

Assessing the ecosystem impact of scallop bottom culture through a community analysis and trophic modelling approach

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ABSTRACT: The Peruvian bay scallop *Argopecten purpuratus* is a key resource of the Peruvian diving fishery that has long been harvested along the Peruvian and Chilean coastline. In the last decade, Sechura Bay (North Peru) has developed into a hotspot for its cultivation, which represents an important socio-economic activity for the region. Scallops are cultivated on the bottom and may potentially function as ecosystem engineers in the system by providing settling substrate to other organisms in an otherwise soft-bottom habitat. Community analysis (permutational multivariate analysis of variance, similarity percentage analysis and abundance–biomass comparison) was combined with trophic modelling (Ecopath with Ecosim) to compare the current system state with pre-culture conditions, to evaluate the impact of scallop culture on both the benthic community and overall ecosystem functioning. The results suggest the following effects due to the massive culture: (1) a significant change in benthic community composition; (2) an increase in the predator biomass, paralleled by a decrease in the biomass of their competitors; (3) a change in species diversity and maturity; (4) a system increase in size (in terms of biomass and total flows); and (5) a decrease in energy cycling, indicative of the direct impact of scallop culture on the system's flow structure and functioning. The results suggest that a further expansion of scallop culture may cause the benthic species composition to further shift towards a hard-bottom-associated community, essentially altering the system's structure and functioning. These results are expected to aid the process of suggesting limits to culture and the ecological carrying capacity of the bay's system.

KEY WORDS: Bivalve culture · Aquaculture impact · Community analysis · Trophic modelling

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INTRODUCTION

Bivalve aquaculture is considered to be one of the most sustainable marine activities (Shumway et al. 2003) since cultured individuals exploit naturally occurring phytoplankton at the base of the food chain, and do not need external feed inputs, as is the case for many other types of aquaculture (e.g. Cranford et al. 2003, Dumbauld et al. 2009). Bivalves may even improve water quality due to the filtration activity (Newell et al. 2002) and enhance biodiversity

through the creation of structure and, thus, habitat for other organisms (Dealteris et al. 2004, Tallman & Forrester 2007). The presence of bivalve aquaculture can nevertheless cause changes in energy flow through the respective system, and can induce a shift in dominance from pelagic to benthic energy transfer through enhanced biodeposition (Leguerrier et al. 2004). Compared with more intensive suspended culture, bivalve bottom culture is thought to have relatively little impact due to lower cultivation densities, resulting in comparatively lower organic enrichment

of the benthic environment. However, bottom culture usually increases bivalve densities above natural levels, and the resulting increase in shells and/or the introduction of protective structures such as nets increases habitat complexity, potentially enhancing epibiotic biomass (Powers et al. 2007, Ysebaert et al. 2009) as well as predator densities (Inglis & Gust 2003). Cultured individuals may thus function as ecosystem engineers (after Jones et al. 1994), greatly influencing habitat conditions and the benthic community structure. Moreover, cultured filter feeders may outcompete other bivalve species and filter-feeding organisms such as zooplankton (Gibbs 2004, Newell 2004). Other potential impacts of bivalve bottom culture include local oxygen depletion (NRC 2010), and the redirection and attenuation of water currents (Galinou-Mitsoudi et al. 2006). Given these potential deleterious effects, the evaluation of aquaculture impacts on the adjacent community and the overall ecosystem is crucial for the maintenance of ecosystem health and functioning in the context of ecosystem-based management (Pikitch et al. 2004). In this context, the combination of community analysis and trophic modelling methodologies conducted in this study allowed for holistic evaluation of the effects of scallop aquaculture from 2 different perspectives. The Ecopath approach focuses on alterations in system characteristics and trophic flow structures, while the benthic community analysis allows for a direct assessment of changes in community structure, and the direct testing of a hypothesis. This combination of approaches is, to our knowledge, novel, and aids in providing a holistic assessment of ecological disturbance.

The Peruvian bay scallop *Argopecten purpuratus* (Lamarck, 1819) represents one of the most economically important mollusc species along the Pacific coast of South America due to its comparatively fast growth rates, high productivity and excellent market value. Although it has been fished along the entire Peruvian coastline since the 1950s, the first attempts at cultivation were started in southern Peru (Pisco) in 1983, after a strong El Niño event caused an enormous natural proliferation of the scallop populations (Wolff 1987, 1988). Since 2003, Sechura Bay, located in the north of the country, has become the Peruvian centre for its cultivation. Culture activities continue to increase, but a structured monitoring of the process and an evaluation of the potential impacts of bottom culture on the ecosystem are lacking. The present work aimed to assess the impact of scallop bottom culture on the bay's ecosystem through comparison of the current (culture) state with the pre-

culture state by combining (benthic) community analyses and trophic modelling approaches. These 2 methodologies have not previously been combined for the analysis of system changes, but their combination is expected to yield a better understanding of both the structural and functional consequences of scallop culture at the ecosystem level.

Based on recent scallop production trajectories and recent trophic modelling work (Kluger et al. in press), it was hypothesised that scallops currently represent a more important functional role in the system than during pre-culture, both as dominant primary consumers and as prey to higher trophic levels. Moreover, we hypothesised a shift in community structure favouring hard-substrate-associated species and a general increase in species richness due to an increased variability in substrate. The results of this study are expected to be combined with the results of recent modelling work (Kluger et al. in press) focussing on the ecological carrying capacity of Sechura Bay under different cultivation scenarios.

MATERIALS AND METHODS

Study area

Sechura Bay (5.6° S, 80.9° W; Fig. 1) is located at the northern edge of the Humboldt Current upwelling system, characterised by almost continuous upwelling of cold and nutrient-rich water to surface layers (Tarazona & Arntz 2001). The bay extends over 400 km², and is characterised by sandy substrates and shallow depths (<30 m) (Taylor et al. 2008c). Due to these favourable environmental conditions, the bay has been used for scallop cultivation since 2003. Artisanal fisheries provide livelihoods for most coastal villagers in the region, targeting fish species as well as benthic organisms such as the scallop *Argopecten purpuratus*. At present, 78.6% of the country's scallop production originates from Sechura Bay (in 2011; PRODUCE 2013), with annual export revenues of about US\$158 million (in 2013; ADEX 2014) and 25 000 people involved in the scallop processing chain (J. Proleon pers. comm.). Culture is conducted by artisanal fishermen associations without nets or substrate structures, by transferring scallop seed (recruited individuals) from natural banks into assigned culture areas that are distributed over the entire bay at depths of 5 to 15 m. Natural seed banks can be found within the bay, although most seed originates from banks found at the nearby island Isla Lobos de Tierra (Fig. 1).

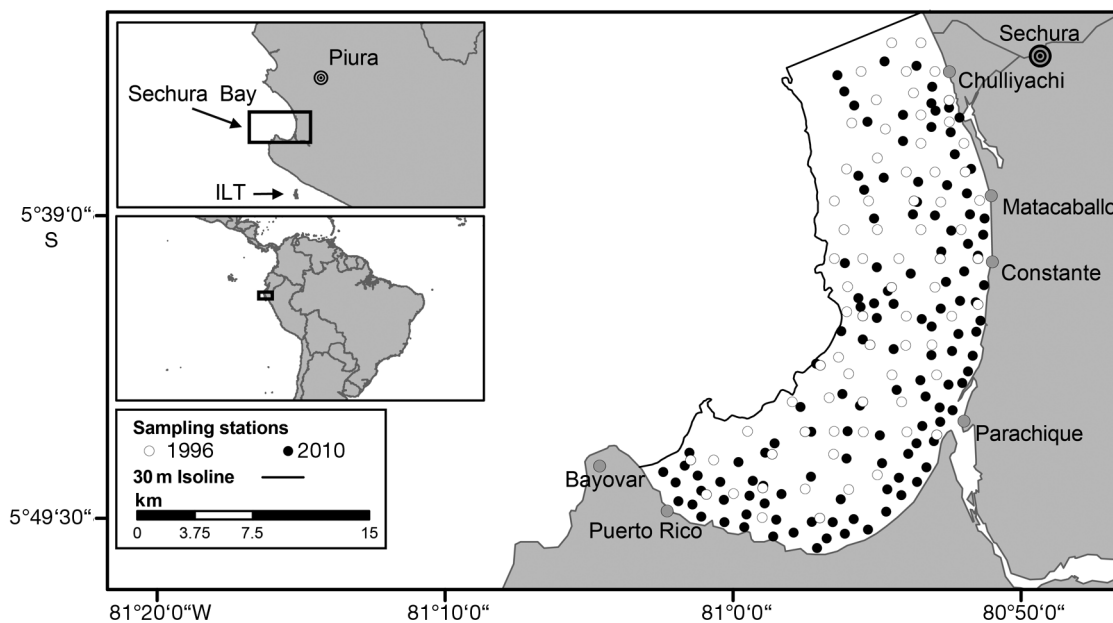


Fig. 1. Location of the study system Sechura Bay in northern Peru. Coastal villages, the isoline of 30 m depth and locations of the benthic evaluation in 1996 (N = 71) and 2010 (N = 124) are indicated. ILT = Isla Lobos de Tierra

Analysis of community changes

Changes in benthic community composition were analysed using benthic survey data from IMARPE (Peruvian Marine Science Institute) for pre-culture and culture conditions (1996 and 2010, respectively). For both cases, sampling was carried out during the spring–summer period (September–December), and locations were randomly distributed over the entire bay's area up to a depth of 30 m (Fig. 1). Sampling of epiflora (macroalgae), epifauna (excluding mobile octopods) and infauna was conducted by divers using replicated 1 m² quadrats. Abundance (if applicable) and weight were identified for each species in the upper sediment layer to a depth of approximately 5 cm, following a standard (thus comparable) procedure of IMARPE (as described in Samamé et al. 1985, Yamashiro et al. 1990, Taylor et al. 2008c).

All statistical analyses were conducted using the statistical and computing environment R (R Core Team 2014). To detect and describe changes in family-based community composition, the following methods were utilised. (1) Rank-abundance plots were used to graphically derive species dominance ranks, richness and evenness for the 2 system states, with species richness and evenness given by the x-axis intercept and the slope of the graph: the shallower the slope, the greater the evenness of a com-

munity (Magurran 2004). A Fisher's log-series model (after Fisher et al. 1943), describing the relation between the number of taxonomic groups and the number of individuals of those groups in a system (Magurran 2004) was fit to the rank-abundance data using the fisherfit function of the R package vegan (Oksanen et al. 2015). The model calculates the parameter of Fisher's α , which provides an informative and robust measure of diversity (Magurran 2004). (2) Similarity percentage (SIMPER) analysis (after Clarke 1993) was applied using the simper function of the R package vegan (Oksanen et al. 2015) to identify groups' contributions to community dissimilarity between pre-culture and culture states. (3) Abundance–biomass comparison (ABC) plots were constructed for both system states (after Warwick 1986) using the abc function of the R package forams (Aluizio 2014) to assess the level of disturbance for benthic communities (Warwick 1986, Magurran 2004). Cumulative abundance and biomass were plotted against the rank of dominant taxonomic groups, with the biomass curve likely to be above the abundance curve for undisturbed communities (that are usually dominated in terms of biomass by few species), while the abundance curve lies above the one for biomass for highly disturbed communities (as those are generally dominated by opportunistic species with high individual numbers, but low biomass) (Magurran 2004). The degree and

direction of separation of these curves is described from Clarke's W statistic and will approach +1 for a community with biomass dominated by a single species and even abundance across species, and $W = -1$ for the inverse case (Clarke 1990, Clarke & Warwick 2001).

As a second step, a 4-way PERMANOVA (permutational multivariate analysis of variance; Anderson 2001) model was applied to test the hypothesis of scallop aquaculture impact according to: (1) year (2-level factor: 1996, 2010), (2) scallop *A. purpuratus* biomass (continuous variable), (3) macroalgae *Caulerpa* sp. biomass, which increased in biomass during culture period (continuous variable), and (4) depth (continuous variable). Analysis was conducted using the `adonis` function of the R package `vegan` (Oksanen et al. 2015), on fourth-root transformed family-based community matrices as derived from the IMARPE data and based on Bray-Curtis distances. Since the PERMANOVA approach is sensitive to heterogeneity of dispersion (Anderson 2001), the multivariate homogeneity of group dispersions was first assessed through the application of the PERMDISP procedure (Anderson 2006). The routine is an analogue to the univariate Levene's test for homogeneity of variances and was conducted using the `betadisper` function of the R package `vegan` (Oksanen et al. 2015).

Observations by fishers have suggested a positive relationship between scallop abundance and abundance of the macroalgae *Caulerpa* sp. due to the fact that the macroalgae are seen to favour scallop shells for attachment over the less stable sandy substrate. Further evidence of a possible symbiotic relationship is suggested by the apparent benefit of the *Caulerpa* sp. structure to scallop juveniles as an important habitat for settlement and shelter (IMARPE 2007) and, vice versa, that scallop excrement may provide important nutrients, such as ammonium and phosphorus, to the macroalgae (Mao et al. 2009). Indeed, the survey data showed a significant positive rank correlation between the biomass of the 2 species groups (Spearman's $\rho = 0.30$), yet the level was low enough that we chose to leave in both species groups as predictor variables to investigate differences in the remaining benthic community. For the same reason, scallops and macroalgae were removed from the community matrix for rank-abundance and ABC plots. In contrast, the SIMPER analysis was done on the full community matrix (including scallops and macroalgae) since it was used as a more descriptive analysis of the overall differences between the 2 sample periods.

Trophic modelling comparison

Model construction

Two trophic models of Sechura Bay representing the pre-culture (1996) and culture (2010) conditions were established using the software Ecopath with Ecosim (EwE) 6.3 (Christensen & Pauly 1992, Christensen & Walters 2004), which allows for the construction of mass-balanced ecosystems models based on the trophic connections between functional groups (or model compartments, consisting of single species or a group of species). Ecopath models use 2 master equations (Christensen & Walters 2004, Christensen et al. 2005), with the first equation defining the individual components of the production term:

$$\text{Production} = \text{catch} + \text{predation} + \text{net migration} + \text{biomass accumulation} + \text{other mortality}$$

The second equation describes the energy balance for each group as:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

For any functional group, the software requires at least 3 of the following 4 parameters: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) and ecotrophic efficiency (EE) (Christensen & Walters 2004). The program further requires information on diet compositions for all groups, as well as exports from the system into fishery or aquaculture harvest.

Model structure

Both models were based on a previous model of Sechura Bay constructed by Taylor et al. (2008c). The model area was defined to cover an area of 400 km², including all depths <30 m (Fig. 1, Taylor et al. 2008c). The reference model included several mobile fish groups, whose biomass in the bay was estimated based on catch data. At present, the focus on aquaculture has shifted the fishery to areas outside the bay, and thus a similar approach could not be used to provide a reliable estimate of biomass in the bay. These fish groups were therefore removed from the present trophic models, and the focus was directed to the benthic community. The model used for the present work now comprised 14 groups including detritus. To facilitate comparison between system states, the reference model from Taylor et al. (2008c) was

accordingly re-constructed as a 14-group model based on original input parameters as can be found on the PANGEA website (Taylor et al. 2008a, b). Table S1 in the Supplement at www.int-res.com/articles/suppl/m547p121_supp.pdf contains a complete list of species contributing to the different functional groups.

Input of model data

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

Phytoplankton biomass was calculated from remote-sensing estimates of sea-surface chlorophyll a (chl a) concentrations (mg m^{-3}) from MODIS (MODIS-Aqua 4 km satellite, taken from <http://disc.sci.gsfc.nasa.gov/giovanni>) for the region $5.17\text{--}5.89^\circ\text{S}$, $80.798\text{--}81.25^\circ\text{W}$, and years 2008–2012. Mean annual values were calculated for this period and spatial extent (i.e. 60 mo by 123 grids). Annual chl a values were first transformed into carbon (ratio 1:40; from Brush et al. 2002) and then to wet weight (ratio 1:14.25; from Brown et al. 1991). To achieve values on a m^2 basis, sea surface biomass was multiplied by a mean water depth of 15 m, assuming a well-mixed water column (following Taylor et al. 2008c). Assuming stable phytoplankton primary production, the same biomass value was used for both models. Estimates of mean zooplankton biomass were taken from IMARPE surveys for the region ($5^\circ\text{--}6^\circ\text{S}$, $<82^\circ\text{W}$, $n = 60$; after Taylor et al. 2008c)

Table 1. Input–output parameters for the 2 balanced steady-state models for Sechura Bay (1996 and 2010). 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; P/R = production/respiration ratio; R/A = respiration/assimilation ratio; F_i = fishing mortality; MO_i = non-predatory natural mortality; $M2_i$ = predation mortality. All parameters calculated by EwE are shown in **bold**

Prey/predator	Year	Trophic level	B_i (t km^{-2})	P_i/B_i (yr^{-1})	Q_i/B_i (yr^{-1})	EE_i	P_i/Q_i	P/R	R/A	Catch (t yr^{-1})	F_i	MO_i (yr^{-1})	$M2_i$ (yr^{-1})
1. Phytoplankton	1996	1.000	33.621	331.815	–	0.316	–	–	–	–	–	197.957	133.858
	2010	1.000	33.621	331.815	–	0.421	–	–	–	–	–	192.270	139.545
2. Macroalgae	1996	1.000	307.769	16.864	–	0.037	–	–	–	–	–	16.243	0.621
	2010	1.000	455.311	16.864	–	0.006	–	–	–	–	–	16.760	0.104
3. Zooplankton	1996	2.175	25.886	32.268	160.662	0.789	0.201	0.335	0.749	–	–	6.803	25.465
	2010	2.177	25.886	35,4948	160,662	0.723	0.221	0.382	0.724	–	–	9.845	25.650
4. Polychaetes	1996	2.061	53.631	0.980	4.645	0.974	0.211	0.358	0.736	–	–	0.026	0.686
	2010	2.063	106.617	0.980	4.641	0.825	0.211	0.357	0.736	–	–	0.172	0.809
5. Scallops	1996	2.000	27.491	1.314	11.629	0.867	0.113	0.165	0.859	2.34	0.085	0.175	1.054
	2010	2.000	147.388	1.314	11.629	0.994	0.113	0.165	0.859	111.445	0.756	0.007	0.551
6. Sea urchins	1996	2.108	22.204	0.528	3.220	0.653	0.164	0.258	0.795	–	–	0.183	0.345
	2010	2.106	3.632	0.581	3.542	0.864	0.164	0.258	0.795	–	–	0.079	0.502
7. Herbivorous gastropods	1996	2.000	21.141	1.139	4.347	0.973	0.262	0.487	0.673	–	–	0.030	1.109
	2010	2.000	3.917	1.139	4.347	0.986	0.262	0.487	0.6723	–	–	0.016	1.123
8. Benthic detritivores	1996	2.000	40.601	1.480	7.437	0.783	0.199	0.331	0.751	0.144	0.004	0.322	1.155
	2010	2.000	15.836	1.480	7.437	0.964	0.199	0.331	0.751	0.081	0.005	0.054	1.421
9. Miscellaneous filter feeders	1996	2.232	22.385	0.921	5.117	0.904	0.180	0.290	0.775	0.001	0.0001	0.089	0.832
	2010	2.250	13.418	1.013	5.628	0.990	0.180	0.290	0.775	0.960	0.072	0.011	0.931
10. Predatory gastropods	1996	3.081	38.750	1.362	4.351	0.894	0.313	0.643	0.609	0.379	0.010	0.145	1.208
	2010	3.180	78.808	1.362	4.351	0.984	0.313	0.643	0.609	1.7734	0.023	0.022	1.318
11. Small carnivores	1996	2.863	14.429	0.523	2.527	0.732	0.207	0.349	0.741	0.001	0.0001	0.140	0.383
	2010	2.946	19.696	0.523	2.527	0.954	0.207	0.349	0.741	–	–	0.024	0.499
12. Predatory crabs	1996	3.169	7.708	1.969	9.207	0.797	0.214	0.365	0.733	–	–	0.400	1.569
	2010	3.231	1.010	1.969	9.207	0.727	0.214	0.365	0.733	–	–	0.538	1.431
13. Octopods	1996	3.731	0.013	5.063	14.064	0.976	0.360	0.818	0.55	0.033	2.539	0.120	2.405
	2010	3.761	0.086	5.063	14.064	0.705	0.360	0.818	0.55	0.212	2.456	1.496	1.112
14. Detritus	1996	1.000	1.000	–	–	0.085	–	–	–	–	–	–	–
	2010	1.000	1.000	–	–	0.080	–	–	–	–	–	–	–

between 1995 and 1999, as more recent data were not available.

Data on benthic macrofauna biomass (including scallops) were obtained from IMARPE, as described above. 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 miscellaneous filter feeders to correct for undersampling (after Taylor et al. 2008c). The biomass of the polychaete group was estimated by Ecopath assuming a similar ecotrophic efficiency (*EE*) as in 1996 (*EE* = 0.825). Biomass of the more mobile group of octopods was estimated from PRODUCE (Peruvian Ministry for Production) assuming that fishery removes half the production (Taylor et al. 2008c).

The artisanal dive fishery targets several benthic species, including scallops. Catch data were obtained from PRODUCE for the 2 main landing sites in Sechura Bay (Parachique and Puerto Rico), and aggregated to the respective functional groups (Table 1).

The construction of diet matrices followed Taylor et al. (2008c) (Table 2). Whenever species composition of a group differed from the author's 1996 model, 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. 2008c). For this approach, a base percentage of detritus feeding (10–20%) was assumed.

Comparing system features

The following system summary statistics as calculated by Ecopath were used to compare the 2 system states with each other and other models: system size (total throughput), mean trophic level of catch, catch/primary production ratio, and maturity (indices of

Table 2. Diet matrices for steady-state models of Sechura Bay for 1996 (from Taylor et al. 2008c) and 2010. Blank cells indicate that this predator does not feed on this prey species

Prey/predator	Year	3	4	5	6	7	8	9	10	11	12	13
1. Phytoplankton	1996	0.750	0.300	0.800				0.700				
	2010	0.750	0.300	0.800				0.700				
2. Macroalgae	1996				0.800	0.800	0.200					
	2010				0.800	0.800	0.200					
3. Zooplankton	1996	0.150	0.050					0.200				
	2010	0.150	0.050					0.200		0.006		
4. Polychaetes	1996				0.100				0.110	0.110	0.100	
	2010				0.100				0.218	0.183	0.127	
5. Scallops	1996								0.110	0.110	0.090	0.115
	2010								0.220	0.091	0.112	0.112
6. Sea urchins	1996									0.210		
	2010									0.037		
7. Herbivorous gastropods	1996							0.090	0.090	0.070	0.090	
	2010							0.000	0.072	0.066	0.083	
8. Benthic detritivores	1996							0.180	0.180	0.140	0.163	
	2010							0.028	0.233	0.127	0.158	
9. Miscellaneous filter feeders	1996							0.070	0.070	0.060	0.079	
	2010							0.029	0.045	0.029	0.096	
10. Predatory gastropods	1996							0.210		0.160	0.179	
	2010							0.299		0.108	0.193	
11. Small carnivores	1996							0.020	0.020	0.020	0.024	
	2010							0.006	0.135	0.097	0.121	
12. Predatory crabs	1996									0.170	0.179	
	2010									0.135	0.158	
13. Octopods	1996											0.169
	2010											0.079
14. Detritus	1996	0.100	0.650	0.200	0.100	0.200	0.800	0.100	0.200	0.200	0.200	
	2010	0.100	0.650	0.200	0.100	0.200	0.800	0.100	0.200	0.200	0.200	

cycling, transfer efficiency) (Christensen et al. 2005, Heymans et al. 2014). In addition, the index of keystone-ness for any functional group i (KS_i) was calculated from the mixed trophic impact analysis as provided by Ecopath for each functional group following Libralato et al. (2006). Keystone species were defined after Power et al. (1996) as those having a comparatively low biomass but a high overall impact (i.e. $KS_i \geq 0$; Heymans et al. 2014). In addition, the index of species dominance (KD_i) that aims at identifying dominant functional groups (or structural groups), was determined after Heymans et al. (2014). KD_i results in high values for groups that have both high biomass proportions and high overall trophic impact (i.e. $KD_i \geq -0.7$; Heymans et al. 2014).

RESULTS

Changes in benthic species community composition and biodiversity

Comparison of benthic species composition

Rank-log abundance analysis revealed differences in the abundance dominance pattern between the 2 system states (Fig. 2, Table S2 in the Supplement at www.int-res.com/articles/suppl/m547p121_supp.pdf). In 1996, the families Majidae, Columbelloidae and Porcellanidae (being part of the EwE functional groups benthic detritivores (BD), herbivorous gastropods (HG), and BD, respectively) were the most dominant in terms of individual numbers. In contrast, Gammaridae, Xanthidae and Majidae (being all part of the BD group) dominated the system in 2010.

The number of taxonomic groups (families) decreased from 40 (in 1996) to 37 (in 2010), and species evenness decreased, indicating the increased dominance of certain groups in the community in 2010. Similarly, the diversity (i.e. the Fisher's α) decreased from 5.934 in 1996 to 5.496 in 2010. Twenty-eight taxonomic groups occurred in both years, with 14 groups only occurring in 1996. Among those were Lottiidae (HG), Pinnotheridae (BD) and Hiattellidae (miscellaneous filter feeders, MF) (abundance rank positions 5, 8 and 10, respectively). In contrast, 11 families were only present in 2010, e.g. Calyptraeidae (BD) and Diogenidae (BD) (abundance rank positions 5 and 8, respectively).

Results of the SIMPER analysis indicated that the pre-culture and culture communities differed by 74.96% from each other. Macroalgae Caulerpaceae

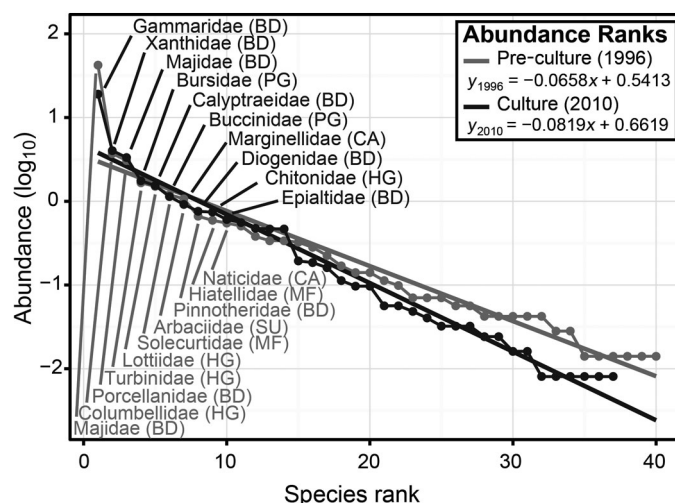


Fig. 2. Rank-log abundance plots for family-based benthic communities of Sechura Bay for 1996 and 2010. Functional groups as used for the EwE model are given: sea urchins (SU), herbivorous gastropods (HG), benthic detritivores (BD), miscellaneous filter feeders (MF), predatory gastropods (PG), small carnivores (CA) and predatory crabs (PC). Table S2 in the Supplement contains a complete list of taxonomic groups, abundance and biomass values, and respective ranks

(MA), scallops Pectinidae (SC), decapod crabs Xanthidae (BD), and the gastropod families Bursidae (PG) and Buccinidae (small carnivores CA) contributed 31.95% to overall dissimilarity, all (except Xanthidae) with higher biomasses in 2010 (Fig. 3, Table S3 in the Supplement).

Degree of disturbance

The results from the abundance–biomass comparison (ABC) plots classified both system states as ‘highly disturbed’, as indicated by the abundance curve being above the biomass curve and a negative W value (Fig. 4). The W statistic increased from 1996 to 2010, suggesting that the biomass of the culture system was comparatively more dominated by a fewer number of species, with individual numbers increasingly equally distributed across species. This is supported by the biomass curve of 2010 being above the 1996 one, and the abundance curve being below that of 1996.

Aquaculture as predictor for community changes

Results of the PERMANOVA analysis confirmed that benthic communities from 1996 and 2010 were

significantly different ($F = 17.94$, $p = 0.001$; Table 3). Scallop biomass ($F = 4.83$, $p = 0.001$), as well as Caulerpaceae biomass ($F = 7.07$, $p = 0.001$) were both significantly correlated with community differences. The multivariate dispersion as tested with PERMDISP differed significantly between the 2 years ($F = 16.988$, $p < 0.001$).

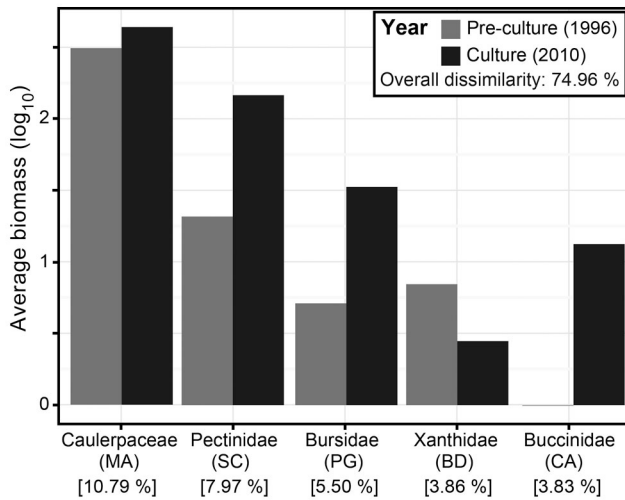


Fig. 3. Results of the SIMPER analysis considering year as a factor. Biomass of the 5 most important families (contributing most to overall dissimilarity) is compared between 1996 (grey) and 2010 (black), standardized per m² by dividing by the number of sampling stations. The individual contribution of groups to the overall dissimilarity is presented below the x-axis labels, with all similarity calculations based on fourth-root transformed data. The functional groups as used for the EwE model are given: macroalgae (MA), scallops (SC), predatory gastropods (PG), benthic detritivores (BD) and small carnivores (CA). Table S3 in the Supplement contains a complete list of the SIMPER results

Comparison of system states using the EwE approach

General aspects

System size (total throughput, T) increased by 16.0% from the pre-culture to culture state (Table 4), reflecting the introduction of large quantities and biomass of scallops. The total biomass to total throughput (B/T) value increased by 11.1%, reflecting the increase in system biomass (+47.0%). Total primary production to total respiration (PP/R) decreased by 8.4%. The 2010 system state also differed from the pre-culture state by higher absolute flows to consumption (+25.3%) and respiration (+25.8%), as well as into exports (+12.6%) and detritus (+13.0%). For both system states, however, the different flow types (consumption, respiration, exports and detritus) were of similar proportion to T .

Table 3. Results of the PERMANOVA model testing for the continuous variables of scallop and macroalgae *Caulerpa* sp. biomass, as well as the factors year (1996, 2010) and depth, and their interaction (Year × Depth) on the benthic community of Sechura Bay. Shown are the degrees of freedom (df), sums of squares (SS), mean sums of squares (MS), F value and p -value

	df	SS	MS	F	p
Scallop biomass	1	1.410	1.4099	4.8272	0.001
<i>Caulerpa</i> sp. biomass	1	2.064	2.0645	7.0683	0.001
Year	1	5.241	5.2407	17.9429	0.001
Depth	1	2.816	2.8162	9.6421	0.001
Year × Depth	1	1.338	1.3378	4.5804	0.001
Residuals	171	49.945	0.2921		
Total	176	62.814			

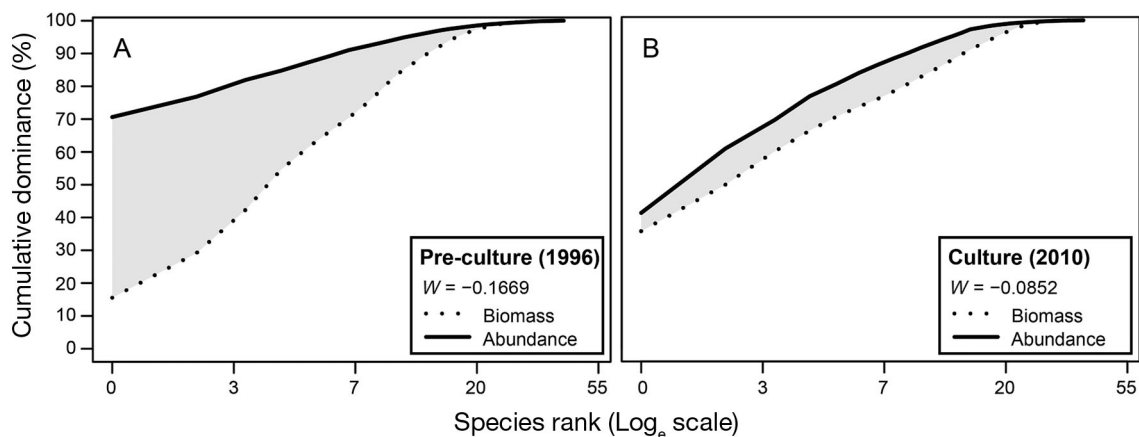


Fig. 4. Abundance–biomass comparison plots and Clarke’s W statistic for the family-based benthic communities of Sechura Bay for (A) 1996 and (B) 2010. Table S2 in the Supplement contains a complete list of taxonomic groups, abundance and biomass values, and respective ranks

Table 4. Comparison of system statistics of the models for Sechura Bay from 1996 and 2010, indicating percentage change

System statistics	1996	2010	% change
Trophic indicators			
Total system throughput (T) ($\text{t km}^{-2} \text{yr}^{-1}$)	35870.34	41600.80	+15.98
Sum of all consumption ($\text{t km}^{-2} \text{yr}^{-1}$)	5583.78 (15.57 %)	6994.04 (16.81 %)	+25.26
Sum of all exports ($\text{t km}^{-2} \text{yr}^{-1}$)	12980.83 (36.19 %)	14619.74 (35.14 %)	+12.63
Sum of all respiratory flows ($\text{t km}^{-2} \text{yr}^{-1}$)	3350.98 (9.34 %)	4214.60 (10.13 %)	+25.77
Sum of all flows into detritus ($\text{t km}^{-2} \text{yr}^{-1}$)	13954.76 (38.90 %)	15772.43 (37.91 %)	+13.03
Total net primary production ($\text{t km}^{-2} \text{yr}^{-1}$)	16346.19	18834.34	+15.22
Total biomass (excl. detritus) ($\text{t km}^{-2} \text{yr}^{-1}$)	615.63	905.23	+47.04
Mean transfer efficiency (%)	5.5	4.3	-21.82
Fishery indicators			
Total catches (TC) ($\text{t km}^{-2} \text{yr}^{-1}$)	2.898	114.471	+3850.02
Mean trophic level of catch	2.16	2.02	-6.22
Gross efficiency (catch/net PP)	0.0002	0.0061	+3328.20
Primary production required (PPR)/catch	10.11	8.98	-11.18
Community energetics			
Primary production/total production (PP/P)	0.94	1.07	+15.92
Total PP /total respiration (PP/R)	4.88	4.47	-8.39
Total PP /total biomass (PP/B)	26.55	20.81	-21.64
Total biomass and T (B/TST) (yr^{-1})	0.0196	0.0218	+11.09
Network indicators			
Finn's cycling index (FCI)	2.74	2.70	-1.46
Predator cycling index (PCI)	8.44	7.30	-13.51

System maturity

The Finn's cycling index (FCI) was relatively low in 1996, suggesting a low degree of development, and further decreased by 1.5% in 2010, indicating that a lower proportion of total flows was recycled during the culture state (Table 4). Similarly, the related predator cycling index (PCI) decreased by 13.5%. A drop in mean transfer efficiency by 21.8% from pre-culture to culture conditions indicated a less efficient transport of energy from low to higher trophic levels, reflecting the increased harvest rates at lower trophic levels.

Fishery

Total harvest from the bay system increased from 2.9 t km^{-2} (in 1996) to 114.5 t km^{-2} (in 2010) (Table 4), representing 0.008% and 0.275% of the total system throughput, respectively. This was mainly due to the increase in the scallop *Argopecten purpuratus* harvest, which increased from 2.34 t km^{-2} (in 1996) to 111.5 t km^{-2} (in 2010), with predatory gastropods, miscellaneous filter feeders and octopods contributing most of the remaining catches. Accordingly, the mean trophic level of catch decreased by 6.2% (from 2.16 to 2.02) and gross efficiency (catch/net primary

production) increased from 0.02% in 1996 to 0.61% in 2010, due to the low trophic level of the targeted scallops. In 1996, PP required per unit of catch was relatively low (10.1), further decreasing by 11.2% in 2010 mainly due to the decrease in lower trophic level of catch, but also from an increase in total primary production due to the increase in macroalgae biomass.

Analysing changes in trophic flow structure

The flow diagram shows the prominent role of scallops within the trophic structure of Sechura Bay (Fig. 5), which increased their contribution to the total system's biomass from 4.5% (of 615.6 t in 1996) to 16.3% (of 905.2 $\text{t km}^{-2} \text{yr}^{-1}$ in 2010). The increase in total system biomass was not only due to the scallops, but also resulted from increases in biomass of other groups, e.g. macroalgae, polychaetes, predatory gastropods, small carnivores and octopods (Fig. 5). Benthic primary consumers (sea urchins, herbivorous gastropods, benthic detritivores and miscellaneous filter feeders) decreased in biomass. The analysis of trophic flows further revealed that phytoplankton was consumed to a higher extent in 2010, as indicated by an increase of ecotrophic efficiency (EE) from 0.316 (in 1996) to 0.402 (in 2010) (Table 1).

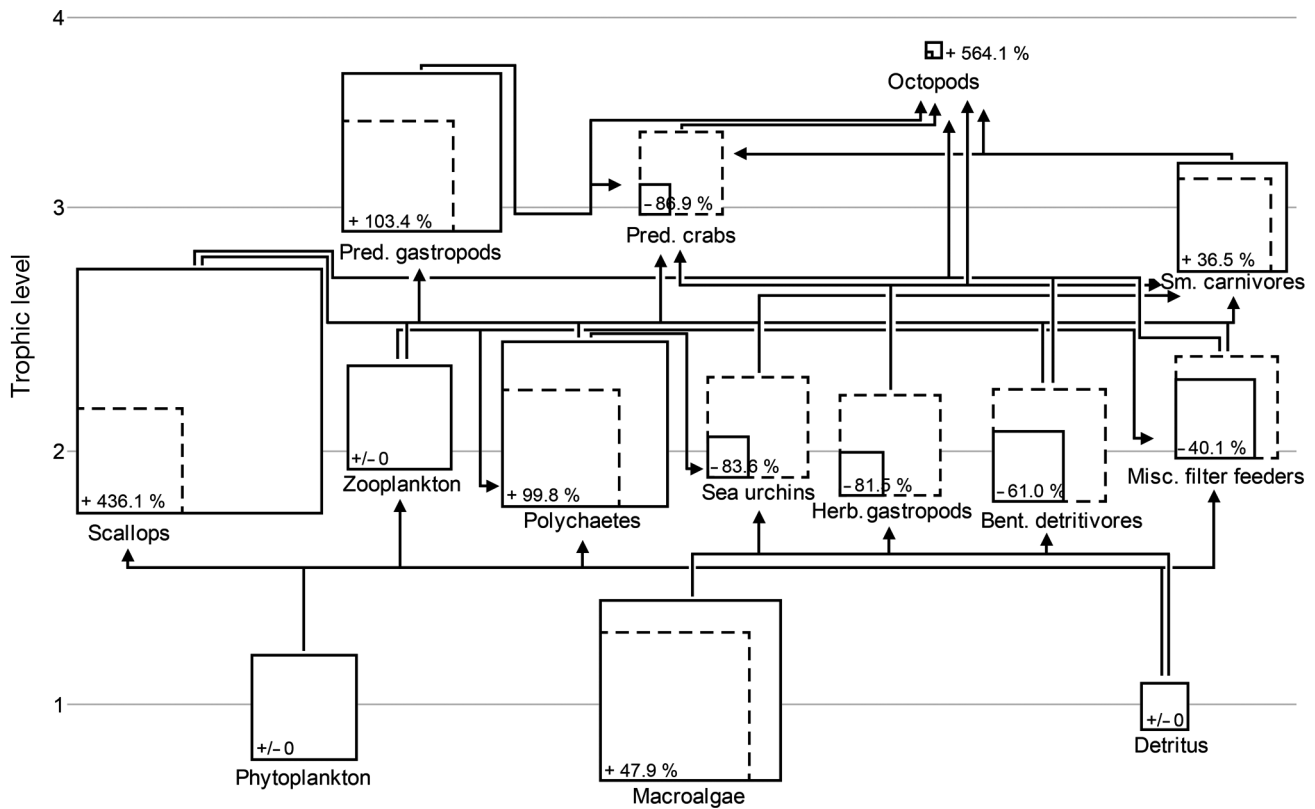


Fig. 5. Trophic flow diagram of the Sechura Bay ecosystem in pre-culture (1996, dashed lines) and culture (2010, solid lines) system states, demonstrating the percentage change in functional group biomass between both states. Actual biomass values and trophic levels as calculated by EwE are given in Table 1

Keystoneeness

No clear keystone group could be identified (i.e. $KS_i \geq 0$) for the pre-culture or culture conditions. For several groups (including scallops, predatory crabs and octopods) the KS_i value increased, however, indicating their increased importance (Table 5). For both system states, macroalgae represented a dominant functional group (as described by $KD_i \geq -0.7$) due to its high biomass and overall impact.

DISCUSSION

Bivalve aquaculture might be less impacting than other types of mariculture, as cultured organisms exploit natural food sources, but a system disturbance can occur under situations of intensive cultivation (e.g. Dumbauld et al. 2009). While the use of the term 'disturbance' may imply a negative impact, the systemic effects of this type of aquaculture have been described both negatively, e.g. by depleting a food source for other organisms (Newell 2004) and positively, e.g. by providing settling structure and, thus, habitat to other organisms (Filgueira & Grant 2009),

which may ultimately increase biodiversity (Dealteris et al. 2004, Tallman & Forrester 2007). Due to this complex set of possible aquaculture–environment interactions, an ecosystem-based approach for its impact assessment is necessary (Cranford et al. 2012).

Results of this combined approach suggest scallop aquaculture impacted the Sechura Bay system through significant changes in the community assemblages (PERMANOVA analysis, Table 3), including a decrease in benthic biodiversity and species evenness in the culture period (rank plots, Fig. 2), and shifts in dominant species. Scallops, macroalgae Caulerpaceae and predatory gastropods Bursidae contributed most to the overall dissimilarity between system states (SIMPER analysis, Fig. 3), with increased biomass in the culture system state. The observed biomass increase of the gastropod family Bursidae is likely due to a bottom-up trophic response from the increased biomass of their scallop prey. These results agree with other studies reporting the positive effect of bivalve aquaculture on its predators, e.g. fish and macroinvertebrate species (e.g. McKindsey et al. 2006, D'Amours et al. 2008) and a general shift in the relative dominance of

Table 5. Results of the calculation of the keystone index KS_i (after Libralato et al. 2006), and the species dominance index KD_i (after Heymans et al. 2014) for all functional groups of the pre-culture (1996) and culture (2010) system states. Keystone groups are defined by $KS_i \geq 0$, and dominant (structural) groups by $KD_i \geq -0.7$ (Heymans et al. 2014)

Group name	Keystone index (KS_i)			Dominance index (KD_i)		
	Pre-culture	Culture	% change	Pre-culture	Culture	% change
1. Phytoplankton	-0.1302	-0.1782	-26.90	-1.3685	-1.5919	-14.03
2. Macroalgae	-0.4739	-0.4411	7.44	-0.4741	-0.4359	8.74
3. Zooplankton	-0.3515	-0.5131	-31.50	-1.7091	-2.0442	-16.39
4. Polychaetes	-0.8444	-0.6623	27.49	-1.8647	-1.5368	21.34
5. Scallops	-0.6357	-0.4961	28.14	-1.9660	-1.2072	62.85
6. Sea urchins	-0.5710	-0.7263	-21.38	-1.9979	-3.1211	-35.99
7. Herbivorous gastropods	-0.5260	-0.5899	-10.81	-1.9751	-2.9518	-33.09
8. Benthic detritivores	-0.5276	-0.2780	89.79	-1.6788	-2.0275	-17.20
9. Miscellaneous filter feeders	-1.0150	-1.0618	-4.41	-2.4383	-2.8844	-15.47
10. Predatory gastropods	-0.1408	-0.2873	-50.99	-1.3136	-1.3080	0.43
11. Small carnivores	-0.1899	-0.1555	22.06	-1.8096	-1.8084	0.07
12. Predatory crabs	-0.7567	-0.3557	112.70	-2.6536	-3.3077	-19.78
13. Octopods	-2.8388	-0.7006	305.18	-7.5142	-4.7212	59.16

trophic groups (Cranford et al. 2012). Several taxonomic groups were part of the community in 1996 that were not present in 2010, and vice versa. Among those found only in 2010 was the gastropod family Calyptraeidae, whose species generally prefer hard-bottom habitat. For the genera *Crepidula* found in Sechura Bay, an epizoic life style, e.g. living on *Argopecten purpuratus* or other bivalves was described (Paredes & Cardoso 2007).

These results suggest that scallop aquaculture may have also altered the physical benthic structure by providing settling substrate and shelter to other organisms, thus functioning as ecosystem engineers (after Jones et al. 1994). The results of our study agree with those of I. Vivar (pers. comm.), who experimentally investigated the impact of scallop culture on the benthic community in Sechura Bay through the introduction of varying densities of scallops to experimental plots and subsequent analysis of benthic community changes over an entire year. In that study, gastropod species of the families Buccinidae (e.g. *Solenosteira* sp.) and Bursidae (e.g. *Bursa* sp.) were found to contribute most to dissimilarities between benthic communities of culture and non-culture plots. Similarly, our study's results showed that these gastropod families together accounted for 9.33% of overall dissimilarity between the pre-culture (1996) and culture (2010) system states (Fig. 3, Table S3 in the Supplement).

The results described above are consistent with the Ecopath analysis, which revealed changes in trophic flow structure and ecosystem functioning. Scallops, as well as their predators (i.e. predatory gastropods, small carnivores and octopods) increased largely in

biomass, reflecting the bottom-up effect of the scallop group. Other benthic groups (e.g. miscellaneous filter feeders, herbivorous gastropods) decreased in biomass, most likely due to inter-specific competition and top-down control through increased consumption by predatory groups as a reflection of a scallop-induced increase of their biomass.

Besides the potential positive effects of bivalve culture on the community surrounding it, impacts may also be negative if the introduced ecosystem engineer threatens niches within the ecosystem (Jones et al. 1997). In Sechura Bay, several other filter-feeding species (e.g. zooplankton and other bivalves such as the clam *Tagelus dombeii*) represent competitors to scallops, and could be negatively affected if culture activities were further expanded. Moreover, the increase of scallop predators may also have increased the predation pressure exerted on other benthic organisms, such as herbivorous gastropods, with possibly deleterious effects when expanding culture activities. In addition, our results do not support the hypothesis of increased biodiversity due to bivalve culture (as suggested e.g. by Dealeris et al. 2004, Tallman & Forrester 2007), although in the case of these studies, aquaculture structures were introduced into the system together with the cultured bivalves, which might have increased the amount of available hard substrate and complicated a direct comparison. These considerations are important as the culture-state model was established (due to data availability) for 2010 only, and culture activities in Sechura Bay have continued to increase. It may therefore be reasonable to believe that the benthic community has since further changed, as suggested

by the results of Kluger et al. (in press). The authors proposed that while the addition of scallops and their associated changes in the substrate may initially enhance biodiversity, these benefits are likely to be lost as scallop densities increase beyond a certain threshold (i.e. the ecological carrying capacity (ECC)). If the ECC is significantly exceeded, bivalve culture may potentially lead to changes in ecosystem structure, loss of benthic biodiversity, disease outbreaks or mass mortalities due to oxygen depletion (e.g. Inglis et al. 2000, Ferreira et al. 2013). It is therefore crucial to implement continuous monitoring, and to establish thresholds for culture development based on indicators of ecosystem health. In this context, the concept of ECC, defined as the maximum amount of cultivated organisms that does not yet cause 'unacceptable' impacts on the ecosystem, could be used (e.g. Inglis et al. 2000, McKindsey et al. 2006). For example, one threshold might be to define the point at which the impact of culture on other species results in a decrease to <10% of its original biomass (Worm et al. 2009). Such criteria have recently been applied to functional groups within the context of the ECC of scallop culture in Sechura Bay using EwE (Kluger et al. in press).

As filter feeders, bivalves can clear large volumes of water, potentially altering flows of energy and matter (Dowd 2003, Cranford et al. 2012), and exerting a top-down control on phytoplankton standing stocks (Dame & Prins 1998, Newell 2004, Huang et al. 2008, Petersen et al. 2008). The results of our study suggest, however, that phytoplankton availability is not, in contrast to expectations, a limiting factor for a further culture expansion in Sechura Bay. Although the ecotrophic efficiency (describing the percentage of a group's production that is utilised within the system) of phytoplankton increased from pre-culture to culture conditions, the value of 0.421 in 2010 can still be considered low, indicating a potential scope for growth of culture activities. This is in line with the results of Kluger et al. (in press), who suggested that besides the bivalve–phytoplankton relationship, other inter-specific relations (i.e. bottom-up effects on predators, top-down control of competitors) may be more important for long-term sustainable culture levels. Nevertheless, a sound understanding of *in situ* phytoplankton availability, including intra- and inter-annual variability over a period of several years, should first be established before being able to draw any recommendation in this context.

For both system states, the primary production required (*PPR*) per unit of catch was low compared with the value of 25.1% presented by Pauly & Chris-

tensen (1995) for other upwelling systems, but could be explained by the focus of the local fisheries on low-trophic-level benthic organisms. Accordingly, a further decrease in *PPR*/catch ratio from 1996 to 2010 reflects the decrease in the mean trophic level of catch. This is mainly due to an increased proportion of scallops (trophic level = 2.0) in the catches, while the relative catch composition of other species remained similar.

System cycling, indicative of system maturity, was similarly low for both system states when compared with other bay systems along the South American coastline (FCI of 5.1% for Independence Bay, South Peru (Taylor et al. 2008d), and 10.1% for Tongoy Bay, Chile (Wolff 1994)). A further decrease in the cycling indices (FCI, PCI) from pre-culture to culture conditions may suggest that the culture system is even less mature and more disturbed (Odum 1969), but it would need more than 2 year's system states comparison for a sound conclusion in this respect. Similarly, the decrease in transfer efficiency reflects a less efficient transport of energy towards higher trophic levels, likely a result of the increased harvest at lower trophic levels. This result is in line with those of Díaz López (2011), who analyzed the systemic impact of the establishment of a finfish aquaculture facility by comparing 2 Ecopath models representing pre-culture and culture conditions. Similar to our results, they found that the introduction of large amounts of cultured biomass into the system caused the FCI to decrease. The decrease in cycling within the system as a result of aquaculture is crucial as cycling represents an important feedback mechanism contributing to system stability (Odum 1969) and to resistance to perturbations (DeAngelis et al. 1978, DeAngelis et al. 1989). The reduced cycling from pre-culture to culture conditions may (partly) be explained by the increase in harvest rates, which are considered as exports in Ecopath (Christensen et al. 2005), representing a substantial loss to the system when it comes to its ability to recycle energy and to withstand perturbations. Although scallops were already targeted in 1996, the introduction of aquaculture activities increased the percentage of the system's throughput that is removed from the system as harvest, demonstrating the direct impact of aquaculture on the system's flow structure and functioning.

These results are in contrast to the abundance–biomass comparison (ABC), which described the culture state as less disturbed than the pre-culture system, as indicated by a slightly higher *W* statistic value. This discrepancy may be explained by the focus of the different approaches (community level vs. systemic

view). The W statistic describes the degree and direction of separation of the biomass and abundance curves, and an increase in the W statistic from pre-culture to culture conditions suggests that the biomass of the culture system state is more dominated by single taxonomic groups than it was in 1996 (Clarke 1990), reflecting the dominance in biomass of secondary consumers, such as predatory gastropods Bursidae and Buccinidae, that are at the same time relatively abundant. The calculation of cycling, on the other hand, describes the fraction of an ecosystem's throughput that is recycled (after Finn 1976, Christensen et al. 2005).

It is important to mention that this work represents a comparison between 2 states only, and although trends of changes can be detected, a final conclusion should not be drawn. In particular, the context of ecosystem maturity and stability needs a long-term investigation to support the arguments above. The comparison of system states is based on the assumption that the system of 1996 represents a contrasting system state (i.e. pre-culture conditions). It must be considered, however, that the dive fishery has operated in this and other Peruvian bays for many decades, and has always fished scallops to very low (unnatural) levels. The system state observed in 2010 may thus simply resemble another natural state that is still within the range of natural variability. With culture activities still expanding, it nevertheless remains unclear how the system may behave in the future, and when limits of natural variability will be reached. We recommend time series analyses of the benthic community and complementary Ecosim modelling to predict future changes in ecosystem structure and functioning following further culture expansion.

In summary, the introduction of large scallop quantities to Sechura Bay appear to have positively impacted the system by increasing system size (Eco-path analysis), while simultaneously increasing the level of disturbance (reduced cycling) and decreasing biodiversity and species evenness (rank plot). The results of the community (PERMANOVA and SIMPER) analysis suggest scallop aquaculture represents a 'disturbance' that has caused the system of Sechura Bay to change. The 2 system states differ significantly in terms of their community composition, with some increases in hard-bottom-associated species for the culture state. System functioning, as viewed by the relative proportions of flows into consumption, respiration, etc., is observed to be less impacted. Phytoplankton availability suggests a scope for growth of scallop culture, but an assess-

ment of ecosystem effects of further expansion should be conducted and limits to acceptable changes should be carefully defined. Whether these changes in the ecosystem are acceptable (or even desirable) or not depends, in the end, on the social carrying capacity, e.g. particular management and conservation targets (i.e. species of interest, Dumbauld et al. 2009) and stakeholder perceptions. From an ecological point of view, the loss of species as a result of any culture activity may be considered critical, yet the enhanced scallop production in Sechura Bay would primarily be seen as positive by those who are the beneficiaries of the mariculture. Future research should address the bay's limits to scallop culture, i.e. the ecological and social carrying capacity, to enable long-term sustainable use of this important coastal system and its valuable resources.

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