



Carrying capacity simulations as a tool for ecosystem-based management of a scallop aquaculture system



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ABSTRACT

Over the past decade, Sechura Bay has become an important center for mariculture in Peru, where the Peruvian bay scallop (*Argopecten purpuratus*) is grown in bottom cultures. Currently, the business involves 5000 artisanal fishermen and yields an export value of more than 158 million US\$ per year. However, intensity and area extent of cultivation activities continue to increase. Overstocking of scallops combined with critical environmental changes may cause mass mortalities and severe consequences for the ecosystem. Accordingly, the ecosystem-based assessment of the current situation and the determination of long-term sustainable limits to scallop culture for the bay are crucial. Using a trophic food web model, the further expansion of culture activities is explored by forcing scallop biomass to increase to four different levels (458, 829, 1200, and 1572 t km⁻²) and the impact on other groups and the ecosystem are investigated. The ecological carrying capacity (ECC) is defined as the maximum amount of scallop biomass that would not yet cause any other group's biomass to fall below 10% of its original biomass. Results suggest that (a) the current magnitude of scallop bottom culture (147.4 t km⁻²) does not yet exceed ECC, (b) phytoplankton availability does not represent a critical factor for culture expansion, (c) a further increase in scallop biomass may cause scallop predator biomasses to increase, representing in turn a top-down control on other groups of the system, and (d) exceeding scallop biomass levels of 458 t km⁻² may cause other functional groups biomasses to fall below the 10% threshold. The applicability and potential of the here presented ECC simulations as an ecosystem-based approach to sustainable bivalve culture are discussed. Results of this study are expected to guide both local fishers and managers in their challenging task of finding sustainable long-term levels for this important socio-economic activity in Sechura Bay.

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1. Introduction

Bivalves such as clams, oysters, mussels, and scallops represent valuable marine resources worldwide that have been harvested for centuries. During the last decades, aquaculture became an important means for enhancing the production of these resources for human consumption without overexploiting their natural populations. However, the development of aquaculture has often been a bottom-up process, without systematic planning, previous identification of adequate culture areas, or consideration of environmental constraints (Ferreira et al., 2013). Since intensive, industrial-scale culture may lead to changes in ecosystem structure, loss of benthic biodiversity, disease outbreaks, or may cause even mass mortalities due to self-pollution, or whole systems to collapse (e.g. Inglis et al.,

2000; Ferreira et al., 2013), a system-scale assessment of bivalve aquaculture is crucial to ensure long-term sustainable usage of these important marine resources.

Along these lines, many authors have focussed on the concept of carrying capacity, which defines the maximum culture levels before unacceptable changes are incurred to the system (e.g. Inglis et al., 2000). Carrying capacity (CC) has been distinguished into physical, production, ecological, and social CC (Inglis et al., 2000; McKindsey et al., 2006), with physical carrying capacity being the area geographically available and physically suitable for the cultivation of a species in a certain location, and the production carrying capacity describing the bivalve stocking density optimizing long-term harvest. On the ecological level, carrying capacity is approached more holistically, with limits to culture that are set as to optimize production without causing unacceptable impacts on the ecosystem. The social CC considers thresholds of production in a socio-economic context (Inglis et al., 2000; McKindsey et al., 2006). Modeling approaches to carrying capacity have so far often dealt

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with hydrodynamics, food availability and production, as well as with bivalve feeding physiology (Inglis et al., 2000; McKindsey et al., 2006; Gibbs, 2007; Ferreira et al., 2013; McKindsey, 2013), thus targeting physical and production CC. Index models, as an example, have been used to evaluate the impact of bivalve culture on the respective system, comparing the filtration of seston (Dame and Prins, 1998), the production of ammonia (Gillibrand and Turrell, 1997) or biodeposits (Grant et al., 2005) with its tidal renewal as presented by a simple ratio. Other authors estimated carrying capacity as the stocking density maximizing production rates without negatively affecting individual growth rates (Carver and Mallet, 1990) or depleting available oxygen (Uribe and Blanco, 2001), or by the amount of waste production that can be assimilated, removed, or dispersed by the system of concern (e.g. Weise et al., 2009).

By definition, ecological carrying capacity describes the maximum standing stock of the cultured species that does not yet cause “unacceptable” impacts on the ecosystem (e.g. Inglis et al., 2000). The characterization of what represents such an unacceptable change is, however, difficult, and depends on both the environmental settings as well as the social context (e.g. the perception of the involved stakeholders). A holistic approach is nevertheless important, as certain carrying capacity levels may be “unacceptable” to other compartments of the system, e.g. when stocking densities result in cascade effects within the trophic structure of the system (Jiang and Gibbs, 2005). On the other hand, positive effects of culture may also be possible, when the cultured species provides a new habitat structure (Meyer, 2014) and/or an increased food source for benthic fishes and macroinvertebrates associated with bivalve culture sites (McKindsey et al., 2006). In addition to that, cultured bivalves may impact the system by an excessive partitioning of food resources (Newell, 2004), increase in water clarity (Shumway et al., 2003), competition for space (Gibbs, 2004) and increased sediment deposition (La Rosa et al., 2002). As yet, co-occurring species have not been included in most CC models, although they may be important for preservation biodiversity (Worm et al., 2006), due to their role in regulating ecosystem structure and functioning. These concerns, however, are especially important when an ecosystem-based management approach is followed to avoid surpassing carrying capacity limits with a resulting degradation of the system function (Byron et al., 2011a). Some authors used the trophic modeling (Ecopath) approach to estimate carrying capacity by a step-wise increase of the biomass of cultured bivalves, until more food is required than available in the system (ecotrophic efficiency >1, e.g. Wolff, 1994; Jiang and Gibbs, 2005; Byron et al., 2011a, 2011b). This approach, however, uses a steady-state model of constant flow rates between the compartments, and does only focus on the phytoplankton–bivalve interaction, without considering that bivalve culture may significantly impact other parts of the ecological community, or the overall system itself.

The present work aims at addressing ecological carrying capacity of the Sechura Bay ecosystem in northern Peru, which is subjected to an intensive and growing scallop bottom culture, in a more holistic way. The possible impact of a further increase in culture activities on other species groups and possible ecosystemic changes is evaluated by the use of Ecosim. Based on scallop production trajectories of the last years, it was hypothesized that current biomass levels of scallops are already close to the ecological carrying capacity and that phytoplankton standing stocks will soon be depleted if culture activities are expanded at the current pace. The potential of using the definition of stock collapse (after Worm et al., 2009), i.e. if any group biomass falls below 10% of its original biomass, as an approach for defining “unacceptable” ecosystem-based thresholds is explored. Possible management (adaptations) scenarios are discussed in order to ensure the long-term sustainable use of this marine ecosystem and its valuable (fisheries) resources.

2. Methods

2.1. Description of study site

Sechura Bay is located in the North of Peru (5.6°S, 80.9°W) in a transition zone between the northern edge of the Humboldt Current and the southern end of the tropical equatorial region. Due to this geographic position, the bay's sea surface temperatures (SST) are usually higher than those of the central region of the Humboldt system to the south. The bay's inner part is shallow, containing a large area with depths between 5 and 10 m, with depths greater than 30 m found further offshore. The bay, which extends over an area of 400 km², has in recent years developed into a hotspot for scallop (*Argopecten purpuratus*) bottom culture. The species has been extracted along the Peruvian and Chilean coastline since the 1950s, and its fishery represents one of the economically most important bivalve species of the Pacific coast of South America. Due to its comparatively fast growth rate and high productivity, it represents an important portion of the aquaculture exports from Peru, with an export value of about 158 million US\$ per year (in 2013, ADEX Association of Exporters Perú, 2014). In Sechura Bay, approximately 5000 artisanal fishers and 20,000 additional personnel are currently involved in the scallop production and subsequent processing. At present, about 41% of the bay's area (165 km⁻²) is assigned to different associations of artisanal fishermen allowing them to conduct scallop bottom culture (PRODUCE–Ministry of Production, 2015). This is done without the use of large nets or substrate structures, by placing newly recruited individuals (“seed”) onto the ground at densities sometimes up to 300 ind. m⁻² (Mendo et al., 2011). Seed is collected at natural banks within the bay or at a nearby island called *Isla Lobos de Tierra* (ILT, see Fig. 1).

2.2. Model description and data input

A trophic model of Sechura Bay was constructed using the software Ecopath with Ecosim (EwE) 6.4.3 (Christensen and Walters, 2004a), and was based on a previous model by Taylor et al. (2008), which represents the pre-aquaculture conditions of the year 1996. The updated model is comprised of 19 functional groups, representing both benthic and pelagic species groups (Fig. 2).

Input parameters for the different functional groups were obtained from various sources including regional catch statistics, empirical relationships shown in other studies or models, and assumed estimates (after Taylor et al., 2008; see Table 1). Values for production/biomass (P/B), consumption rate (Q) and conversion efficiency (GE) were based on former estimates of Taylor et al. (2008).

Phytoplankton biomass was calculated from remote sensing estimates of sea surface Chlorophyll *a* (Chl *a*) (mg m⁻³) from MODIS (MODIS-Aqua 4 km satellite, taken from <http://disc.sci.gsfc.nasa.gov/giovanni>) for the region 5.17–5.89°S, 80.798–81.25°W. Annual values were first transformed into wet weight using conversion ratios from Brush et al. (Brush et al., 2002; Chl *a*: Carbon - 1:40) and Brown et al. (Brown et al., 1991; Carbon: wet weight - 1:14.25) and were then multiplied by a mean water depth of 15 m to convert values to a m² basis, assuming a well-mixed water column (after Taylor et al., 2008). Phytoplankton biomass was averaged for the years 2008–2012, to diminish the effect of inter-annual variability. Estimates of zooplankton biomass were taken from surveys conducted by the Peruvian Marine Research Institute (IMARPE) for the region (5°–6°S, <82°W, *n* = 60; after Taylor et al., 2008) between 1995 and 1999, as more recent data was not available. Benthic macrofauna biomass estimates, including scallops, were based on data of a benthic survey in Sechura Bay conducted during December 2010 by IMARPE. Hereby, epifauna and infauna was sampled at 124 stations using replicated quadrants of 1 m² each. Abundance and

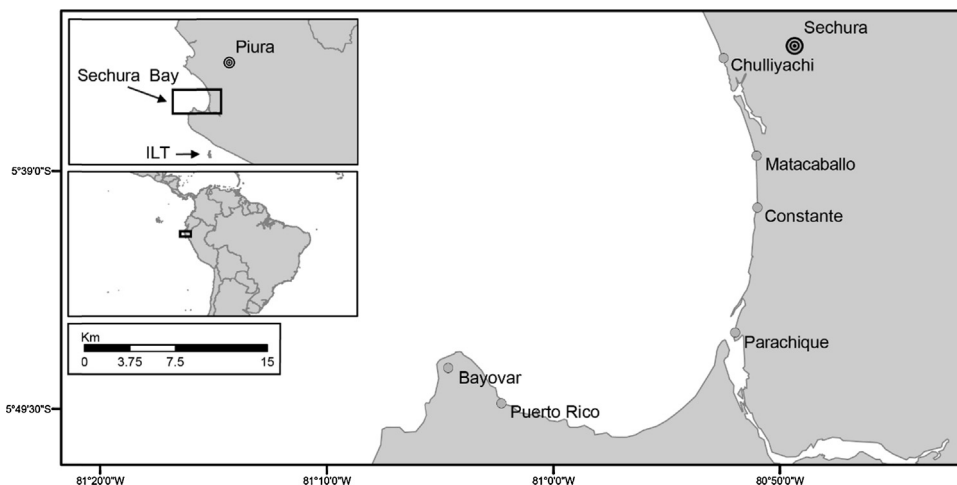


Fig. 1. Location of the study system Sechura Bay in North Peru, with the indication of coastal villages. ILT = Isla Lobos de Tierra, the island where scallop seed is collected.

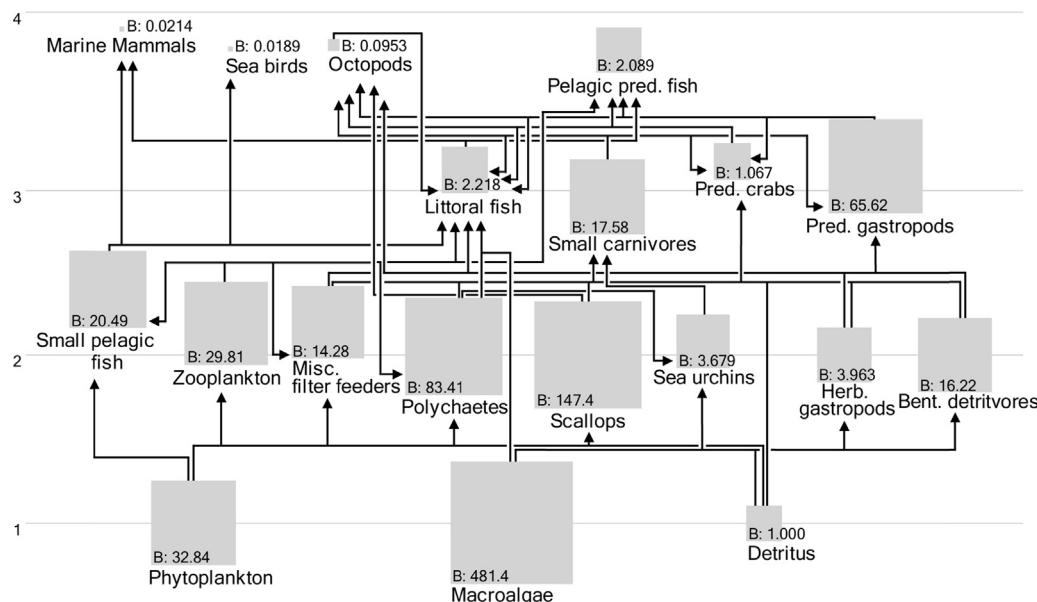


Fig. 2. Flow diagram of the trophic structure of the Sechura Bay ecosystem for the initial steady-state model. Each box represents one functional group scaled proportional to its biomass. Y-axis shows the calculated trophic level (TL) of each functional group.

Table 1
Input–Output parameters for the steady-state model of Sechura Bay. B_i Biomass; P_i/B_i Production rate; Q_i/B_i Consumption rate; EE_i Ecotrophic efficiency; P_i/Q_i conversion efficiency; UA_i/Q_i unassimilated portion of consumption; P/R production/respiration ratio; R/A respiration/assimilation ratio; F_i fishing mortality; MO_i non-predatory natural mortality; $M2_i$ predation mortality. Values in bold were estimated by Ecopath.

Group name	TL	B_i (t km ⁻²)	P_i/B_i (year ⁻¹)	Q_i/B_i (year ⁻¹)	EE_i	P_i/Q_i	P_i/R_i	R/B (year ⁻¹)	Catch (year ⁻¹)	F_i	MO_i (year ⁻¹)	$M2_i$ (year ⁻¹)
1. Phytoplankton	1.00	33.621	331.815		0.421	–	–	–	–	–	192.298	139.517
2. Macroalgae	1.00	455.790	16.864		0.007	–	–	–	–	–	16.748	0.116
3. Zooplankton	2.25	25.886	40.059	160.662	0.997	0.249	0.453	88.471	–	–	0.120	39.940
4. Polychaetes	2.06	100.845	0.980	4.016	0.825	0.244	0.439	2.233	–	–	0.172	0.809
5. Scallops	2.00	147.388	1.314	11.629	0.955	0.113	0.165	7.989	111.445	0.685	0.060	0.498
6. Sea urchins	2.11	3.675	0.528	3.220	0.897	0.164	0.258	2.048	–	–	0.055	0.474
7. Herb. gastropods	2.00	4.011	1.139	4.347	0.927	0.262	0.487	2.339	–	–	0.083	1.056
8. Bent. detritivores	2.00	16.391	1.480	7.437	0.926	0.199	0.331	4.470	0.081	0.005	0.110	1.365
9. Misc. filt. feeders	2.25	13.591	1.094	5.042	0.961	0.217	0.372	2.939	0.960	0.067	0.042	0.981
10. Pred. gastropods	3.27	77.115	1.693	4.351	0.971	0.389	0.947	1.788	1.773	0.027	0.048	1.621
11. Small carnivores	2.95	18.806	0.523	2.527	0.949	0.207	0.349	1.498	–	–	0.027	0.496
12. Predatory crabs	3.21	1.021	1.969	9.207	0.931	0.214	0.365	5.397	–	–	0.137	1.832
13. Octopods	3.71	0.100	4.739	14.064	0.996	0.337	0.728	6.512	0.143	1.501	0.021	3.288
14. Littoral fish	3.17	2.242	1.177	12.134	0.918	0.097	0.138	8.530	0.750	0.338	0.096	0.747
15. Small pelagic fish	2.50	19.059	1.823	20.954	0.742	0.087	0.155	11.797	13.630	0.665	0.471	0.637
16. Pelagic pred. fish	3.57	1.979	0.853	7.685	0.931	0.111	0.189	4.526	0.864	0.414	0.059	0.357
17. Marine Mammals	3.72	0.019	0.114	57.000	0.000	0.002	0.003	45.486	–	–	0.114	–
18. Sea birds	3.57	0.020	0.040	40.000	0.000	0.001	0.001	29.560	–	–	0.040	–
19. Detritus	1.00	1.000	–	–	0.077	–	–	–	–	–	–	–

weight were identified for each species in the upper sediment layer to approximately 5 cm of depth (for further information see references in Taylor et al., 2008). Biomass of groups of small epifauna (herbivorous gastropods, benthic detritivores, miscellaneous filter feeders, and small carnivores) was increased by 25% and by 100% in the case of misc. filter feeders) to correct for undersampling (after Taylor et al., 2008). Biomass of the polychaete group was estimated by Ecopath using the ecotrophic efficiency (EE) value of the 1996 model (EE = 0.825). Biomass for marine mammals and sea birds was used after Taylor et al. (2008), as newer estimates were not available. Biomass for the detritus group was set to 1 t km⁻². Biomass for pelagic groups (i.e. small pelagic fish, littoral fish, predatory pelagic fish, and octopods) was estimated from PRODUCE fisheries statistics from the most important landing sites (Parachique and Puerto Rico) within the bay assuming that the fishery takes out half of the production (Taylor et al., 2008). Landings, however, differed greatly from those in 1996, with a greater species diversity of landed fish, increase in catch and the “presence” of species that occupy habitats not found inside the bay. This is due to a change in fishery practices, i.e. technical improvement of fishing gears and boats allowing fishermen to extend the spatial scale of their activities. Between February and May 2014, interviews were therefore conducted with local fishermen in order to determine catches coming from within the bay (Table 2). Catch data of the artisanal fishery for species considered in the model were obtained from PRODUCE and summed according to its functional group. The construction of the diet matrix followed Taylor et al. (2008, Table 3). Whenever species composition of a group differed from the author’s model of 1996, the diet matrix was adjusted based on the biomass proportions of the group’s composite species. For predatory macroinvertebrate groups (predatory gastropods, small carnivores, predatory crabs, and octopods), the diet matrix was constructed reflecting opportunistic feeding based on iteratively estimated availability of prey biomass and consumption rates of predators (after Taylor et al., 2008), assuming a base percentage of detritus feeding (10–20%).

2.3. Ecosim explorations of the expansion of scallop bottom culture

Scallop aquaculture expansion was simulated for a period of 30 years under four scenarios of differing final scallop biomass that was incrementally increased between years 2 and 6 of the simulation and was then held constant for the remaining years. The introduced biomasses assumed an expansion of activities within culture area (in 165 of 400 km⁻²) and corresponded to

Table 2
Species comprising the different model compartments for the steady-state model of Sechura Bay.

Functional group	Species
2. Macroalgae	<i>Caulerpa</i> sp. (96.1%), <i>Chondracanthus chamosoi</i> (1.6%), <i>Rhodymenia</i> sp. (1.3%), <i>Rhodophyta</i> (0.4%), <i>Ulva fasciata</i> (0.2%), <i>Codium fragile</i> (0.2%), <i>Grateulopia doriphora</i> (0.1%), <i>Ulva</i> sp. (0.1%)
4. Polychaetes	Nereidae
5. Scallops	<i>Argopecten purpuratus</i>
6. Sea urchins	<i>Encope</i> sp. (54.9%), <i>Arbacia spatuligera</i> (45.1%)
7. Herb. gastropods	<i>Aplysia juliana</i> (32.1%), <i>Tegula picta</i> (55.9%), <i>Mitrella</i> sp. (6.9%), <i>Chiton</i> sp. (2.6%), <i>Mitra swainsonii</i> (1.6%), <i>Anachis</i> sp. (0.9%)
8. Benth. detritivores	<i>Cycloanthops sexdecimdentatus</i> (18.0%), <i>Hepatus chiliensis</i> (15.8%), <i>Holothuria</i> sp. (15.2%), <i>Crepidula</i> sp. (10.6%), <i>Inachoides microhynchus</i> (8.5%), <i>Dromia</i> sp. (8.1%), <i>Turritella broderipiana</i> (6.7%), <i>Acanthonix petiverii</i> (5.0%), <i>Gammarus</i> sp. (3.0%), <i>Pleuroncodes monodon</i> (2.5%), <i>Petrochirus californiensis</i> (1.7%), <i>Panopeus</i> sp. (1.5%), <i>Pilumnoides</i> sp. (1.2%), <i>Ophiuroidea</i> (0.6%), <i>Microphrys platysoma</i> (0.6%), <i>Dardanus</i> sp. (0.4%), <i>Euripanopeus</i> sp. (0.3%), <i>Mursia gaudichaudii</i> (0.2%), <i>Pachycheles</i> sp. (0.1%), <i>Crucibulum monticulus</i> (0.1%), <i>Alpheus</i> sp. (0.1%), <i>Crepidatella</i> sp. (0.0%), <i>Petrolisthes</i> sp. (0.0%)
9. Misc. filter feeders	<i>Tagelus dombeii</i> (77.9%), <i>Transennella pannosa</i> (15.0%), <i>Porifera</i> (6.6%), <i>Pennatulacea</i> (0.3%), <i>Cnidaria</i> (0.1%), <i>Megabalanus</i> sp. (0.1%)
10. Pred. Gastropods	<i>Bursa ventricosa</i> (42.7%), <i>Stramonita chocolata</i> (32.9%), <i>Sinum cymba</i> (11.3%), <i>Conus regularis</i> (5.5%), <i>Ocenebra buxea</i> (2.8%), <i>Hexaplex brassica</i> (2.5%), <i>Conus patricius</i> (2.1%)
11. Small carnivores	<i>Solenosteira gatesi</i> (46.0%), <i>Solenosteira fusiformes</i> (37.8%), <i>Prunum curtum</i> (10.1%), <i>Polinices uber</i> (4.0%), <i>Nassarius</i> sp. (1.0%), <i>Nassarius gayi</i> (1.0%), <i>Pseudosquillopsis</i> sp. (0.1%), <i>Ephitonium</i> (0.0%)
12. Pred. crabs	<i>Portunus asper</i> (77.7%), <i>Arenaeus mexicanus</i> (22.3%)
13. Octopods	<i>Octopus mimus</i>
14. Littoral fish	<i>Cynoscion analis</i> (55.5%), <i>Paralabrax humeralis</i> (17.6%), <i>Ophichthus remiger</i> (10.1%), <i>Paralanchurus peruanus</i> (5.5%), <i>Isacia conceptionis</i> (4.6%), <i>Sciaena deliciosa</i> (8.8%), <i>Peprilus medius</i> (2.2%), <i>Genypterus maculatus</i> (0.1%), <i>Muraena lentiginosa</i> (0.1%), <i>Trinectes fluviatilis</i> (0.0%), <i>Anisotremus scapularis</i> (0.0%), <i>Menticirrhus ophicephalus</i> (0.0%), <i>Scorpaena mystes</i> (0.0%)
15. Small pelagic fish	<i>Engraulis ringens</i> (80.0%), <i>Mugil cephalus</i> (15.3%), <i>Anchoa nasus</i> (4.3%), <i>Ethmidium maculatum</i> (0.5%), <i>Odontesthes regia</i> (0.0%)
16. Pelagic predatory fish	<i>Scomber japonicus</i> (47.4%), <i>Sarda chiliensis</i> (28.8%), <i>Auxis rochei rochei</i> (16.7%), <i>Mustelus lunulatus</i> (7.1%), <i>Carcharhinus</i> sp. (0.0%)

Table 3
Diet matrices for the steady-state models of Sechura Bay. Values of 0.000 indicates a proportion of <0.0005.

Prey\predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. Phytoplankton	0.700	0.300	0.800				0.700						0.598			
2. Macroalgae				0.800	0.800	0.200						0.185				
3. Zooplankton	0.200	0.050					0.200					0.197	0.402	0.147		
4. Polychaetes				0.100				0.200	0.178	0.127		0.133				
5. Scallops								0.200	0.108	0.112	0.112					
6. Sea urchins									0.037							
7. Herb. gastr.								0.000	0.066	0.066	0.083	0.009				
8. Bent. detri.								0.014	0.233	0.127	0.158	0.098		0.171		
9. Misc. filt. feed.								0.029	0.050	0.029	0.096	0.033				
10. Pred. gastr.								0.351	0.154	0.193	0.136			0.121		
11. Sm. carniv.								0.006	0.129	0.097	0.121	0.003				
12. Pred. crabs										0.089	0.158	0.011		0.034		
13. Octopods											0.079	0.008				
14. Littoral fish												0.024		0.044	0.250	0.101
15. Small pel. fish												0.146		0.44	0.701	0.899
16. Pel. pred. fish														0.043	0.049	
17. Mar. mammals																
18. Sea birds																
19. Detritus	0.100	0.650	0.200	0.100	0.200	0.800	0.100	0.200	0.200	0.200		0.017				

Table 4
System statistics and flow indices of the Sechura Bay steady-state model.

Parameter	Value
<i>Trophic indicators</i>	
Sum of all consumption (t km ⁻² year ⁻¹)	7335.11 (17.5%)
Sum of all exports (t km ⁻² year ⁻¹)	14,592.82 (35.9%)
Sum of all respiratory flows (t km ⁻² year ⁻¹)	4249.60 (10.2%)
Sum of all flows into detritus (t km ⁻² year ⁻¹)	15,673.13 (37.5%)
Total system throughput (TST) (t km ⁻² year ⁻¹)	41,850.65
<i>Fishing</i>	
Total catch (t km ⁻² year ⁻¹)	129.65
Mean trophic level of the catch	2.09
Gross efficiency (catch/net p.p.)	0.0069
Primary Production (PP) required/catch	11.88
<i>Community energetic</i>	
Total primary production (PP)/total respiration	4.43
Total PP/total biomass	20.45
Total biomass/total throughput (year ⁻¹)	0.02
Total biomass (excl. detritus)	921.56
<i>Network indicators</i>	
Finn's cycling index (FCI) (% of TST)	3.15
Ascendency (%)	39.6

grow-out densities of 10, 20, 30, and 40 individuals per m⁻², while the biomass in the non-culture areas (235 of 400 km⁻²) was maintained at background population biomass levels of 147.4 t km⁻² (approximately 1.6 ind. m⁻²). An average culture size (shell height) of 77 mm and average body wet weight of 90 g for scallop individuals (including shells) was assumed (after Meyer, 2014), and final biomass (B_{final}) values to be introduced for the scenarios were obtained for the whole model area as follows (Table 4):

$$B_{\text{final}} = (B_{\text{culture}} \times A_{\text{culture}}) + (B_{\text{non-culture}} \times A_{\text{non-culture}})$$

Here, B_{culture} represented the scallop biomass for within culture as described above (i.e. 900, 1800, 2700, 3600 t km⁻² for scenarios 1–4, respectively), and $B_{\text{non-culture}}$ was maintained at 147.4 t km⁻² as for the initial EwE model. A_{culture} and $A_{\text{non-culture}}$ represented the proportion of culture (165/400 km²) and non-culture (235/400 km²) areas, respectively. Accordingly, for the four scenarios $B_{\text{final}} = 458, 829, 1200, \text{ and } 1572 \text{ t km}^{-2}$, respectively. Scenarios were based on a previous study done in conjunction with local fishers regarding the influence of grow-out densities on scallop growth (Mendo et al., 2011), which showed a decrease in growth performance associated with high scallop densities (>30 ind. m⁻²), possibly due to oxygen rather than food limitation. Therefore, scenarios of the densities were chosen that did not extensively exceed these levels. The vulnerabilities (v) in Ecosim, describing the flows and type of trophic control (bottom-up, intermediate, or top-down) between predator and prey, were set to be proportional to the trophic level of the functional group (following Cheung et al., 2002, Buchary et al., 2003, Chen et al., 2008):

$$V_i = 0.1515 \times \text{TL}_i + 0.0485 \quad (1)$$

where TL_i represents the trophic level of a functional group as calculated by Ecopath. Vulnerability settings as proposed by the above-mentioned authors ranged from 0 to 1, with 0.0 representing a bottom-up control, 0.3 a mixed effect, and 1.0 describing a top-down impact (Christensen and Walters, 2004a). A linear conversion was therefore applied to derive at values for v ranging from 1-Inf (as used for the EwE version 6.4.3, Table 5):

$$\log(V_{\text{new}}) = 2.301985 \times V_i + 0.001051 \quad (2)$$

Result of the individual scenario simulations (including biomasses and ecological network analysis indicators, see Table 6) were downloaded from Ecosim and via the Ecosim network analysis form in Ecopath. The development of ecological network analysis indicators over simulation time was compared with initial values.

Table 5

Vulnerability settings used for the Ecosim simulations in order to mimic a more realistic trophic control regime in the ecosystem. Vulnerability values (v) are linearly proportional to trophic levels (TL) of each functional group.

Functional group	Trophic level (TL)	Vulnerability setting (v)
3. Zooplankton	2.2376	2.4426
4. Polychaetes	2.0631	2.2984
5. Scallops	2.0000	2.2484
6. Sea urchins	2.1063	2.3333
7. Herb. gastropods	2.0000	2.2484
8. Benthic detritivores	2.0000	2.2484
9. Misc. filter feeders	2.2500	2.4532
10. Pred. gastropods	3.1772	3.3898
11. Small carnivores	2.9480	3.1293
12. Predatory crabs	3.2142	3.4338
13. Octopods	3.5938	3.9198
14. Littoral fish	3.1508	3.3586
15. Small pelagic fish	2.4975	2.6744
16. Pelagic pred. fish	3.5551	3.8672
17. Marine Mammals	3.7127	4.0857
18. Sea birds	3.5635	3.8786

Table 6

Description of ecological network analysis indicators used.

Indicator	Description
Total system throughput (TST)	The sum of all flows through the ecosystem, measure of system size (Ulanowicz, 1986).
Capacity	The product of TST and entropy represents the upper limit to the ascendency (Heymans et al., 2007).
Ascendency	The product of the growth (TST) and development (AMI) of the system (Ulanowicz, 1986, 2004).
Average mutual information (AMI)	The organization of the exchange among components (Mageau et al., 1998).
Entropy	The total number and diversity of flows within the system, a measure of the total uncertainty embodied in a given configuration of flows (Mageau et al., 1998).
Kempton's Q	Relative index of biomass diversity, including species or functional groups with a TL > 3 (Kempton and Taylor, 1976, Christensen and Walters, 2004b), expressing both species richness and evenness (Ainsworth and Pitcher, 2006).
Finn's cycling index (FCI)	The percentage of the ecosystem throughput that is recycled, serves as an indicator of stress and structural differences (Finn, 1976).
Transfer efficiency (TE)	For a given trophic level (TL) the ratio between the sum of the exports and the flow transferred to the next TL, and the throughput on the TL (Christensen and Walters, 2004a), in this context the mean TE for TL > 2 is used.

The impact of scallop biomass increase on the other functional groups was then evaluated comparing changes in biomasses to the initial steady-state model for each functional group for all four scenarios. An ecosystem state scenario was considered not sustainable, if any functional group fell below 10% of its original biomass standing stock. This approach follows the definition of a collapsed stock in fisheries science, describing a stock as collapsed if its biomass falls below 10% of its unfished biomass (Worm et al., 2009). At such a low abundance, recruitment of a population may be severely limited (Worm et al., 2009).

3. Results

3.1. Overall system effects

The increase in scallop biomass generally caused system size to increase, as can be seen from the increase in total system biomass and throughput, the capacity, and the ascendency, with values leveling off once scallop biomass was stabilized (Fig. 3). However,

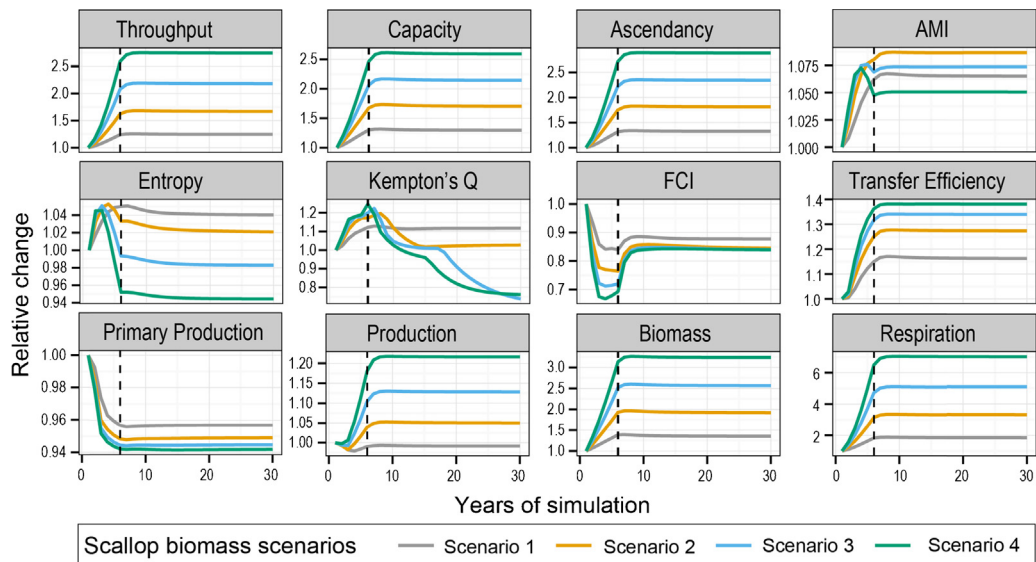


Fig. 3. Relative changes in ecological network analysis indices for the scenarios 1 to 4 (increasing scallop biomasses to 458, 829, 1200, and 1572 t km⁻², respectively) when compared with the initial balanced EwE model. The vertical dashed black line indicates the point in time after which scallop biomass levels were held constant (i.e. year 6). AMI = Average mutual information, FCI = Finn's cycling index, PP = Primary Production.

a poorer cycling within the system due to the introduction of large scallop biomass quantities was indicated by a decrease of the Finn's cycling index (FCI) and an increase in the average mutual information (AMI). However, an increase in the transfer efficiency (TE) suggested a more efficient transport of energy from low to high trophic levels. Diversity of flows, as described by the system's entropy, peaked for all scenarios during the first 5 years of simulation, and fell thereafter, with values dropping below initial ones for scenarios 3 and 4. A further increase in scallop biomass to levels of scenarios 1 and 2 had a positive effect on biodiversity and evenness, as described by an increase in the Kempton's Q indicator. Exceeding these values (i.e. reaching scallop biomass levels of scenarios 3 and 4), caused the index to decrease (Fig. 3), reflecting a decrease in upper trophic level biomass and the drastic decrease in biomass of several functional groups. Primary production decreased as a result of decreased phytoplankton biomass (see also part 3.2). Total system respiration increased in response to the increase in total system biomass. Its relative change was, however, higher than for biomass, indicating a change in community structure, i.e. a shift in dominant species (functional groups) contributing more to overall system respiration when compared with the initial state.

3.2. Effects on other functional groups

The further expansion of scallop culture generally caused total system biomass to increase (Fig. 4), and induced a change in community structure due to the bottom-up effect of scallop on its predators (e.g. predatory gastropods, small carnivores, predatory crabs, octopods, littoral fish, predatory pelagic fish, Figs. 4 and 5), that increased in biomass. Scallop competitors (e.g. polychaetes, sea urchins, herbivorous gastropods, benthic detritivores, misc. filter feeders, and small pelagic fish), on the other hand, decreased in biomass (Figs. 4 and 5), caused by the top-down control induced by increasing predator biomasses, with some groups being nearly completely depleted. Scallops, initially contributing 16% of system's biomass, represented for all scenarios, the most important functional group in terms of biomass at the end of simulation. Predatory gastropods represented a second group that initially held a comparatively low percentage (8%), but that greatly increased its contribution to overall system biomass, in scenarios 3 and 4 even surpassing macroalgae that otherwise represented the second

highest biomass contribution. The phytoplankton biomass never fell below 81% of its original standing stock, indicating that the top-down control of scallops on its food source only plays a minor role.

Only when remaining scallop biomass at 458 t km⁻² (scenario 1) all functional groups stayed above the threshold of 10% (of its original standing stock biomass). A further increase (i.e. exceeding 829 t km⁻², scenario 2) caused polychaetes and misc. filter feeders biomasses to fall below 10% (Fig. 5). Several other groups, including sea urchins, herbivorous gastropods, and benthic detritivores, also drastically decreased in biomass, but did not fall below the 10% threshold. The group of benthic detritivores dropped to 12% in scenario 4. Both marine mammals and sea birds continued to decrease during simulation time, while all other groups leveled off at a certain point.

4. Discussion

4.1. Systemic effects

The exploration of ecological indicators reveals that a further expansion of scallop culture would represent an impact on the ecosystem. System size increases, as demonstrated by an increase in system throughput, ascendancy, and capacity, and the increase in trophic efficiency indicates an increase in development and maturity. On the other hand, several indicators suggest a poorer cycling within the system, a severe change in flow structure and the increasing dominance (in terms of biomass) of certain groups. As an example, a rise in average mutual information (AMI) indicates that the system is becoming more constrained due to a channeling of flows along more specific pathways (Ulanowicz and Abarca-Arenas, 1997), but also channeling of flows through secondary production (e.g. via scallops). Accordingly, predator biomass increases, while competitor biomass decreases. Mature systems are assumed to be low in entropy and to represent a higher degree in cycling within the system (Odum, 1969). According to this, the introduction of scallop biomasses up to 829 t km⁻² (i.e. scenario 2) would cause a decrease in system maturity, as indicated by an increase in system's entropy, and increase when surpassing this limit. Similarly, a drop in system cycling (i.e. Finn's cycling index, FCI) in all scenarios suggests the system would decrease in maturity with increased

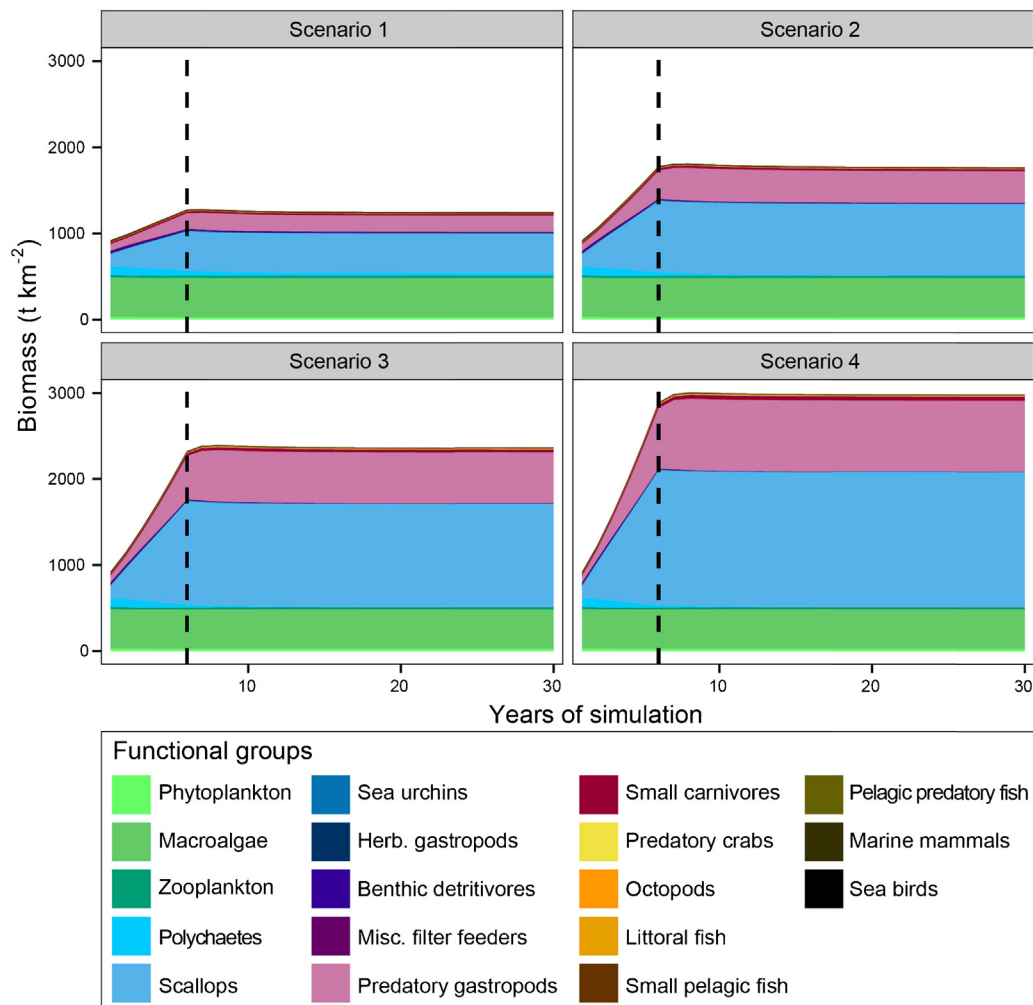


Fig. 4. Biomass contribution of each functional group to overall system biomass during simulation time for the scenarios 1 to 4 (increasing scallop biomasses to 458, 829, 1200, and 1572 t km^{-2} , respectively). The vertical dashed black line indicates the point in time after which scallop biomass level was held constant (i.e. year 6).

scallop biomass (Christensen, 1995). In contrast to this, increasing scallop biomass levels to 829 t km^{-2} (i.e. scenarios 1 and 2) causes a net increase in biodiversity as indicated by the Kempton's Q, while higher biomasses (scenarios 3 and 4) caused the indicator to decrease, suggesting that scallop culture may be expanded until 829 t km^{-2} before negatively impacting species diversity.

Scallop bottom culture can be physiologically limited if grow-out densities of 30 ind. m^{-2} are exceeded (Mendo et al., 2011), most likely due to small scale oxygen limitations. Based on oxygen considerations, we would therefore only expect the scenario 4 (1572 t km^{-2} , corresponding to 40 ind. m^{-2} within the culture area) to cause a problematic situation for the culture. However, total system respiration as calculated by Ecosim increased during simulations by up to seven times, while this increase was not directly proportional to the increase in total system biomass (which increased by the factor of 3). This reflects a change in community composition and corresponding biomass decrease of groups such as zooplankton, small pelagic fish, and marine mammals, that had comparatively higher respiration to biomass (R/B) ratios in the initial EwE model used for the simulation (Table 1), with simultaneous increase in total system respiration indicates that respiratory demands of other groups, most likely scallops and higher level predators, must have increased due to a respective rise in biomass. In addition, the real oxygen consumption of the community may even be higher than the values calculated here, since microbial cycling was not included into the model, but

can contribute significantly contribution to community respiration through the mineralization of organic matter (Nizzoli et al., 2005). The potential depletion of oxygen at bottom layers was described as an important impact of bivalve bottom culture (NRC, 2010), both to the benthic community and the cultivated bivalve themselves. Bottom culture is especially susceptible to oxygen limitation due to decreased concentration with water depth and higher bottom water residence times from reduced current speed. In contrast, suspended cultures are less susceptible, due to its position in the more oxygenated upper part of the water column. But, suspended mussel lines and scallop cages can promote the development of macrofaunal communities that increase oxygen consumption and the release of nutrients (Richard et al., 2007), which may ultimately impact benthic communities. The disproportional increase of total system respiration when compared with the increase in total biomass stresses the importance of including the factor of oxygen into carrying capacity estimations, since an expansion of scallop culture in Sechura Bay would not only increase respiratory demands of the increased scallop population, but of the whole community. It is thus recommended to not only to consider oxygen depletion by the cultured individuals, but by the entire community. This is supported by Dankers et al. (1989) who conducted a study comparing oxygen consumption by mussel beds in tanks and their natural environment (Dutch Wadden Sea). Their results suggest considerably higher oxygen consumption for the latter, which they attributed to benthic organism and biogeochemical

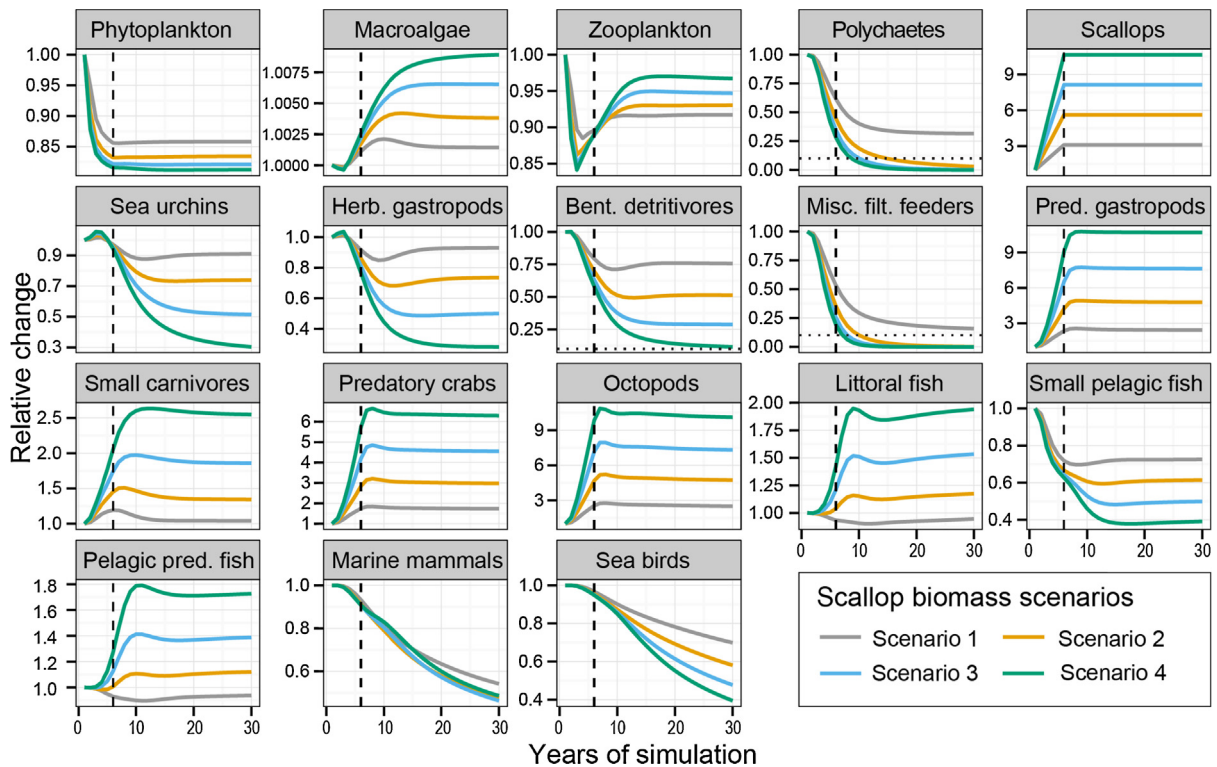


Fig. 5. Relative changes in biomass of all functional groups for the scenarios 1 to 4 (increasing scallop biomasses to 458, 829, 1200, and 1572 t km⁻², respectively) when compared with the initial balanced EwE model. The vertical dashed black line indicates the point in time after which scallop biomass level was held constant (i.e. year 6). The horizontal red dotted line represents the 10% threshold of initial biomass stocks.

processes associated with the mussel bed. Similarly, [Richard et al. \(2006\)](#) found that the metabolism of (suspended) cultured bivalves and their associated fauna as well as the degradation of associated organic matter causes an increase in oxygen consumption and nutrient release to adjacent waters. In addition, cultivated bivalves and its associated fauna can generate considerable amounts of organic matter ([Callier et al., 2006](#)), which can ultimately accumulate within aquaculture structures ([Nizzoli et al., 2006](#)).

According to a study by [Tam et al. \(2012\)](#) assessing the carrying capacity of Sechura Bay considering the factors oxygen and food (i.e. phytoplankton production) limitation, oxygen was estimated to be the more important limiting factor to the expansion of scallop culture in this system. They presented, however, a CC value higher than the biomass level of scenario 4, but this difference may be explained by the fact that they calculated the productive carrying capacity, which often is higher than ecological CC (e.g. in [Jiang and Gibbs, 2005](#); [Byron et al., 2011a](#)), and have not included the respiratory demands of other groups in the system.

The results of our explorations emphasize the need to permanently monitor oxygen concentrations within a system subjected to bivalve culture, and to consider the total community respiration, including microbial respiration, when estimating carrying capacity. Further environmental studies would need to specifically address oxygen dynamics in our particular system.

4.2. Impact on other groups

In contrast to many studies focusing on ECC for bivalve culture, the results of this work contradict the hypothesis that food (phytoplankton) availability generally represents the most limiting factor for the extension of culture. For our case, phytoplankton biomass never fell below 81% of original standing stock for any of the explored scenarios, which may be explained by the vulnerability value of 2.25 used for scallop ([Table 5](#)), ultimately limiting

the increase in predation pressure on phytoplankton, as well as the a relatively low ecotrophic efficiency ($EE = 0.45$) in the steady-state model used for the simulations, representing the potential scope for growth of the scallop population without depleting the phytoplankton resource. This makes also sense considering that Sechura Bay is a relatively large open bay system with a comparatively low water residence time of 5.29–7.93 days ([Quispe, 2012](#)) when compared with other bay systems that were modeled to estimate ecological carrying capacity (e.g. 26 days in Narragansett Bay in eastern USA ([Byron et al., 2011a](#))), with the frequent flushing diminishing the possibility of food limitation for cultured bivalves. Our results suggest that besides the phytoplankton–bivalve relationship other inter-specific relations in the ecosystem may in fact be more important for evaluating the carrying capacity of the system. The increase in predator's biomass due to an increase in scallop abundance, as an example, represents a top–down control on other benthic groups such as benthic detritivores and miscellaneous filter feeders, increasing the losses in these groups' biomasses with an expansion of scallop culture. The zooplankton group never fell below 91% of its original standing stock. This is somehow counter-intuitive, as this group represents one of the most important food competitors for scallops. In fact, several authors have defined (production) carrying capacity as the point at which cultivated bivalves outcompete zooplankton (e.g. [Gibbs, 2004](#), [Jiang and Gibbs, 2005](#), [Byron et al., 2011a](#)). In our study system, zooplankton is not only preyed upon by benthic filter feeders such as bivalves and polychaetes, but also by the different fish groups (see [Fig. 2](#) and [Table 3](#)), with small pelagic fishes being the most important predator. The increase in scallop biomass indirectly caused (via the enhanced biomass of predatory fish groups) the standing stock of small pelagic fishes to decrease, reducing in turn the predation pressure on the zooplankton. Similarly, the decrease in other benthic groups as described above is likely not caused by inter-species competition for food (phytoplankton), but

by indirect trophic effects. The assumption that bivalve aquaculture may eventually outcompete other filter feeders in the system was conclusively not observed for our case.

Bivalve aquaculture is considered as one of the more sustainable types of aquaculture (Shumway et al., 2003) as cultured individuals exploit naturally occurring phytoplankton at the basis of the food chain, and do not need external feed inputs as other types of aquaculture (Dumbauld et al., 2009). Culture (facilities), however, may alter environmental conditions such as seston levels or by providing settling structure, thus habitat, to other organism (Filgueira and Grant, 2009), which may increase biodiversity (Dealeris et al., 2004; Tallman and Forrester, 2007). Suspended bivalve culture was shown to increase the abundance and biomass of sessile organisms such as benthic invertebrates in the water column by providing substrate for the settlement and growth (Lesser et al., 1992, Ross et al., 2004, McKindsey et al., 2006, Richard et al., 2007). Benthic macrofaunal biomass, in contrast, was suggested to be negatively impacted by suspended bivalve cultures (Hatcher et al., 1994, Grant et al., 1995, Christensen et al., 2003). Our results, in contrast, suggest that a further expansion of culture activities may affect ecosystem structure and biodiversity as indicated by the collapse of entire functional groups (here defined as a decrease in biomass to <10% of its original standing stock) and a corresponding drop in Kempton's Q as a measure of biodiversity. These results emphasize the need to evaluate the possible expansion of bivalve culture in the ecosystem context, for which the trophic modeling approach appears useful. The increase in biomass of higher trophic level groups as a potential result of an increase in scallop biomass supports what other studies have found with respect to potential benefits from bivalve culture to wild animals. Several authors described that the production of fish can be increased in areas with mussel culture (Chesney and Iglesias, 1979), and that the diet of various fish (López-Jamar et al., 1984) as well as crab (Freire and Gonzalez-Gurriaran, 1995) species consisted to larger parts of epifauna from mussel culture (facilities). This development may on the other hand represent a potential benefit to fisheries in the region, as many of the species joined in the functional groups benefitting from culture represent fishery target species. However, the increase in biomass of potential predators may cause a loss in culture production, as in Sechura cultured individuals usually are not enclosed by any protective structures such as cages, and are therefore directly impacted by an increase in predation pressure.

Considering the trophic network surrounding scallop bottom culture in Sechura Bay, culture activities may be expanded to a scallop biomass level of 458 t km⁻² (i.e. scenario 1) before negatively impacting other groups of the system.

4.3. Estimating ecological carrying capacity in the context of trophic interactions

The use of Ecosim for the estimation of carrying capacity allows for the temporal exploration of potential impacts of a further increase of culture activities based on species interaction. To our knowledge, this represents a novel approach. The only similar study we found was conducted by Lin et al. (2009), who used Ecosim to investigate the possible consequences of the complete removal of oyster racks on Tapong Bay in southern Taiwan. This was done by increasing the relative fishing effort on cultured bivalves (and directly associated (epi-) fauna) to simulate removal of oyster racks. The authors found a significant negative feedback of cultured oysters on biomass of almost all other groups in the system, but did not use their results in an ECC context.

From a physiological point of view, scallop bottom culture in Sechura should be conducted without exceeding mean individual densities of 30 ind. m⁻², in order to ensure best grow-out results (Mendo et al., 2011). However, an accordant increase in cultivation

levels to this target density for the whole cultivable area (corresponding to a total biomass of 1200 t km⁻², scenario 3) could already result in major changes on ecosystem structure and in particular may represent an unacceptable change for other functional groups, as shown by their decrease of biomass to below the threshold of 10%. When considering ecological carrying capacity (ECC) as the scallop biomass level at which all other groups remain above the 10% threshold (of its original value), scallop biomass should not be increased further than 458 t km⁻² (scenario 1). Accordingly, current biomass levels of 147.4 t km⁻² do not yet exceed ECC. However, the introduction of large scallop biomass quantities to the present level due to the initiation of culture activities in 2003 has already changed the community composition in Sechura Bay (Kluger et al., in preparation). The authors compared the pre-culture and culture states of the system (as represented by EwE models for the years 1996 and 2010), and found that the latter system state is already more dominated by certain species (i.e. scallops, macroalgae, and predatory gastropods). Accordingly, the model used for the hypothetical explorations as presented in this work may represent already a biased baseline, but as the focus of the present work was to explore potential impact of a future expansion of culture activities, it was still considered a viable start for simulation. The ECC value of 458 t km⁻² is much lower than the value presented by Tam et al. (2012) for Sechura Bay. The authors concluded that the culture should not exceed 6090 10⁶ scallop individuals, corresponding to a biomass of 1352 t km⁻². However, they calculated production carrying capacity (based on oxygen), which is expected to result in higher values as for ecological carrying capacity (e.g. Jiang and Gibbs, 2005; Byron et al., 2011a).

For comparison, ecological carrying capacity was calculated from the initial steady-state EwE model following the approach used by many authors (e.g. Wolff, 1994, Jiang and Gibbs, 2005, Byron et al., 2011a, 2011b). For this, scallop biomass was increased until the ecotrophic efficiency of any group exceeded one (EE > 1). Results suggest that scallop biomass could be increased to 841.6 t km⁻². This value, however, would exceed both physiological thresholds of scallops (i.e. the biomass corresponding to a density of 30 ind. m⁻² that was identified as physiologically feasibility in terms of growth) and of other functional groups in the system (as indicated by the drop in biomass below the threshold of 10% for several groups already at a biomass level of 829 t km⁻² (scenario 2)). This approach to ECC using Ecopath is somehow simplified as it neither includes any oxygen considerations, nor the assessment of potential indirect trophic effects of bivalve culture on other groups of the systems. Allowing the culture to expand until an average biomass of 841.6 t km⁻² would, for our case, over-estimates the capacity of the system to sustain bivalve culture, thus put it under the threat of local species extinction. The change in community composition may have unpredictable impacts in terms of ecosystem functioning. This result emphasizes the necessity to address ECC in the ecosystem context, considering species interactions, rather than focusing on the phytoplankton–bivalve relationship only.

Besides the factor of phytoplankton depletion, most studies have not yet presented carrying capacity limits that are transferable to other systems. This is mainly due to the great variability of system's spatial dimensions, environmental conditions, and trophic structures, requiring CC models to be developed and applied on a site-specific basis. The approach of estimating carrying capacity presented here may be an alternative as it is based on ecosystemic thresholds. Furthermore, new developments in the EwE software allow for the monitoring of biodiversity while exploring expansion scenarios for bivalve culture. Not allowing any group to be depleted further than 10% of its original biomass could be used as an ecosystem-based indicator of how much change, as induced by scallop culture, is acceptable, and may be applied

to other systems exposed to bivalve culture. It may be recommendable, however, to extend studies on individual capabilities of the species present in the system of concern in order to ensure long-term sustainability. The 10% threshold used for this study represents a useful approximation of how much change in group's biomass is acceptable, but is based on the assumption that at 10% of its original standing stock, a species will be severely restricted in terms of recruitment and may not be able to perform its ecological role (Worm et al., 2009). At this stage, the species may be lost already to the system and in order to ensure the maintenance of ecosystem functioning it may therefore be necessary to adjust the threshold to the point at which a species group is still able to maintain its population given its individual live traits characteristics (e.g. growth rates, reproduction, or movement pattern).

4.4. Management considerations

The approach to carrying capacity as presented in this work allows for a more holistic, thus realistic, exploration of potential consequences of further extended scallop culture on the ecosystem level. Considering only measures of scallop growth performance for carrying capacity estimations, i.e. the maximum grow-out density of 30 ind. m^{-2} to obtain highest production yields, was shown to already cause “unacceptable” changes to other functional groups of the system. Defining the ecological carrying capacity as the quantity of scallop biomass that not yet causes any group to be reduced to below 10% of its original biomass, the scallop culture activities in Sechura Bay should not be extended further than 458 $t km^{-2}$ in order to ensure the maintenance of the ecological community and ultimately ecosystem functioning. From an ecological point of view, the extinction of entire groups as a consequence of bivalve culture is not acceptable, and should be avoided when developing management strategies. On the other hand, culture at optimum densities to ensure highest production yields will be in the interest of culturists. Any management plan for Sechura Bay, as for any other system exposed to bivalve culture, has therefore to be a balance between ecological thresholds and compliance of involved stakeholder demands.

Assuming that an expansion of culture activities should not exceed the scallop biomass level of 458 $t km^{-2}$ (scenario 1) before causing other functional groups of the system to become depleted, this translates into an annual harvest of 138,477 t as the ecological carrying capacity for Sechura Bay. The results of this work are based on the system state of 2010, as the model was constructed with data for the year for which most information was available. Comparing this potential harvest value with what has been produced in Sechura Bay in the year of highest production since then (2013), it becomes clear that culture has already intensified since the moment for which the model was constructed. According to SANIPES (=Organismo Nacional de Sanidad Pesquera; J. Proleón, personal communication), the annual harvest value was at 150,000 t for the year 2013, suggesting that current culture is at the ecological carrying capacity of the bay, and should not be expanded further. In order to obtain long-term sustainable use of this important marine resource while maintaining ecosystem functioning, a continuous monitoring and meaningful management measures are required. These may include the control of grow-out densities and the implementation of individual harvest limits for each fishermen association (e.g. depending on the size of their respective culture area, and/or the location within the bay).

One aspect to also consider is the effect of scallop bottom culture on higher trophic level predator production. As most of those species represent target species to the local artisanal fishery, any management plan considering to allow the extension of scallop culture activities would therefore have to aim at developing strategies for harvesting these groups as well. A further expansion of scallop

bottom culture and a corresponding increase in predator biomass would thus allow the fishery to increase fishing pressure on the latter, but the process would have to be evaluated carefully in order to develop meaningful multi-species management measures.

Moreover, it is important to consider the spatial extension of culture that currently expands over 165 km^2 out of 400 km^2 within the bay. For this work, average densities for these 165 km^2 were assumed, but in reality culture is often conducted exceeding grow-out densities of 40 ind. m^{-2} (Mendo et al., 2011). Nevertheless, culture usually occupies only about 60% of the area assigned to this purpose, meaning that although intense bottom culture may exceed the ecological carrying capacity on a small-scale, it may represent the chance to spatially release the ecological community from the pressure that scallop culture exposes. To ensure the optimal effect, it may moreover be recommendable to change areas used for cultures in a rotational manner, i.e. to implement area closures that are open to fishery/culture only for a certain period of time. This is a concept that has been successfully applied to manage the Atlantic sea scallop (*Placopecten magellanicus*) fishery at Georges Bank off the northeastern USA (Hart, 2003). Scallop bottom culture in Sechura does not involve any culture facilities (nets, etc.), but this idea would nevertheless be difficult to implement, as culture areas are officially assigned to single fishermen associations, and the effort needed for the spatial re-allocation of culture would most likely exceed feasibility. Large-scale monitoring of culture activities in Sechura has yet to be implemented, mainly due to the large size of the bay. An alternative could therefore be the rotational use of the area of individual culture units allocated to fishermen associations (instead of using always the same patches as is currently practised, personal observation), and limiting the scallop grow-out densities to 30 ind. m^{-2} . As a next step toward an even more realistic carrying capacity estimation for the Sechura Bay ecosystem it may further be recommendable to extend carrying capacity explorations spatially, e.g. by applying the Ecospace module, and to include socio-economic aspects in order to identify social carrying capacity (SCC) thresholds. In this context, SCC may be defined as the maximum level of aquaculture activity that not yet causes adverse social impacts, but analytical methods for its estimation are still under development (Byron and Costa-Pierce, 2013). As SCC may be an important driver for management (Byron et al., 2011c) it will therefore be addressed in a future publication aiming at the holistic guidance of decision-making in Sechura Bay.

4.5. Conclusions

The use of Ecosim proved to be a useful tool for the estimation of ecological carrying capacity (ECC) and ecosystem-based thresholds to bivalve aquaculture development. ECC was defined as the maximum amount of scallop biomass that would not yet cause any other group's biomass to fall below 10% of its original biomass. This threshold represents an ecosystem-based limit to bivalve culture and is expected to be applicable to other systems. Simulations of a further culture expansion suggest that phytoplankton may not be significant for our case, which is in accordance with a first CC study from the region (Tam et al., 2012). More important seem to be interspecific trophic consequences, e.g. when an increase in bivalve predator's populations impose a top-down control on other (benthic) groups of the system. Exceeding scallop biomass levels of 458 $t km^{-2}$ may cause other functional groups biomasses to fall below the 10% threshold (of its original standing stock), potentially threaten ecosystem functioning, emphasizing the necessity for an ecosystem-based approach to ECC. In order to develop meaningful management strategies it may be recommendable to extend carrying capacity explorations to include spatial processes for added realism.

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