased rainfall
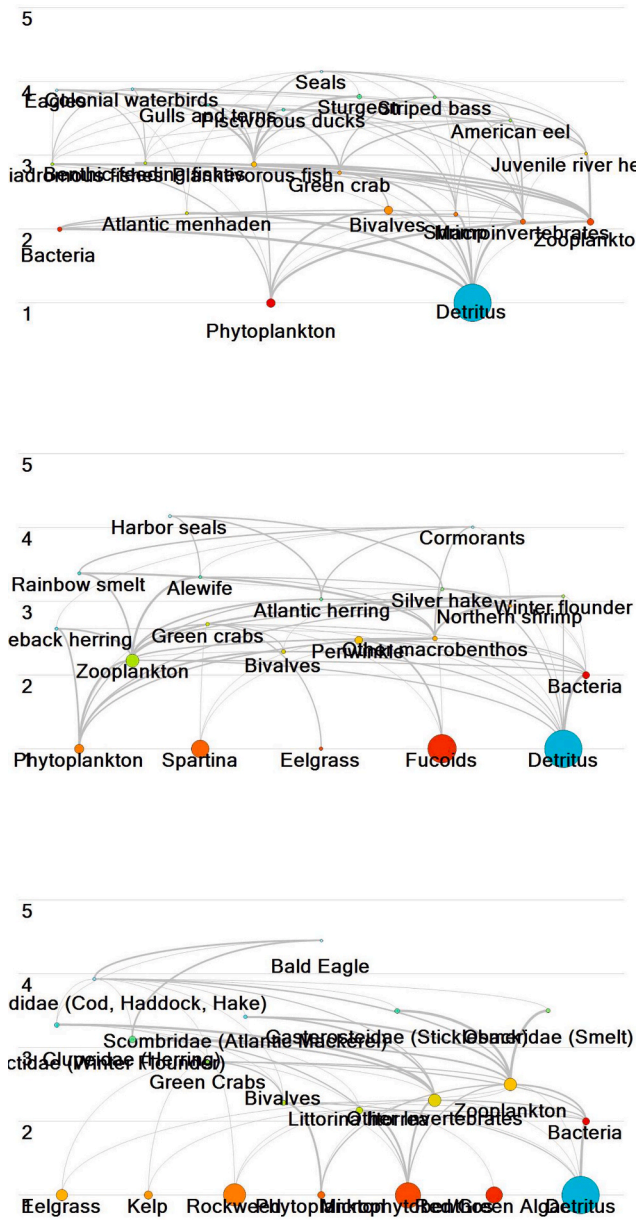
Fig. 2. Ecopath ecosystem food webs along the coast of Maine from Southern Maine in Saco Bay (top panel), Midcoast in Penobscot Bay (middle panel), and (bottom panel) Northern Maine in Cobscook Bay. Food web diagrams show energy flow and trophic levels between different food web components. The y-axis depicts trophic level and size of the spheres are scaled to biomass in ecosystem.

events and freshwater inputs into nearshore Gulf of Maine ecosystems. With increased rainfall and freshwater loading into nearshore ecosystems, higher levels of terrestrial DOC are predicted to enter coastal ecosystems. These higher levels of terrestrial DOC affect coastal ecosystem food webs by physically darkening the color of the water, which decrease primary productivity and phytoplankton biomass (Balch et al., 2016). Decreased levels of phytoplankton lower available energy in the ecosystem food web, potentially decreasing the biomass of higher trophic levels in the food web. To simulate the effects of increased DOC loading in nearshore ecosystems, we investigated the ecosystem effects of decreasing phytoplankton 10, 20, and 30% based on the potential effects of DOC loading described by Balch et al. (2016).

Our second scenario explored synergisms between various ecosystem food web stressors. This scenario explicitly considered the interaction of

invasive species, historical overfishing, and effects of climate change on ecosystem food web structure and function (Harris and Tyrrell, 2001). The depletion of the groundfish fishery and increasing rates of species invasions are thought to alter benthic community composition through increased abundances of green crab (*Carcinus maenas*), common periwinkle (*Littorina littorea*), and other benthic community invertebrates (Harris and Tyrrell, 2001). To simulate the effects of these interacting stressors, we modified the current biomass of benthic dwelling species by increasing the abundance of green crab, periwinkle, and other benthic invertebrates by 20, 80, and 200% to reflect differing magnitudes of invasion. We increased green crab, periwinkle abundance by 20% based on predicted effects of warming on population abundances (Grosholz and Ruiz, 1996; Young et al., 2017). We modified the current biomass of green crab, periwinkle, and other benthic invertebrates by 200%, the level of increase required to unbalance our ecosystem food web models (EE > 1). This approach allowed us to establish the level of invasion that may unbalance current food web functioning. Finally, we used 80% as an intermediate scenario between predicted effects and upper limit scenario of 200%.

Our final scenario focused on the effects of ocean warming and acidification. A recent study highlighted that the interaction between ocean warming and acidification could cause marine food web destabilization through changes in ecosystem energy flow (Ullah et al., 2018). It is predicted that combined acidification and ocean warming will disrupt energy flow between trophic levels, leading to an increase in detrital and bacterial biomass. To simulate this effect of climate change, we modified input model parameters by decreasing the biomass of secondary and tertiary trophic levels 25, 50, and 75% and increasing the biomass of bacteria by 200% (Table 3). We decreased secondary and tertiary trophic levels by 25, 50, and 75% and increased the biomass of bacteria by 200% based on work by Ullah et al. (2018). The trophic level was determined by Ecopath as the feeding position of organisms within the food web.

3. Results

3.1. Ecology of food webs along the Maine coastline

Along the coast of Maine, food web composition and the interactions between food web components differ. These compositional differences drive important functional differences between food webs (Fig. 2; Table 4). For example, metrics of ecosystem function differ along the coast of Maine with changes in ecosystem structure. Compared to Penobscot and Cobscook Bays, Saco Bay has an order of magnitude lower: total biomass, total system throughput, net primary production, and sum of respiratory flows (Table 4). Since the sum of respiratory flows and net primary production are scaled in each bay, the ratio of total primary production to total respiration is similar across food webs and ranges from 1.29 to 1.45. Functionally, Penobscot and Cobscook Bay more resemble each other compared to Saco Bay: Penobscot and Cobscook Bays have similar total biomass of 1.98×10^5 and 2.86×10^5 kg km^{-2}. The ratio of total primary production to total biomass is 18.67 in Saco Bay, 58.67 in Penobscot Bay, and 38.00 in Cobscook Bay.

3.2. Bivalve carrying capacity along the coastline

The baseline biomass of bivalves in each bay was of similar orders of magnitude and varied from 7.1×10^3 kg km^{-2} in Penobscot Bay to 1.1×10^4 kg km^{-2} in Cobscook Bay (Table 5). Saco Bay had an intermediate baseline biomass of bivalves of 9.9×10^3 kg km^{-2}. The bivalve carrying capacity—the biomass of bivalves the model can support before becoming unbalanced—varied more between bays than the baseline (current state) of bivalve biomass along the coastline. The bivalve biomass that could theoretically be supported given the currently available energy and resources in the ecosystem was the lowest in Saco Bay at 3.3×10^4 kg km^{-2}. Cobscook Bay could support an intermediate

Table 2

Ecological food web model input parameters for Cobscook Bay. Trophic level and ecotrophic efficiency are values solved by Ecopath. Biomass, Production/biomass (P/B), and Consumption/biomass (C/B) are values derived from the literature and references are noted within table. P/B and C/B represent turnover rates per year and biomass is in kg km^{-2}.

Group	Trophic level	Biomass (kg km^{-2})	Production/biomass (y^{-1})	Consumption/biomass (y^{-1})	Ecotrophic efficiency
Haliaeetus leucocephalus[a]	4.454	17.38	0.200	0.750	0.000
Gadidae[b,b]	3.929	666.6	0.380	2.580	0.564
Scombridae[b]	3.414	1334	0.190	4.400	0.468
Pleuronectidae[b]	3.309	2668	1.900	3.800	0.027
Gasterosteidae[b]	3.500	2705	0.540	9.700	0.106
Clupeidae[b]	3.114	7146	0.600	10.100	0.034
Osmeridae[b]	3.500	1734	0.390	2.900	0.203
Carcinus maenas[c]	2.804	1333	1.400	3.000	0.413
Bivalves[d]	2.250	3766	0.700	4.000	0.463
Littorina litterea[e]	2.150	6666	0.483	18.000	0.315
Other invertebrates[f]	2.285	20,000	2.000	14.000	0.996
Zooplankton[g]	2.500	20,000	69.000	150.00	0.050
Zostera marina[h]	1.000	17,809	0.391		0.431
Kelp[i]	1.000	10,499	3.542		0.253
Ascophyllum nodosum[j]	1.000	60,406	0.546		0.619
Phytoplankton[k]	1.000	8200	125.0		0.611
Microphytobenthos[k]	1.000	80,000	125.0		0.084
Red/green algae[l]	1.000	33,300	8.000		0.023
Bacteria[m]	2.000	7400	500	1500	0.431
Detritus[m]	1.000	200,000			0.816

[a] Todd et al., 1982
[b] Vieser 2010
[c] Tyrrell 2006
[d] Beal 2015 unpublished data
[e] Ugarte et al., 2010
[f] Determined from model prebalancing
[g] Johnson et al., 2011
[h] Beal et al., 2004
[i] Vadas et al., 2004b
[j] Vadas et al., 2004c
[k] Phinney et al., 2004
[l] Vadas et al., 2004a
[m] Campbell 2004

Table 3

Effects of climate change scenarios and corresponding model modifications to investigate the effects of climate change on bivalve carrying capacity.

Scenario	Climate change effects	Model action	Reference
1	Increase in terrestrial DOC loading into ocean	Decrease phytoplankton biomass in model by 10, 20, and 30%	Balch et al. (2016)
2	Benthic community change driven by synergism between climate change, overfishing, and invasion	Increase green crabs, periwinkle, and "other invertebrates" by 20, 80, and 200%	Harris and Tyrrell (2001)
3	Ocean warming and acidification alter ecosystem energy flow, creating a more detritus driven system	Decrease secondary and tertiary trophic level biomass by 25, 50, and 75%; increase bacteria biomass in model by 200%	Ullah et al. (2018)

theoretical biomass of 5.1×10^5 kg km^{-2} and Penobscot Bay could support 7.4×10^5 kg km^{-2} before the model became unbalanced. The difference in the current biomass of each bay to the modeled maximum biomass of bivalves represented a 3.3 fold increase in Saco Bay, a 45.1 fold increase in Cobscook Bay, and a 103.7 fold increase in Penobscot Bay (Table 5). In our models, two different elements of the food web became destabilized when bivalve biomasses exceeded the carrying capacity. In Saco Bay, zooplankton populations became destabilized, whereas in Penobscot and Cobscook Bays, phytoplankton populations became destabilized with increasing bivalve biomass.

Table 4

Ecosystem metrics derived from balanced Ecopath models in Saco, Penobscot, and Cobscook Bays.

Parameters	Saco Bay	Penobscot Bay	Cobscook Bay	Units
Sum of all consumption	1.52×10^6	1.71×10^7	1.46×10^7	kg km^{-2} y^{-1}
Sum of all exports	2.54×10^5	3.60×10^6	2.58×10^6	kg km^{-2} y^{-1}
Sum of all respiratory flows	6.17×10^5	8.0×10^6	8.79×10^6	kg km^{-2} y^{-1}
Sum of all flows into detritus	1.46×10^6	1.57×10^7	1.40×10^7	kg km^{-2} y^{-1}
Total system throughput	3.85×10^6	4.44×10^7	4.00×10^7	kg km^{-2} y^{-1}
Sum of all production	1.47×10^6	1.73×10^7	1.65×10^7	kg km^{-2} y^{-1}
Calculated total net primary production	8.72×10^5	1.12×10^7	1.13×10^7	kg km^{-2} y^{-1}
Total primary production/ total respiration	1.41	1.45	1.29	unitless
Net system production	2.54×10^5	3.60×10^6	2.58×10^6	kg km^{-2} y^{-1}
Total primary production/ total biomass	18.67	58.67	38.00	unitless
Total biomass (excluding detritus)	4.67×10^4	1.98×10^5	2.86×10^5	kg km^{-2}

3.3. Effects of enhanced DOC loading on coastal ecosystem function (scenario 1)

When we explicitly considered the effects of climate change on coastal ecosystem food webs, we found varying degrees of ecosystem

Table 5
Baseline bivalve and carrying capacity biomass in each bay along the coast of Maine. Each component of each food web model becomes unbalanced when bivalve biomass exceeds the carrying capacity biomass. The ecological rationale for food web destabilization is provided in the final column. Bivalve biomass is in kg km^{-2}.

Model	Baseline bivalve biomass	Bivalve carrying capacity biomass	Magnitude of increase	Food web destabilizer	Ecological rationale
Saco Bay	9.9×10^3	3.3×10^4	3.3	Zooplankton	Relative high abundance of planktivorous fish that compete with bivalves
Penobscot Bay	7.1×10^3	7.4×10^5	103.7	Phytoplankton	Lack of groundfish pressure on lower trophic levels
Cobscook Bay	1.1×10^4	5.1×10^5	45.7	Phytoplankton	Macroinvertebrates, zooplankton compete with bivalves for phytoplankton

resilience to becoming unbalanced. In the case of increased DOC loading on coastal ecosystems, we found a marked decrease in the biomass of bivalves that could be supported given the effects of climate change in each food web model. In Saco Bay, when decreasing phytoplankton biomass by 10% we saw a ~60% decrease in the biomass of bivalves from 3.3×10^4 kg km^{-2} to 1.3×10^4 kg km^{-2}. In Cobscook Bay, the reduction in bivalve biomass was ~68% (3.8×10^5 kg km^{-2} to 1.3×10^5 kg km^{-2}) from the same scenario. In Penobscot Bay, a 20% reduction in phytoplankton biomass corresponded to an unbalanced food web. We found that Cobscook Bay was the only food web model that did not become unbalanced when modifying biomass of phytoplankton to levels that are consistent with the predicted effects of increased DOC loading. When we decreased biomass of phytoplankton by 10% none of the ecosystem food webs along the coast became unstable. However, in Penobscot Bay, decreasing phytoplankton by 20% destabilized the ecosystem food web. The Saco Bay food web destabilized at a 30% reduction in phytoplankton, and Cobscook Bay remained stable. Our three distinct food web models along the Maine coastline exhibited different outcomes from increased DOC loading predicted from climate change.

3.4. Effects of synergisms between multiple stressors on coastal ecosystem function (scenario 2)

The next scenario we simulated with our food web models was the effect of the synergisms between multiple stressors associated with human intervention: climate change, overfishing, and invasive species introductions. With the exception of Saco Bay, the change in benthic community composition altered food web energy flow significantly and influenced the ability of Penobscot and Cobscook bays to support bivalve biomass. For example, when we increased biomass of green crab, periwinkle, and other invertebrates by 20% in the model, only Penobscot Bay destabilized. When we increased biomass of these benthic species by 80%, Cobscook bay destabilized. It took a biomass increase of 200% in the modeled benthic community to destabilize the Saco Bay food web. Different food web components led to the destabilization of the food web in each bay along the coastline. When we increased the biomass of green crab, periwinkle, and other invertebrates by 200% in Saco Bay, a decrease in benthic-feeding fish destabilized the food web. In Penobscot Bay, increasing a benthic community biomass by 20% caused bivalve biomass to decrease and contribute to food web destabilization. In Cobscook Bay, when the benthic community biomass was increased by 80%, rockweed biomass decreased via periwinkle consumption, destabilizing the food web. We did not find a biomass of bivalves that these food webs could support given the conditions where benthic community composition increased (Table 3). The effects of the synergisms between multiple stressors on ecosystem food webs varied by orders of magnitude and the identity of the food web destabilizing component along the coast of Maine.

3.5. Effects of altered energy flows from climate change on coastal ecosystem function (scenario 3)

In our final scenario, we investigated the effect of climate change-induced altered energy flows between trophic levels within a food web. When we decreased tertiary and secondary trophic levels by 25% and increased bacterial biomass by 200%, only the Saco Bay food web remained stable. Penobscot and Cobscook Bay food webs were particularly sensitive to this scenario. In these two models, elevating bacterial biomass increased pressure on the detrital food web component, causing the food web to become unbalanced. In fact, every level of decrease of tertiary and secondary consumer biomass and increase in bacterial biomass caused these food webs to be unbalanced. Saco Bay remained balanced with a decrease of tertiary and secondary consumer biomass by 75% and a 200% increase of bacterial biomass. We found that the predicted effects reported in the literature—25-75% decrease in tertiary and secondary consumers and a 200% increase in bacteria—would destabilize ecosystem energy flow in Penobscot and Cobscook Bay, and would subsequently not support bivalve biomass for aquaculture. In Saco Bay, bivalve biomass decreased from 2.5×10^4 kg km^{-2} to 8.1×10^3 kg km^{-2} representing a 68% decline in bivalve biomass. The simulated effects of the modeled scenarios destabilized our ecosystem food webs and decreased or eliminated the potential for bivalve aquaculture. Much like with the scenarios above, the climate change induced altered energy flows between trophic levels had various outcomes depending on ecosystem food web structure.

4. Discussion

We used a combination of existing and new ecosystem food web models to investigate the potential for bivalve aquaculture along the coast of Maine in the face of climate change. We independently considered multiple mechanisms of climate change on coastal ecosystem food webs and the resulting effect on bivalve carrying capacity. Additionally, the topology and constituent taxa of our ecosystem food webs reflected the differing habitat types driven by the gradient of biogeomorphic conditions found along the entire coast of Maine. Thus, our investigation of the expected effects of climate change on ecosystem energy flow provides a holistic assessment of the potential for aquaculture along the coast of Maine in the future (D'Antoni, 2009; Merino et al., 2012). In the following section we discuss the dynamics of ecosystem models across each bay, the effects of climate change on ecosystem food web dynamics, and the effects of climate change on the potential for aquaculture.

4.1. Characteristics of the ecosystem food web models across each bay

Ultimately, the extent to which an ecosystem could support aquaculture depends on available energy and energy flow within the ecosystem. Along the coast of Maine, differences in food web composition contribute to differing energy flows and food web dynamics between bays. Landscapes become less sandy and increasingly rocky and heterogeneous from south to north. These northern landscapes support increasingly complex and diverse primary producer communities. Larger, more diverse primary producer communities in Penobscot Bay and Cobscook Bay compared to Saco Bay may have contributed to differences in ecosystem function metrics between Saco Bay and Penobscot and Cobscook Bays. This finding is consistent with the notion that more

spatially heterogeneous landscapes contribute to species diversity through a variety of interacting mechanisms (Menge, 1976; Tews et al., 2004; Miller and Etter, 2008).

Parameters of food web dynamics such as consumption, exports, respiratory flows, flows into detritus, and production are comparable with other estuarine systems around the world (Wolff et al., 2000; Ullah et al., 2012; Abdul and Adekoya, 2016). These results suggest that despite differing ecosystem structure and composition, there are emergent and fundamental principles guiding ecosystem function. The ratio of total primary production to total respiration is similar and greater than 1 across all three bays along the coast of Maine. When primary production to respiration ratios are greater than 1, the ecosystem is considered to be autotrophic. Our primary production to respiration ratios were slightly lower than reported in other studies and all of the estuarine food web studies had primary production to respiration ratios greater than 1, a finding that is not surprising given that estuaries are frequently listed among the most productive ecosystems on the planet (Mitsch et al., 2009; Barbier et al., 2011). Across our study systems, Penobscot and Cobscook Bays more closely resembled each other functionally than Saco Bay, and all three systems were functionally similar to other global estuarine systems. An understanding of ecosystem energy flow and food web dynamics is fundamental to informing aquaculture siting and development.

4.2. Effects of climate change on ecosystem food web dynamics

Climate change directly and indirectly influences ecosystem energy flow and food web dynamics. The indicators used in our scenarios that simulate the effects of climate change had profound effects on ecosystem food web dynamics. Given the magnitude of the effects of increasing DOC and invasive species on primary production, community composition, and ecosystem energy flow across these bays, it is not surprising how fundamentally vulnerable these systems are to expected mechanisms of change (Brown et al., 2010; Niiranen et al., 2013; Serpetti et al., 2017). Previous studies have demonstrated ecosystem food web vulnerability and decreasing ecosystem service provisioning when explicitly considering the effects of climate change (Ainsworth et al., 2011; Serpetti et al., 2017), however, another model simulation predicted that primary productivity may increase and have positive conservation and fishery outcomes near Australia (Brown et al., 2010). The influence of multiple drivers such as eutrophication and climate change and their relative importance in shaping food web dynamics is not well understood (Ehrnsten et al., 2019). The disparate influences of climate change on ecosystem structure and function highlight the need to develop models with regionally specific scenarios and investigations (Boyd and Doney, 2002). Our study approach represents a holistic investigation of the regional effects of climate change on food web dynamics in the Gulf of Maine (Moloney et al., 2011).

4.3. Effects of climate change on the Maine aquaculture industry

The influence of climate change on bays along the coast of Maine will undoubtedly influence the capacity of these systems to support aquaculture. Beyond influencing ecosystem food web dynamics, each of our modeled scenarios had detrimental effects on the potential for shellfish aquaculture. Increased DOC loading from increased freshwater inputs into the Gulf of Maine is expected to alter the color of the ocean, decreasing phytoplankton biomass (Balch et al., 2016). Since bivalves consume phytoplankton, a decrease in phytoplankton primary productivity and biomass will decrease available energy within the ecosystem that may be used to support bivalve aquaculture. Likewise, a change to benthic community assemblages by the synergism between climate change, species invasion, and overfishing may decrease the biomass of bivalves within the ecosystem (Harris and Tyrrell, 2001). An increase in green crabs will increase direct predation on bivalves and an increase in periwinkles may decrease food sources available to bivalves (Miron

et al., 2005; Tan and Beal, 2015). Finally, the additive effects of ocean warming and acidification are expected to alter ecosystem energy flow, creating a bottleneck of energy flow between trophic levels (Ullah et al., 2018). Acidification has direct negative effects on shell-forming organisms by decreasing $CaCO_3$ saturation state in the water column (Kurihara, 2008; Beniash et al., 2010). Given these direct negative effects of climate change on ecosystem, community, and population dynamics, it is not surprising that our scenarios simulating effects of climate change decreased the maximum bivalve biomass that these food webs could support.

Our results suggest that effects of climate change will negatively impact the potential production and the carrying capacity of bivalves through aquaculture, potentially decreasing food security and economic well-being. Our results also provide bivalve biomasses that each of the study bays could theoretically support both with and without explicitly considering effects of climate change. These modeled biomasses could inform the number of aquaculture leases and harvester licenses approved. By modeling a range of predicted bivalve biomass outcomes while considering the effects of climate change, our estimates provide a coarse span of bivalve biomass with varying levels of harvest "risk." Decisionmakers could consider these biomass ranges generated from the ecosystem model while assessing ecological, economic, and social considerations.

5. Conclusion

Increasing global population, shifts in diets, and stagnation in capture fishery production are all leading to the development and proliferation of aquaculture to meet the rise in seafood demand. With high levels of primary productivity, proximity to markets, and dynamic habitat, coastal bays and estuaries represent potential ecosystems for aquaculture development. The drivers leading to aquaculture development also operate in the face of climate change and will influence to what extent these systems can provide ecosystem services.

Marine ecosystem food webs face multiple interacting and synergistic stressors that threaten the ability of these systems to provide essential ecosystem services. Additionally, the differential effects of climate change on ecosystem food web structure and function globally necessitate regionally specific model investigations to better inform coastal fishery and aquaculture management. Our results highlight the importance of explicitly considering the effects of climate change on ecosystem function to better inform fisheries and aquaculture management. Our modeled scenarios developed in this study determined that the potential effects of climate change negatively affect ecosystem energy flow and decrease the potential for aquaculture to provide ecosystem services in Maine.

CRediT authorship contribution statement

Eric J. Chapman: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition. **Carrie J. Byron:** Conceptualization, Methodology, Software, Data curation, Writing - original draft, Writing - review & editing. **Rachel Lasley-Rasher:** Data curation, Investigation. **Christine Lipsky:** Data curation, Investigation. **Justin R. Stevens:** Data curation, Investigation. **Rebecca Peters:** Data curation, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.105103.

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