Ecological and socio-economic feasibility of scallop bottom culture in Sechura Bay, Northern Peru




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*"En Sechura, solo hay el desierto y el mar. Y nosotros.
La naturaleza y nosotros somos uno."*

(Fishermen in Sechura, May 2013)

Abstract

Aquaculture has become increasingly important for aquatic protein production, as an alternative to exploiting natural populations. Bivalve aquaculture represents a sector of particular economic potential, because cultured individuals feed on naturally occurring phytoplankton at the bottom of the food chain, reducing production costs and environmental impacts. Production is still increasing, and its further sustainable development should follow an ecosystem approach (EA), allowing aquaculture expansion while at the same time maintaining biodiversity and ecosystem functioning. The concept of the system's ecological carrying capacity (ECC) – describing limits to culture expansion – and the resilience capacity are at the center of EA, though the identification of critical thresholds to development remains difficult. The overall objective of this thesis was therefore to develop a holistic approach for the ecosystem-based exploration of bivalve aquaculture impact and the estimation of ECC that should be applicable to other coastal settings.

For this, a case study system – Sechura Bay in northern Peru – was used, a location which recently developed into a main center for the cultivation of the Peruvian bay scallop *Argopecten purpuratus*. This bivalve species has been harvested by small-scale diving fishermen along the Peruvian and Chilean coastline since the 1950's. Today, its cultivation and related activities constitute an important socio-economic sector for the region of Sechura, with about 25000 people involved into the production chain and annual export values of >150 million US$. Due to this, Peru is currently the world's third most important scallop producer (in terms of aquaculture production), with main markets in Europe and the USA. In Sechura Bay, scallops are cultivated on the seafloor. By providing settling substrate to other organisms in an otherwise soft-bottom habitat they may potentially function as ecosystem engineers in the system. Overstocking of scallops combined with critical environmental changes such as oxygen reduction may cause scallop mass mortalities, potentially impacting other organisms and overall ecosystem functioning. Accordingly, the ecosystem-based assessment of the current situation and the determination of long-term sustainable limits to scallop aquaculture for the bay became crucial.

As a first step, this thesis investigated if the initiation of intense scallop bottom culture has induced changes in the benthic community structure and ecosystem functioning. This was done by contrasting the current system state with pre-culture conditions through the combined application of community ecology analyses (permutational multivariate analysis of variance, *PERMANOVA*; similarity percentage analysis, *SIMPER*; abundance-biomass comparison, *ABC*) and trophic modelling (Ecopath with Ecosim, *EwE*). Comparing the two system states, a significant change in benthic community composition and a concomitant decrease in species diversity was detected. Scallop predator biomasses (e.g. predatory gastropods and octopods) increased, leading to a top-down control on other groups of the system, such as scallop competitors (e.g. other bivalves). In addition, a decrease in energy cycling and reduction in ecosystem maturity was observed.

As a second step, the bay's ecological carrying capacity for scallop aquaculture was determined. An approach was developed that uses Ecosim for the simulation and exploration of ecosistemic effects of a further aquaculture expansion. A novel ecosystem-based threshold for ECC is proposed, i.e. defined as the maximum amount of bivalve biomass that not causes the biomass of any other group in the system to fall below 10% of its original biomass. Results proposed that scallop aquaculture levels could be enhanced by 10 % before reaching the system's ECC, and that a further expansion would lead to a loss of system compartments such as polychaetes and other filter feeders.

The third part of this thesis combined the abovementioned ECC simulations with the exploration of the system's resilience capacity. A newly developed resilience indicator and a measure of functional diversity, both based on the distribution of consumption flows within the trophic network, were combined for the analysis of aquaculture impact on the food web's structure. Findings confirmed the explorations of the aforementioned study. Current scallop biomass levels are slightly above the one resulting in maximum resilience, and further enhancing culture intensity will continuously decrease the system's resilience. When exceeding the ECC threshold, the risks of the aquaculture operation would start to comprise ecosystem health, causing the system's structure to collapse and increasing the potential for the occurrence of a regime shift.

The fourth part of this thesis used a socio-ecological system's approach for the analysis of the long-term potential for Sechura Bay to remain an important location for scallop production on the Latin American level. The ecological, economic, and societal factors that have allowed Sechura to successfully develop were identified. Results proposed the combination of favourable environmental conditions and the low production costs to have facilitated the rise in scallop production in Sechura Bay. The bottom-up approach through which the aquaculture operations were initiated, i.e. the small-scale nature of activities, has additionally provided a basis for its lasting performance. Nevertheless, specific obstacles including the lack of permanent seed supply will have to be overcome in order to ensure a long-term sustainable future of the mariculture activities.

In conclusion, scallop aquaculture has essentially altered the system's trophic flow structure and functioning, which emphasizes the need for the development of meaningful management measures to culture expansion. Results of this thesis are expected to guide local decision makers and furthermore contributes substantially to our understanding of ecosystem responses to bivalve aquaculture. As a major output, a general EA to aquaculture is proposed that is based on several novel methodologies for the integrated assessment of (1) impacts of aquaculture on ecosystem functioning and resilience, (2) effects of management decisions on harvest through ECC simulations, and (3) societal and environmental factors important for long-term sustainability. Considering the importance of the ever expanding aquaculture industry worldwide, the approach may provide guidance for future studies in different aquaculture settings that aim at determining sustainable limits to growth.

Keywords: Bivalve culture management, aquaculture impact assessment, trophic modelling, ecological carrying capacity, functional diversity, resilience capacity, socio-ecological sustainability, ecosystem approach to aquaculture

Resumen

La acuicultura se ha convertido en una fuente de producción de proteína en ambientes acuáticos, y en una alternativa a la explotación de poblaciones naturales en estos ambientes. La acuicultura de bivalvos representa un sector de particular importancia comercial pues los organismos cultivados se pueden alimentar de fitoplancton disponible en el ecosistema en la base de la cadena trófica, reduciendo de esta manera los costos de producción y los potenciales impactos ambientales. La producción acuícola sigue creciendo, y la sostenibilidad de su desarrollo dependerá de la aplicación del enfoque ecosistémico (EE) en sus planes de manejo, de manera que se permita tanto la expansión de la acuicultura, como el mantenimiento de la biodiversidad y funcionalidad de los ecosistemas en donde esta actividad se lleva a cabo. El concepto de capacidad de carga ecológica (CCE) – describiendo limites para la expansión de los cultivos acuícolas – y la capacidad de resiliencia, son parte central del EE. Sin embargo, la identificación de limites críticos para el desarrollo acuícola es aún difícil.
El objetivo general de esta tesis fue el desarrollar una aproximación holística para la exploración del impacto de la acuicultura de bivalvos y la estimación de CCE que pueda ser aplicable a otros ambientes costeros. Para ello, se seleccionó como sistema de estudio la Bahía de Sechura, en el norte de Perú; un lugar recientemente identificado como centro principal para el cultivo de concha de abanico (*Argopecten purpuratus)*. Esta especie de bivalvo ha sido explotada por pescadores artesanales a lo largo de las costas peruanas y chilenas desde 1950. Hoy en día, el cultivo de la concha de abanico y las actividades relacionadas constituyen un importante sector socio-económico en la provincia de Sechura, donde cerca de 25000 personas están involucradas en la cadena de producción, con valores anuales de exportación mayores a 150 millones de US$. Debido a esto, Perú es actualmente el tercer productor (en acuicultura) mundial de pectínidos, con mercados principales en Europa y Estados Unidos. En la Bahía de Sechura, la concha de abanico es cultivada en el fondo marino. Al proveer sustrato a otros organismos en un fondo que originalmente es blando, la concha de abanico posiblemente juega un rol de ingeniero ecosistémico en el sistema. La sobrepoblación de conchas de abanico combinada con cambios ambientales críticos como la reducción del oxígeno en el agua, pueden causar mortalidades masivas de estos pectínidos, impactando potencialmente a otros organismos y afectando el funcionamiento general del ecosistema. En tal sentido, una evaluación de la situación actual de la actividad acuícola en la Bahía de Sechura, aplicando un enfoque ecosistémico es de vital importancia para la determinación de límites de manejo que permitan un desarrollo sostenible con beneficios a largo plazo en base a esta actividad.

Como un primer paso, esta tesis investigó si la iniciación del cultivo intensivo de fondo de la concha ha inducido cambios en la estructura de la comunidad bentónica y el funcionamiento del ecosistema. Esto fue realizado contrastando el estado actual del ecosistema con las condiciones anteriores al cultivo, aplicando la combinación de diferentes análisis de ecología de comunidades (Permanova, Simper, comparaciones de abundancia-biomasa) con modelamiento trófico (Ecopath con Ecosim, EwE). Se observó un cambio significativo en la composición de la comunidad bentónica y una dismunición de la diversidad de especies. La biomasa de los depredadores de conchas de abanico (e.g. gasterópodos depredadores y pulpos) incrementó, ocasionando un control *top-down* sobre otros grupos del sistema, como lo pueden ser competidores de la concha de abanico (e.g. otros bivalvos filtradores). Adicionalmente, se observó un descenso en la circulación de la energía y una reducción en la madurez del ecosistema.

En un segundo paso, se determinó la capacidad de carga ecológica de la bahía ante el cultivo de concha de abanico. Se desarrolló una metodología que usa Ecosim para la simulación y exploración de los efectos a nivel ecosistémico de la expansión de las actividades de acuicultura. Se propone un nuevo límite basado en el ecosistema para calcular la CCE, i.e. definido como la máxima cantidad de biomasa de conchas de abanico que no causan que la biomasa de otro grupo del sistema se sitúe por debajo del 10% de su biomasa original. Los resultados de este enfoque sugieren que los niveles actuales de acuicultura de concha de abanico en la Bahía de Sechura están ya sobre la CCE, y que una expansión del cultivo podría llevar a una perdida de compartimentos del sistema como los poliquetos y otros organismos filtradores.

La tercera parte de esta tesis combinó las simulaciones de CCE antes mencionadas con la exploración de la capacidad de resiliencia del sistema. Un nuevo indicador de resiliencia y una medida de diversidad funcional, ambos basados en la distribución de los flujos de consumo dentro de la red trófica, fueron combinados para el análisis del impacto de la acuicultura en la estructura de la red trófica. Los resultados de este análisis confirmaron los resultados obtenidos anteriormente. Los niveles de biomasa actuales de conchas de abanico se encuentran ligeramente arriba de los que resultarían en máxima resiliencia, por lo que un incremento en la intensidad del cultivo generará un descenso continuo en la resiliencia del sistema. Si se exceden los limites de CCE, los riesgos de la operación acuícola empezarán a comprometer la salud del ecosistema, causando un colapso en la estructura del sistema e incrementando el potencial de la ocurrencia de un cambio de régimen.

La cuarta parte de la tesis usó un enfoque de sistema socio-ecológico para analizar el potencial a largo plazo de la Bahía de Sechura para permanecer como un lugar importante de producción de concha de abanico en Latinoamérica. Los factores ecológicos, económicos y sociales que permitieron que Sechura se desarrollara exitosamente como centro de producción de concha de abanico fueron identificados. Los resultados del análisis mostraron que la combinación de condiciones ambientales favorables y los bajos costos de producción han facilitado el crecimiento de la producción de concha de abanico en la Bahía de Sechura. El enfoque *bottom-up* con el que se iniciaron las actividades de acuicultura en esta área (i.e. la naturaleza de escala-pequeña de las actividades) ha brindado adicionalmente una base para su desempeño duradero. Sin embargo, algunos obstáculos específicos, que incluyen la falta de una fuente permanente de semillas, necesitarían ser superados para garantizar un futuro sostenible a largo plazo de dicha actividad acuícola.

Se puede concluir que la acuicultura de concha de abanico en la Bahía de Sechura ha alterado la estructura trófica y el funcionamiento del sistema; lo cual permite enfatizar en la necesidad de desarrollar estrategias de manejo ante el potencial de expansión de los cultivos. Como uno de los mayores resultados de este trabajo, se propone aquí un EE general para la acuicultura el cual esta basado en varias metodologías novedosas para el diagnostico integrado de: (1) los impactos de la acuicultura sobre el funcionamiento del ecosistema y su resiliencia, (2) los efectos de la decisiones de manejo en las cosechas de concha a través de simulaciones de la CCE, y (3) los factores sociales y ambientales más importantes para la sostenibilidad a largo plazo del cultivo. Considerando la importancia que representa la expansión continua de la industria de la acuicultura a nivel mundial, el enfoque presentado en este trabajo puede proveer guías importantes para estudios futuros en otros sistemas que pretendan establecer limites sostenibles al crecimiento acuícola.

Palabras clave: Manejo de cultivo de bivalvos, diagnóstico del impacto de la acuicultura, modelamiento trófico, capacidad de carga ecológica, diversidad funcional, capacidad de resiliencia, sostenibilidad socio-ecológica, enfoque ecosistémico para la acuicultura.

Zusammenfassung

Aquakultur ist für die aquatische Proteinproduktion eine zunehmend wichtige Alternative zur Nutzung natürlicher Populationen geworden. Die Kultivierung von Bivalven stellt einen ökonomisch besonders interessanten Sektor dar, da gehälterte Individuen sich von natürlich vorkommendem Phytoplankton an der Basis der Nahrungskette ernähren. Dies verringert die Produktionskosten und den Einfluss auf die Umwelt. Da die Produktion weiter ansteigt, sollte ein Ökosystemansatz (engl. Ecosystem Approach, EA) der den Ausbau von Aquakultur mit der Erhaltung von Biodiversität und Ökosystemfunktionen in Einklang bringt zur nachhaltigen Entwicklung verwendet werden. Das Konzept der ökologischen systemischen Tragweite (engl. ecological carrying capacity, ECC) – welches Wachstumsgrenzen der Zuchten beschreibt – und die Resilienzkapazität befinden sich im Fokus von dem EA, jedoch ist die Identifizierung von entsprechenden Grenzwerten schwierig ist. Das übergreifende Ziel dieser Dissertation war deshalb die Entwicklung eines ganzheitlichen Ansatzes für die ökosystem-basierende Untersuchung des Einflusses einer Muschelzucht und der Abschätzung der ökologischen Tragweite, welcher auch auf andere Systeme übertragen werden können sollte.

Zu diesem Zweck wurde eine Fallstudie – die Sechura-Bucht im Norden Perus – verwendet, welche sich unlängst in ein Hauptzentrum für die Kultivierung der Pilgermuschelart *Argopecten purpuratus* entwickelt hat. Diese Bivalvenart wurde seit den 1950er Jahren entlang der Peruanischen und Chilenischen Küste von tauchenden Kleinstfischern genutzt, und dessen Zucht und damit verbundene Aktivitäten stellen für die Region von Sechura heutzutage einen wichtigen sozioökonomischem Sektor dar. Etwa 25000 Personen arbeiten in der Produktionskette, und Exportwerte betragen >150 Millionen US$, wodurch Peru zurzeit der drittwichtigste Pilgermuschelproduzent der Welt ist (bezogen auf Produktion aus Aquakulturen). Die Region produziert hauptsächlich für den Europäischen und US-Amerikanischen Markt. Die Pilgermuscheln werden in Sechura auf dem Meeresboden gezüchtet, wodurch Substrat für die Ansiedelung von anderen Organismen in ein eigentliches Weichboden-Habitat eingebracht wird und wodurch die Muscheln potenziell als Ökosystem-Ingenieure wirken können. Zu hohe Zuchtdichten der Muscheln können, in Kombination mit kritischen Umweltveränderungen wie die Verringerung von Sauerstoff, zu einem Massensterben der Pilgermuscheln führen, was andere Arten und allgemeine Ökosystemfunktionen beeinflussen könnte. Die ökosystem-basierende Bewertung der aktuellen Situation, sowie die Bestimmung von langfristig nachhaltigen Grenzen für die Pilgermuschelzucht in der Bucht, ist dementsprechend essentiell.

Diese Dissertation untersuchte als ersten Schritt, ob die Initiierung von intensiven Bodenkulturen von Pilgermuscheln eine Veränderung in der Struktur der benthischen Gemeinschaft und der Funktionsweise des Ökosystems verursacht hat. Hierfür wurde mittels der Analyse der ökologischen Gemeinschaft (permutational multivariate analysis of variance, *PERMANOVA*; similarity percentage analysis, *SIMPER*; abundance-biomass comparison, *ABC*) und trophischer Modellierung (Ecopath with Ecosim, *EwE*) der aktuelle Systemzustand mit dem vor Beginn der Kultivierung kontrastiert. Ein signifikanter Unterschied in der Zusammensetzung der benthischen

Gemeinschaft und eine gleichzeitige Reduzierung der Biodiversität konnte beim Vergleichen der beiden Systemzustände beobachtet werden. Die Biomasse der Prädatoren der Pilgermuscheln (z.B. räuberische Gastropoden und Oktopoden) erhöhte sich, welches zu einer Top-down-Steuerung anderer Gruppen des Systems (z.B. andere Bivalven) führte. Außerdem wurde eine Verringerung der Energiewiederverwertung und Reduzierung der Ökosystemreife entdeckt.

Als zweiter Schritt wurde die ökologische Tragweite des Systems für Pilgermuschel-aquakultur bestimmt. Hierfür wurde ein Ansatz entwickelt, der für die Simulation und Untersuchung der ökosystemischen Effekte einer weiteren Zuchtausweitung Ecosim verwendet. Ein neuartiger ökosystem-basierender Grenzwert wurde vorgeschlagen, der als die maximale Muschelbiomasse definiert ist, die für keine andere Gruppe des Systems eine Verringerung dessen Biomasse unter 10% der ursprünglichen Biomasse bewirkt. Die Ergebnisse zeigten, dass die gegenwärtige Intensität der Muschelzucht bereits der Tragweite des Systems entspricht, und dass eine weiterführende Ausweitung den Verlust von Systemkompartimenten, wie Polychäten und anderen Filtrierern, zur Folge hätte.

Der dritte Teil dieser Dissertation verbindet die oben erwähnte Tragweiten-simulationen mit der Bestimmung der Ökosystemresilienz. Zwei neu entwickelte Indikatoren zur Abschätzung der Resilienz und der funktionalen Diversität wurden verwendet, um den Einfluss von Aquakultur auf die Struktur des Nahrungsnetzes zu untersuchen. Die Ergebnisse bestätigten die Untersuchungen der dieser Arbeit vorausgegangenen, und legten überdies nahe, dass das derzeitige Niveau der Pilgermuschelbiomasse bereits leicht über dem Biomassenwert liegt der eine optimale Resilienz erzielt. Eine weitere Ausweitung der Aktivitäten hätte eine beständige Verringerung der Ökosystemresilienz zur Folge. Mit dem Überschreiten der Grenze der ökosystemischen Tragweite würde das Risiko der Aquakultur die Funktionsweisen des Ökosystems gefährden, möglicherweise einen Zusammenbruch dessen Struktur verursachen, sowie die Wahrscheinlichkeit eines *regime shift* erhöhen.

Im vierten Teil dieser Arbeit wurde ein sozio-ökologischer sowie systemischer Ansatz verwendet, um Sechuras langfristiges Potential zu analysieren, ein wichtiger Standort für die Pilgermuschelproduktion auf dem Südamerikanischen Niveau zu bleiben. Die ökologischen, ökonomischen und sozialen Faktoren, die zu der erfolgreichen Entwicklung Sechuras beigetragen haben, wurden identifiziert. Die Kombination von vorteilhaften Umweltbedingungen und niedrigen Produktionskosten haben gemäß den Ergebnissen den Aufstieg der Pilgermuschelzucht in Sechura begünstigt. Der Bottom-up-Ansatz mit dem die Aktivitäten begonnen wurden, und insbesondere deren kleiner Maßstab, hat zusätzlich eine Basis für eine nachhaltige Leistung geschaffen.

Zusammenfassend hat die Pilgermuschelzucht die Struktur der trophischen Flüsse und die Funktionsweise des Ökosystems wesentlich verändert, was die Notwendigkeit der Entwicklung von bedeutsamen Managementmaßnahmen betont. Es ist zu erwarten, dass die Ergebnisse der vorliegenden Arbeit die lokalen Entscheidungsfindungsprozesse unterstützen können, und unser allgemeines Verständnis bezüglich der Resonanz von Ökosystemen auf Muschelaquakultur vergrößern werden. Als Hauptergebnis schlägt diese Arbeit einen auf verschiedenen neuen Methoden beruhenden Ökosystemansatz für die integrierte Evaluierung (1) des

Einflusses von Aquakultur auf die Funktionsweise und Resilienz von Ökosystemen, (2) der Auswirkungen von Entscheidungen des Managements durch die Simulation der ökologischen Tragweite, and (3) der sozialen sowie umgebungsbedingten Faktoren die für eine langfristige Nachhaltigkeit wichtig sind. Unter Berücksichtigung der weltweit immer weiter expandierenden Aquakulturaktivitäten kann dieser Ansatz eine Orientierungshilfe für zukünftige Studien bieten, die versuchen für andere Aquakulturstandorte nachhaltige Grenzen des Wachstums zu bestimmen.

Schlüsselwörter: Management von Muschelaquakultur, Folgenabschätzung von Aquakultur, trophische Modellierung, ökologische Tragweite, funktionale Diversität, Resilienzkapazität, sozio-ökologische Nachhaltigkeit, Ökosystemansatz für Aquakultur

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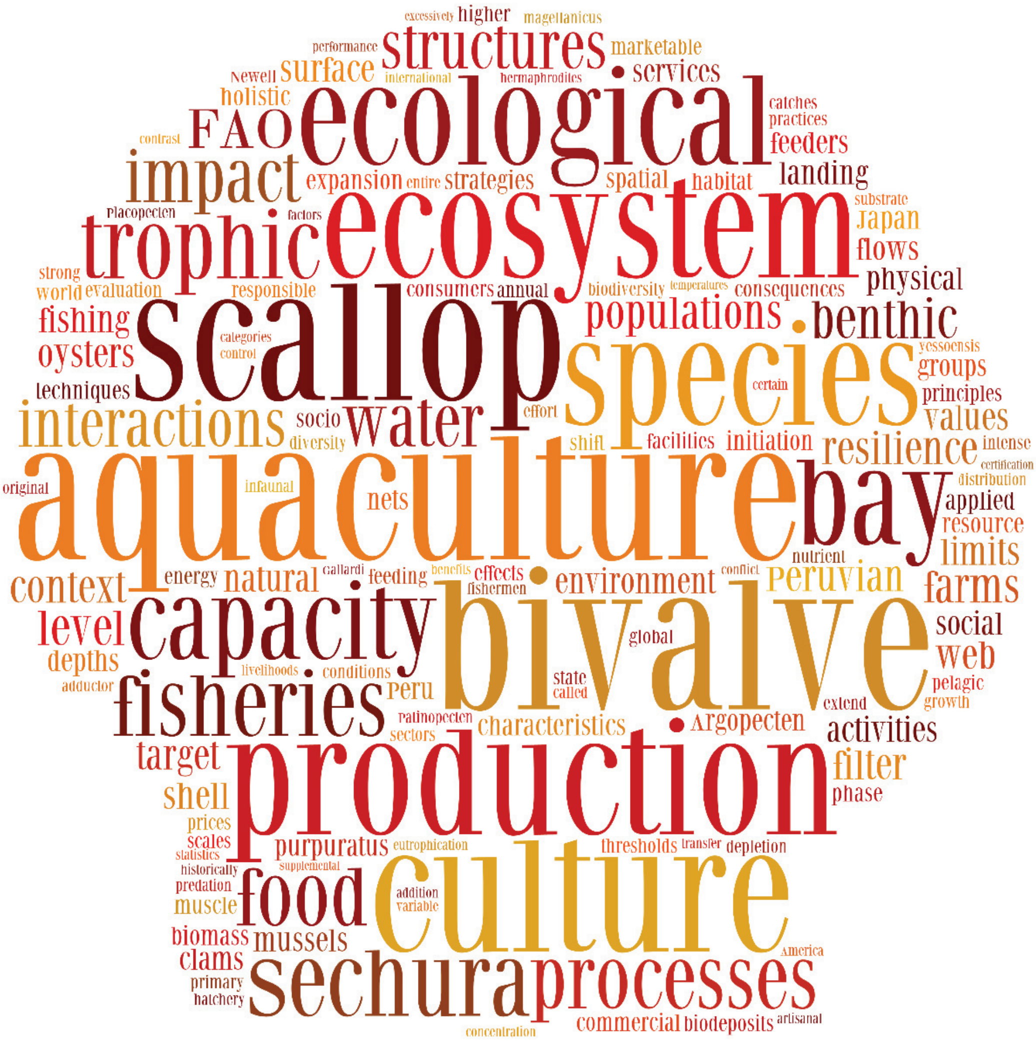
CHAPTER 1

– General Introduction –



1.1 BIVALVE AQUACULTURE – POTENTIAL FOR A SUSTAINABLE FOOD PRODUCTION?

1.1.1 Bivalves – a valuable resource

Bivalves are sessile or low mobile molluscs with two shell valves and a soft body inhabiting a wide range of inter- and subtidal aquatic habitats across the globe. The class of Bivalvia consists of about 7500 species of oysters, mussels, scallops, and clams, most of which are marine (Gosling 2003). Individuals may live (permanently) attached to hard substrate or to each other – as is the case for mussels, oysters, and some clam species. Some species are surface-dwelling (e.g. scallops), or burring into a variety of substrates (e.g. clams) at nearly all water depths. Most bivalves are dioecious (i.e. with separate sexes), but may also be asynchronous or simultaneous hermaphrodites (e.g. most scallops). They generally reproduce via a pelagic larval phase of three to five weeks duration, after which juvenile specimen settle (mainly in the size range of 250-300 µm; Gosling 2003). All bivalves form byssus threads for temporary attachment when young, but for most species of oysters, scallops, and clams the byssus apparatus is subsequently lost (Gosling 2003). As filter feeders, these organism pump water through their mantle cavity and retain suspended particles (i.e. phytoplankton, detritus) with their enlarged gills (Gosling 2003). In doing so, bivalves exert a wide range of key ecological roles and also provide important ecosystem services to humans (see section 1.1.2).

Bivalves represent comparatively high-value species that provided a basis for human livelihoods since pre-industrial times and until today sustain socio-economically important fisheries worldwide. Being hand-collected during low tide from intertidal zones, dredged or gathered by divers from subtidal areas, bivalves are targeted in many different coastal and marine settings by small-scale and commercial fisheries. In the last decades, production was greatly enhanced (Figure 1.1), with an increasing percentage originating from aquaculture (i.e. rising from 50.6 % in 1984 to 90.2 % in 2013; FAO 2016). First culture attempts of bivalves date back to the year 1235 for mussels in France (Gosling 2003) and to 1624 for oysters in Japan (Fujiya 1970, cited in Gosling 2003), though reliable techniques for culturing bivalves were only developed by the late 19th century (Gosling 2003). Since the 1970's, production was greatly augmented by the development of hatchery techniques for bivalve seed production (Gosling 2003), resulting in 12.7 million tons of world bivalve production from aquaculture in 2013, with a total value of 14.9 million US$ (FAO 2016).

As for any other aquaculture operation, bivalve mariculture depends on the constant seed (spat) supply, i.e. small (juvenile) individuals used for grow-out. This seed may either be hand-collected or dredged from natural banks, obtained from artificial seed collectors deployed in the water column, or may be hatchery-raised. Depending on the species, local traditions, and site-specific characteristics, culture techniques may then involve the grow-out within sediments, e.g. for infaunal clams, or on the bottom surface (sometimes being protected by net structures), as is done for some mussels, oysters, and scallops. Off-bottom trestles, rafts or long-lines that are deployed in intertidal areas may be used for oysters and mussels. Suspended culture involves long-lines, mesh bags or (lantern) nets that are installed in the water column for the grow-out of mussels or scallops (McKindsey et al. 2011).

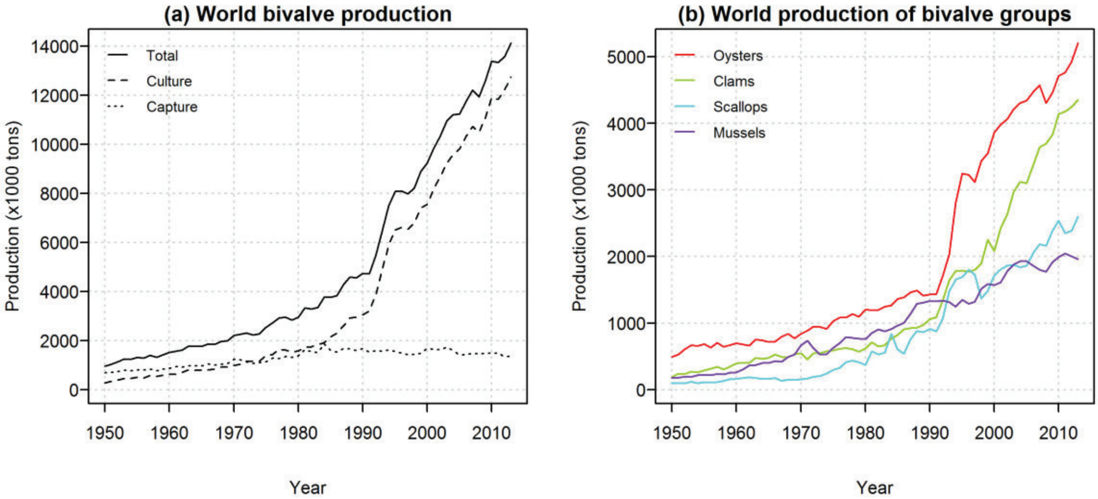


Figure 1.1. *World bivalve production (in tons) during the period 1950-2013, showing (a) the annually produced quantities in capture fisheries (Capture), aquaculture (Culture) and both (Total); and (b) the production (i.e. the sum of culture and capture) of the bivalve groups oysters, clams, scallops, and mussels. Source of data: FAO (2016).*

Among all bivalves, pectinid scallops and their shells have attracted the interest of naturalists and collectors for centuries (Gosling 2003), and are nowadays of special commercial interest. In particular the genera *Pecten*, *Placopecten*, *Patinopecten*, *Aequipecten*, *Argopecten*, and *Chlamys* (Medina et al. 2007) – represent high-priced fisheries products for the European (i.e. French) and North American markets. Scallops' great economic importance becomes apparent when comparing the different bivalve groups in terms of their percentage contribution to total bivalve production and respective economic values (Figure 1.2). In 2013, scallop production contributed 14.5 % to total bivalve production in tonnage, but 22.0 % to the total bivalve economic value, since prices per kg are higher when compared to other bivalve groups (values for aquaculture production; Figure 1.2, Supplemental Table S1.1). In the same year, world scallop production resulted in 2.6 million tons, with China, Japan, the USA and Peru representing the most important scallop producing countries (accounting for 61.9 %, 19.9 % 6.0 %, and 3.5 %, respectively, FAO 2016; Figure 1.3). The principle target species are currently *Patinopecten yessoensis* (mainly produced in Japan), *Placopecten magellanicus* (produced in the USA and Canada), *Argopecten purpuratus* (exclusively produced in Peru and Chile), *Pecten maximus* (mainly produced in the UK and France), and *Zygochlamys patagonica* (Argentina) (in 2013, FAO 2016), as well as *Chlamys farreri* (mainly produced in China, Guo & Luo 2006)).

Scallops have a more extensive global distribution than the other bivalve groups, though individual species' ranges are less broad than those of some oyster and clam species (Gosling 2003). Many scallop fisheries have experienced boom and bust situations, with phases of increased production through fishing effort intensification stimulated by good market prices, followed by a population collapse due to over-exploitation. Examples for this are *Argopecten purpuratus* in Chile (Stotz 2000), *A. ventricosus* in Mexico (Félix-Pico et al. 1997) and Panama (Medina et al. 2007), *Aequipecten techuelchus* in Argentina (Ciocco et al. 2006), *Euvola ziczac* in Brazil (Pezzuto & Borzone 2004), as well as *Placopecten magellanicus* (Murawski et al. 2000) and *Patinopecten caurinus* (Kruse et al. 2005) at the East and West coasts of the USA, respectively. Management strategies such as temporal area closures (*P. magellanicus* at the East coast of the USA, Hart & Rago 2006; *P. yessoensis* in Japan, Uki 2006), the implementation of catch quotas (*Pecten fumatus* in Australia, Dredge 2006)) and stock enhancement /sea ranching (*P. yessoensis* in Japan, Uki 2006)) have promoted the recovery of natural populations in some cases. Nevertheless, aquaculture has by now often replaced wild fisheries, as is the case for other bivalve species. In 2013, 1.85 million tons of scallops were produced in cultures, which accounts for 71.1 % of total scallop production. China, Japan, and Peru are the most important global producers, contributing 86.9 %, 9.1 %, and 3.7 % to total scallop culture production, respectively (FAO 2016).

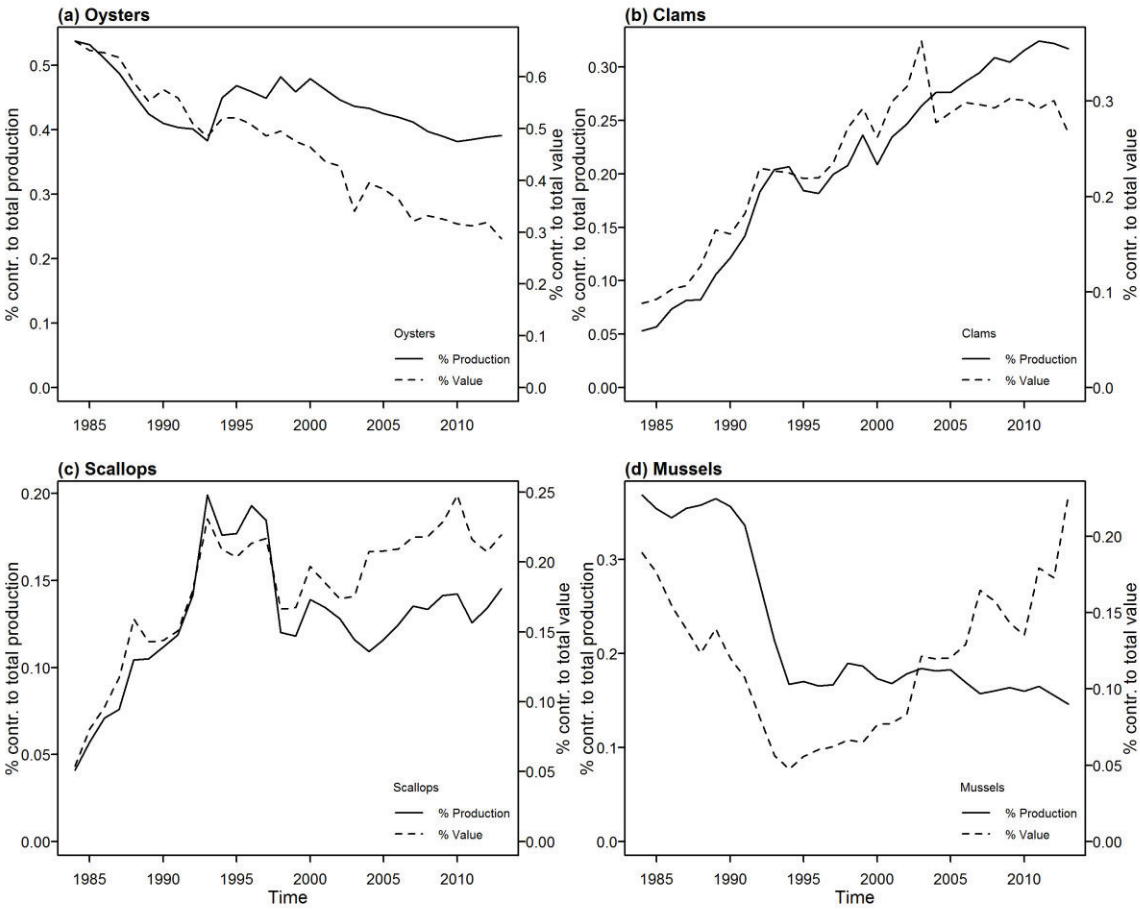


Figure 1.2. *Percentage contribution of (a) oysters, (b) clams, (c) scallops, and (d) mussels to annual world bivalve production originating from aquaculture (primary y-axis) and to the respective total economic value of bivalve aquaculture production (secondary y-axis). Development is shown for the years 1984 to 2013. Source of data: FAO (2016).*

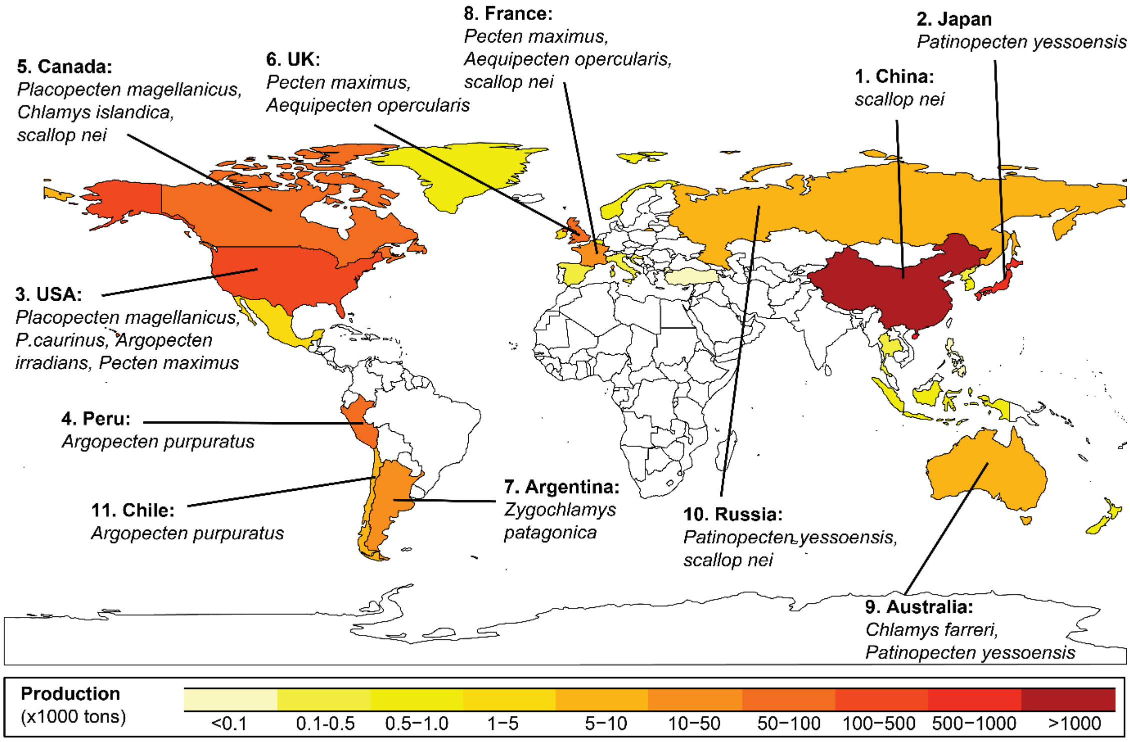


Figure 1.3. *World scallop production (in tons) by the most important scallop producing countries (producing >5000 tons) for the year 2013, indicating scallop species produced. Please note that other species may be harvested that are not registered with the FAO. According to Guo and Luo (2006), China mainly produces Chlamys farreri and Patinopecten yessoensis, among other species. Source of data: FAO (2016), summing culture and capture production. Please consider Supplemental Table S1.2 for an overview of all scallop producing countries.*

1.1.2 Bivalve aquaculture and environmental interactions

Bivalves may interact with the environment and associated ecological communities in many ways, including both trophic and non-trophic interactions. They contribute to ecosystem functioning through the creation of habitat and refugia for other species from predation, and provide ecosystem services such as eutrophication control (e.g. Coen et al. 2007), the provision of food and recreational values. The introduction of aquaculture facilities may amplify some of these interactions. For a summary of benefits and services see Table 1.1.

As for the pelagic environment, bivalves interact primarily with phytoplankton through filter feeding, exerting a top-down control on phytoplankton populations (e.g. Dame & Prins 1998, Newell 2004). Through the feeding mode, phytoplankton communities may be altered by the selective retention of larger sized phytoplankton (Strohmeier et al. 2012), increasing picophytoplankton abundances (Froján et al. 2014), and decreasing turbidities thus facilitating a shift towards faster growing algae species (Prins et al. 1995). Nutrients excreted by bivalves may be re-mineralized and taken up by phytoplankton (e.g. Asmus & Asmus 1991), a process through which bivalves exert a bottom-up nutrient control on their own food source (Smaal et al. 2001), though this positive feedback would likely be neutralized if increasing bivalve biomass was to reduce primary production (Smaal et al. 2013).

Table 1.1. *Ecosystem services (distinguishing regulating, provisioning, and cultural services) as provided by bivalves and its culture facilities (using the classification of ecosystem functions and services of Farber et al. (2006) who himself used the Millennium Ecosystem Assessment (WRI 2005). Table modified from Beseres Pollack et al. (2013); Petersen et al. (2015).*

Good/Service	Description	Benefits	References
Regulating services: maintenance of essential ecological processes			
• Nutrient uptake	• Uptake of particulate organic nutrients	• Nutrient removal by harvest of mussel biomass. Temporally immobilization of nutrients, eutrophication control	Stybel et al. (2009); Lindahl (2011); Petersen et al. (2014)
• Water regulation	• Filtering of water by mussels leads to flow modification and purification of water	• Reduced seston concentration, increased light penetration	Petersen et al. (2008); Cranford et al. (2014); Nielsen (2014); Schröder et al. (2014)
• Habitat	• Farm structure create habitat in water column	• Increased biodiversity, fish and invertebrate habitat	Murray et al. (2007); Amours et al. (2008); Wilding & Nickell (2013)
Provisioning: natural resources and raw material			
• Food	• Mussels for human consumption	• Commercial and subsistence harvesting	Lindahl (2011); Petersen et al. (2014)
• Feed stuff	• Processed mitigation mussels for feed	• Protein source for pigs and poultry	Jönsson et al. (2011); Nørgaard et al. (2015)
• Raw material	• Shells for building, manufacturing, fuel, soil, fertilizer	• Organic compost • Road base, chicken calcium supplement, cosmetics, spat collectors, smoke gas cleaning	Lindahl 2011; DSC pers. comm. (cited in Petersen et al. (2015))[1]
• Ornamental resources	• Resources for fashion, handicraft, jewelry, etc.	• Belt buckles, ornamental construction	Beseres Pollack et al. (2013)
Cultural services: enhancing emotional, psychological, and cognitive well-being			
• Recreation	• Mussel unit attract birds and fish • Cleaner water • Opportunities for rest, refreshment, recreation	• Fishing, birdwatching, snorkelling • Bathings	DSC, pers. comm. (cited in Petersen et al. 2015) [1]
• Spiritual & historic	• Spiritual or historical information	• Use of nature as national symbols; natural landscapes with significant religious values	Farber (2006); Beseres Pollack et al. (2013))
• Science & education	• Use of natural areas for scientific and educational enhancement	• Outreach dealing with research about nutrient removal, educational programme, seafood festivals	DSC, pers. comm. (cited in Petersen et al. 2015) [1]

[1] DSC dissemination centre is the communication centre from Danish Shellfish Centre, DTU Aqua http://www.skaldyrcenter.dk/ organizing visits of mussel farms, education on biodiversity/mitigation culture/ecology, communication, seafood festival

Through all these processes, large quantities of bivalves introduced into a system for aquaculture purposes may alter seston availability for other consumers (Leguerrier et al. 2004), a process that may be enhanced by filter-feeding activity of biota colonizing aquaculture-associated facilities (Mazouni et al. 2001). Phytoplankton depletion may be strongest in close vicinity to bivalve farms (Newell et al. 1998, Gibbs 2007, Grant et al. 2007), but – depending on bivalve densities and environmental characteristics such as water depths, tidal flushing and water residence times – effects may propagate to larger spatial scales (e.g. Filgueira & Grant 2009, Filgueira et al. 2014). Seston depletion may increase competition for phytoplankton (both intra- and inter-specific), ultimately negatively impacting the growth performance of cultured bivalves (Bacher et al. 2003), but also that of other (benthic) filter feeders and zooplankton (Gibbs 2007). Perturbations of zooplankton population dynamics may in turn propagate throughout the food web, negatively affecting higher trophic level species through decreasing prey availability.

During filtration, bivalves excrete a certain fraction of retained food as unassimilated material (faeces), as well as some uningested matter (pseudofaeces), collectively known as biodeposits (Mckindsey et al. 2011). These biodeposits may influence the benthic environment when sinking to the sea bottom (Newell 2004), inducing a transfer of pelagic energy flows towards benthic food webs (Leguerrier et al. 2004, Cranford et al. 2007). There, biodeposits may be recycled (Dumbauld et al. 2009) through the consumption by infaunal benthic feeders and microbial processes (Valdemarsen et al. 2010), but released ammonium, phosphate, silicate, nitrate and nitrite (Richard et al. 2006, Richard et al. 2007) may also accumulate if water exchange rates are too low. The remineralization requires oxygen, thus excessive organic matter loading from bivalve farms may create anoxic conditions and increase total free sulfide concentrations (especially H_2S) (McKindsey et al. 2011). The accretion of organic matter in the vicinity of aquaculture sites can alter benthic habitat characteristics, which may impact infaunal (Murray et al. 2007) and epifaunal benthic communities (McKindsey et al. 2011). A potential shift in community composition from filter- to deposit-feeders (Gibbs 2007), a decrease in species richness and an altered dominance of trophic groups (Cranford et al. 2012) were observed for some cases. In the end, the magnitude of effects of biodeposits on the benthos will depend on environmental characteristics and the intensity of culture practices (Dumbauld et al. 2009).

In addition, cultured bivalves are considered as ecosystem engineers (after Jones et al. 1994). The physical presence of bivalves and respective aquaculture facilities modifies the environment by introducing three-dimensional physical structures (e.g. McKindsey et al. 2011), which alters hydrodynamics and reduces flow rates (Petersen et al. 2008), and transforms deposition regimes within farms and by that sediment characteristics (McKindsey et al. 2011). These new structures may serve as habitat or shelter from predation for mobile invertebrates and fish species (McKindsey et al. 2006b, and references therein), and/or may induce a shift towards hard-bottom communities (McKindsey et al. 2011) by providing settling substrate for sessile organisms such as macroalgae (Crawford et al. 2003) and tunicate ascidians (Mazouni et al. 2001). This in turn may attract (new) mobile species, e.g. due to enhanced food availability for benthic predators and scavengers (e.g. McKindsey et al. 2011, and references therein). These processes can enhance local diversity and productivity (e.g. Dealteris et al. 2004; Tallman & Forrester 2007; D'Amours et al. 2008). At the same time, larger vertebrate species (e.g. cetaceans) may be negatively impacted by the loss of habitat through the occupation of space by culture facilities, in-water noise caused by culture-associated human activities, by the physical risk of getting entangled in net structures entanglement and the alteration of trophic pathways (Watson-Capps & Mann 2005).

All these processes may alter ecosystem functioning and community structures by modifying energy flows (e.g. benthic-pelagic coupling). If excessively conducted, bivalve aquaculture may also reduce biodiversity, e.g. if cultured organisms out-compete other filter-feeders in the system, such as zooplankton or naturally occurring bivalves (Gibbs 2004, Newell 2004). The maintenance of biodiversity is for ecosystem functioning and the generation of ecosystem services (Chapin et al. 1997, Duffy 2002), and a reduction of the system's species pool may lead to a reduction in the strength of the system to withstand future perturbations, i.e. its resilience (Folke et al. 2004).

Besides environmental consequences of bivalve aquaculture, culture-related operations may conflict with other human activities in the area through boat traffic, dumping of shells, effluents from processing plants, spread of alien species or diseases (ICES 2005). The occupation of space by culture facilities may conflict with a range of other operations such as fishing or tourism. The spatial extend and magnitude of interactions are, nevertheless, site specific (Cranford et al. 2012), requiring integrative and adaptive management strategies. A sound understanding of the potential interactions of the aquaculture-related operations with other anthropogenic activities, as well as the influence on coastal ecosystems are therefore crucial for designing measures for sustainable aquaculture development in the context of integrated coastal zone management (Cranford et al. 2012).

1.1.3 Bivalve aquaculture in the context of coastal management

Besides all the potential interactions as described in the previous section, bivalve aquaculture is considered a less intensive culture technique when compared to other types of aquaculture as that of finfish, since no external feed is added (Gallardi 2014). Still, bivalve-related operations may have strong negative implications if not conducted in an ecologically and socially responsible manner. Considering that (bivalve) aquaculture production is still expanding in many coastal settings around the world, the assessment of potential culture impacts and the definition of sustainable boundaries should be incorporated into bivalve culture management.

After the strong increase in overall aquaculture production during the 1980's and 1990's, the need to conduct farming as "ecological aquaculture" was increasingly recognized, i.e. integrating aquaculture development into the wider ecosystem as to enhance natural aquatic systems and ecosystem services, while being ecologically and socially responsible (Costa-Pierce 2002). Since then, more and more effort has been dedicated to shift management strategies from single-species to ecosystem-based approaches. A workshop organized by the FAO resulted in the formulation of the Ecosystem Approach to Aquaculture (EAA, Soto et al. 2008a) as:

"The ecosystem approach to aquaculture is a strategic approach to development and management of the sector aiming to integrate aquaculture within the wider ecosystem such that it promotes sustainability of interlinked social-ecological systems."

This approach is based on the conservation perspective of the Ecosystem Approach (EA) as adopted by the UN Convention on Biological Diversity (CBD) in 1992 (UNEP/CBD/COP/5/23/ decision V/6, 103-106, Soto et al. 2008a), a concept that initially had been incorporated into management strategies for fisheries (i.e. Ecosystem Approach to Fisheries (EAF, FAO 2003); Ecosystem-Based Fishery Management (EBFM, Pikitch et al. 2004)). EAA further follows the Code of Conduct for Responsible Fisheries (CCRF) that deals with aquaculture in its Article 9 (FAO 1995).

It includes aspects of integrated natural resource management initiatives such as integrated coastal zone management (ICZM) and the planning and management for sustainable coastal aquaculture development (GESAMP 2001, FAO 2010). Accordingly, EAA aims at conserving ecosystem structure, diversity and functioning, while satisfying societal needs in terms of food production (i.e. securing of fisheries/aquaculture yields) (FAO 2003) and integrating the complete range of stakeholders, spheres of influences and other interlinked processes (Soto et al. 2008a). It was proposed that an Ecosystem Approach Aquaculture should be guided by the following three principles (Soto et al. 2008b), i.e. that aquaculture should

1. be developed in the context of ecosystem functions and services (including biodiversity) with no degradation of these beyond their resilience capacity
2. improve human wellbeing and equity for all relevant stakeholders
3. be developed in the context of (and integrated to) other relevant sectors

While the first principle addresses ecological issues as described by the Malawi principles (CBD 1998), the latter two principles target the human dimension of aquaculture, with the third one, in particular, representing a call for the development of multi-sectoral or integrated planning and management systems (FAO 2010). In addition, three scales for the application of EAA approaches were identified: the (1) farm, (2) aquaculture zone or region (concerning the respective waterbody, and (3) global – market-trade related – level (Soto et al. 2008b).

The FAO has further defined seven major risk sectors for the environmental impact assessment of (bivalve) aquaculture (Bondad-Reantaso et al. 2008): risks related to (1) pathogens, (2) food safety and public health, (3) genetics, (4) ecological considerations (e.g. pests and invasive species), (5) environmental issues, as well as (6) financial and (7) social risks. Many countries and international organizations have by now developed according procedures through which the interaction of bivalve culture with its environment may be classified. As an example, best management practices (BMP) and performance standards were proposed (Gallardi 2014) presenting critical environmental thresholds, e.g. e.g. with respect to maximum allowable sulfide concentration around culture sites. Regulatory and certification procedures generally aim for more sustainable, effective and acceptable aquaculture conduction (Gallardi 2014). Examples include the *Global Aquaculture Alliance* (GAA, www.gaalliance.org) and the *Aquaculture Stewardship Council* (ASC, www.asc-aqua.org) that have developed standards for several cultured species (e.g. salmon, shrimps, bivalves), rewarding responsible aquaculture practices with a consumer-oriented label.

An increasing focus for the environmental impact assessment of aquaculture lays on (ecosystem) modelling, allowing for the predictive evaluation of consequences resulting from aquaculture-related management decisions. As an example, the Farm Aquaculture Resource Management (FARM) modelling framework was developed (Ferreira et al. 2007; Ferreira et al. 2009). By that it aims to provide guidance to farmers and managers, e.g. related to the aquaculture site selection process, to the ecological and economic optimisation of culture practices, as well as to the environmental impact assessment (i.e. eutrophication effects) (Ferreira et al. 2007). The approach combines physical (e.g. hydrodynamics), biogeochemical, bivalve growth, and eutrophication assessment models into a management support tool.

Within the framework of EAA, the identification of acceptable limits to culture expansion is crucial. The concept of carrying capacity (CC) was recently recognized to be important in this context, describing the behaviour of a (cultured) population in relation to a determining variable, e.g. the resource on which it depends (Inglis et al. 2000). Considering the change in any state variable (e.g. phytoplankton availability, oxygen concentration, ecosystem biodiversity), the carrying capacity was defined as the maximum amount of cultured biomass that the system may sustain without experiencing "unacceptable" changes (Inglis et al. 2000, McKindsey et al. 2006a, Figure 1.4). Originally conceptualized for the application in terrestrial resource management (Odum 1959, Shelby & Heberlein 1986, both cited in Inglis et al. 2000), the CC concept was first applied to bivalve farming (e.g. Carver & Mallet 1990, Dame & Prins 1998, Smaal et al. 1998, Inglis et al. 2000), before being further adapted to fit finfish aquaculture operations (e.g. Stigebrandt et al. 2004, Geček & Legović 2010, Stigebrandt 2011). At the beginning, carrying capacity was defined as the maximum number of cultured individuals that could be sustained without negatively affecting bivalve growth (Carver & Mallet 1990), as the culture density maximizing annual production (Bacher et al. 1998; Smaal et al. 1998), or as a function of seawater residence time, clearance rate, and primary production (Dame & Prins 1998).

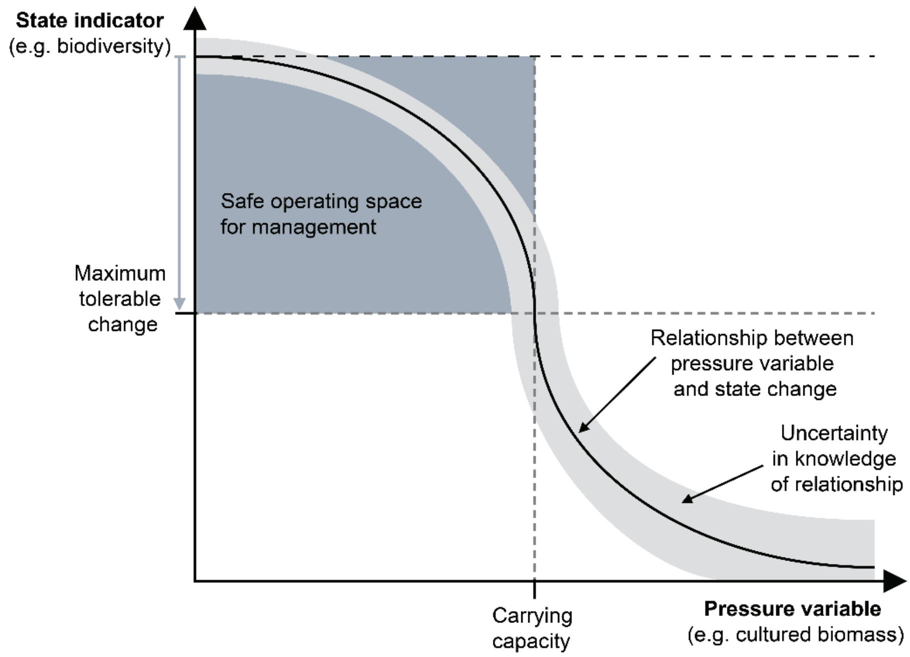


Figure 1.4. *Conceptual framework of carrying capacity (CC), describing the behavior of a certain state indicator (e.g. phytoplankton or oxygen availability, nutrient loading, biodiversity) in response to changes in a pressure variable (e.g. the biomass of cultured species). The carrying capacity is defined here as the maximum amount of cultured biomass that does not yet cause the state variable to exceeding the maximum tolerable change, allowing management decisions within a safe operating space. Constructed following Figure 1 in Tett et al. (2011), originally based on Figure 2 in McKindsey et al. (2006a).*

Inglis et al. (2000) and McKindsey et al. (2006a) broadened the definition by distinguishing four different functional categories of carrying capacity that are today widely accepted:

1. The physical carrying capacity represents the area geographically available and physically suitable for the cultivation of a species in a certain location, limited

by the geography of the area, physical requirements of farm development, and human planning restrictions.

2. The production carrying capacity describes the stocking density of cultured organisms at which the optimum long-term harvest is maximized (Inglis et al. 2000). This may be defined as the maximum stock size at which maximum yield of the marketable cohort is achieved (i.e. the exploitation CC, Smaal et al. 1998), or as the maximum yield constrained by trophic interactions (e.g. the point at which the culture replaces zooplankton, Gibbs 2004).
3. The ecological carrying capacity (ECC) sets limits to aquaculture production as to not cause unacceptable changes in ecological process, species, populations, or communities in the environment (Byron & Costa-Pierce 2013), ideally considering the entire ecosystem (McKindsey et al. 2006a).
4. The social carrying capacity (SCC) considers limits in the socio-economic context, e.g. as culture levels not creating conflicts with other human uses (Inglis et al. 2000), or defined as the point at which the number of aquaculture producers exceeds a profitable cost-benefit ratio for each operation.

Since the first establishment of these categories, assimilative capacity has additionally been proposed as a part of CC, describing the system's ability to process and adapt to changes in organic matter, nutrients or contaminants input, without the alteration of ecosystem state or functioning (Chamberlain et al. 2006, Tett et al. 2011, Ferreira et al. 2013). Recently, the importance of integrating governance into the definition of CC was recognized (Ferreira et al. 2013). The four categories of carrying capacity can be weighted according to region and the type of aquaculture (Ross et al. 2013), i.e. site specific management requirements and targets. They may be mapped as to arrive at an ecosystem approach to aquaculture (Ross et al. 2013, Figure 1.5).

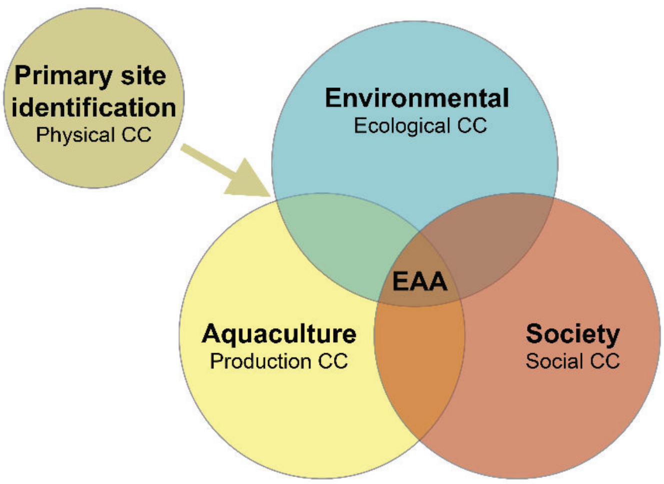


Figure 1.5. *Interaction of the different categories of carrying capacity (CC, i.e. physical, production, ecological, social) to obtain an Ecosystem Approach to Aquaculture (EAA), represented as the overlap of the different CC considerations. Graph constructed following Figure 1 in Ross et al. (2013). Site selection should represent the first step of the EAA framework that could be followed by any of the other areas (Ross et al. 2013).*

However, the definition and implementation of thresholds for carrying capacity is not necessarily straightforward (Ross et al. 2013) and depends on individual system characteristics (Cranford et al. 2012) and on clear definitions of what represents an "unacceptable" change (McKindsey 2013) for the respective system. Accordingly, a wide range of approaches, based on many different variables and concepts have been developed, though most of these studies have addressed production carrying capacity. In contrast, ecological and especially social carrying capacity, have little been addressed due to their comparatively complex estimation (Ferreira et al. 2013, McKindsey 2013) and the lack of adequate techniques (Byron et al. 2011a).

Modeling approaches to CC differ in their spatial and temporal resolution, and may range in their complexity from simple indices to spatially discrete and complex box models and food web models. Index models, as an example, compare physiological demands of bivalves, such as the filtration of seston (Incze et al. 1981, Carver & Mallet 1990) or oxygen requirements (Uribe & Blanco 2001, Tam et al. 2012), or the production of ammonia (Gillibrand & Turrell 1997) or biodeposits (Grant et al. 2005) with its tidal renewal in a simple ratio. As an example, Dame and Prins (1998) used indices representing ratios of water residence time (RT), primary production time (PT) to bivalve clearance time (CT) for the analysis of ECC for bivalve aquaculture in 11 coastal and estuarine systems in Europe and the USA. Since then, these indices (in particular the ratio CT/PT) have often been used for the definition of sustainable aquaculture, e.g. by the Aquaculture Stewardship Council (ASC 2012), though the lack of established, comparable thresholds currently limits applicability (Filgueira et al. 2015).

Box models and fully-spatial models combine hydrodynamic and/or biogeochemical models with bivalve physiology for production and ecological carrying capacity estimation at different spatial resolutions (Raillard & Ménesguen 1994, Dowd 1997, Bacher et al. 1998, Ferreira et al. 1998, Duarte et al. 2003, Dowd 2005, Filgueira & Grant 2009, Filgueira et al. 2010). Although the above mentioned approaches all result in estimates of maximum producible bivalve biomass, most of them do neither consider other (natural) populations of bivalves or different filter-feeders co-occuring with, but consuming the same food source as the cultured individuals (McKinskey 2013), nor other inter-specific interactions for the determination of carrying capacity.

Food web modelling, in contrast, allows to investigate the response of many species' populations to the aquaculture activity at the same time, which is of especial importance for settings in which other species are of commercial interest (e.g. as fishery target species, Filgueira et al. 2015). The few existing approaches for the estimation of CC with a food-web model mainly use Ecopath with Ecosim (EwE, (Christensen & Pauly 1992, Christensen & Walters 2004a), allowing to establish mass-balanced trophic models as a representation of all species in an ecosystem assembled in functional groups. The ECC is then estimated by a step-wise increase of the biomass of cultured bivalves (using a series of consecutive models) until the system gets unbalanced, i.e. until more food is required than available in the system (as demonstrated by an ecotrophic efficiency EE>1, Wolff 1994, Jiang & Gibbs 2005, Byron et al. 2011b, Byron et al. 2011c). Though the approach claims to integrate trophic interactions with co-occurring species, only bivalve biomass was is changed in those successive models, while all other parameters and trophic flows are maintained. Thus, the method actually focusses on the phytoplankton-bivalve interaction, and does not allow for the estimation of effects on the community or ecosystem level (Kluger et al. 2016a). In this context, a recent study presented a novel approach, using

Ecosim for the dynamic simulation of aquaculture expansion, defining the ecological carrying capacity as the bivalve biomass not yet causing any other functional group to get depleted (i.e. to fall below 10 % of its original standing stock, following the definition of depletion from fisheries science, Worm et al. 2009) (Kluger et al. 2016a, i.e. *Chapter 3* of this thesis).

The multitude of existing approaches for the estimation of carrying capacity reflects the effort current research has dedicated to its solution, and the importance the topic has been given in the context of EAA. The site-specific requirements and general difficulties researchers have encountered when trying to define respective thresholds have as yet prevented the development of approaches transferrable to other settings. When aiming at the determination of CC from an ecosystem point of view, food web models may represent an important step towards a holistic approach. The integration of the entire food web surrounding cultures is likely to help balancing aquaculture development with the ecological feasibility, i.e. following an ecosystem-based approach to aquaculture. This is where this thesis comes in, aiming at developing an approach to ECC that is based on a food web model thus integrating inter-specific constrains while being part of a broader ecosystem approach to aquaculture. At the same time, the approach should be applicable to other coastal settings exposed to bivalve aquaculture.

1.2 THE CASE STUDY: SECHURA BAY, PERU

1.2.1 Description of location

The study system represents the Peruvian bay of Sechura, situated in the state of Piura, about 1000 km to the North of the country's capital Lima (5.6 °S, 80.9 °W, Figure 1. 6). The Sechura province is one of eight comprising the state of Piura. The bay of Sechura is a large, semi-enclosed embayment extending over an area of 400 km^2. Large parts of the bay extend over depths between 5 and 10 m but ranging to depths of 30 m, with an average depth of 15 m (Taylor et al. 2008d). Located at the northern edge of the Humboldt Current (HC) upwelling system, the bay is characterized by almost continuous upwelling, transporting cold and nutrient-rich water to the surface layer (Tarazona & Arntz 2001). At the same time, the location benefits from warmer equatorial water that meet the HC just to the north of the bay, with average sea surface temperatures of 20 °C being higher when compared to higher latitudes (Taylor et al. 2008d). This environmental conditions make the bay a highly productive system during normal upwelling conditions. The system's dynamics are influenced by the El Niño Southern Oscillation (ENSO) phenomena, during the warm phase of which the transition zone is shifted southwards by reflected Kelvin waves (Taylor et al. 2008d), resulting in highly elevated sea surface temperatures of up to 29 °C and increased precipitation (30x higher than during non-EN years) in the otherwise arid region (Takahashi 2004).

Several small villages frame the bay, with the main fisheries landing sites being located in Parachique and Puerto Rico (Figure 1.6). In this area, fishing historically played an important role for human livelihood, with 30 % of the economically active population of Sechura being involved in 1993 (Chapa 2005, cited in Badjeck 2008), with purse seine, trawling, and diving as the main types of fishery used (IMARPE 2007). In the years 2000 to 2006, the main fisheries target species represented the Engraulidae (Anchovies) *Engraulis ringens* (92.9 % of all catches) and *Anchoa nasus* (0.6 %), the squid species *Dosidicus gigas* (2.5 %) and Loligo gahi (0.8 %), the snake eel *Ophichthus remiger* (0.6 %), and the mullet *Mugil cephalus* (0.3 %) (IMAPRE 2007). The scallop *Argopecten purpuratus* was only one of many benthic resources targeted by diving fishermen, and contributed 1.1 % to all catches in the aforementioned time period. However, it recently became the main resource landed besides anchovies in the region. In fact, the bay developed into an important scallop producing location – on the regional, national and on the Latin American level – since in 2003 first on-bottom cultures of this species were initiated. By now, 41 % of the bay's area is occupied by culture areas (PRODUCE 2015).

Considering that the Peruvian scallop production contributes to 3.5 % to the total world scallop aquaculture production (FAO 2016), and that this particular bay contributes as much as 80 % to the annual Peruvian scallop production (in 2013, Mendo et al. 2016), this implies that Sechura contributes with 2.9 % to world scallop production from aquaculture. With an increasing cultivation effort during the last years, and the lack of formal management strategies in place, the evaluation of the ecological consequences as imposed by the initiation of aquaculture, as well as the determination of feasible limits to culture expansion became necessary. This bay was therefore chosen as a study location for the development of a holistic approach to the assessment of bivalve aquaculture impact on the ecosystem and social level. Other reasons for selecting this location for the here presented study were the data availability, i.e. the large number of studies already available on the study organisms, the scallop *A. purpuratus* (section 1.2.2), allowing for the establishment of a trophic network model, and the fact that an energy flow model of the bay had already been constructed for the year 1996 (Taylor et al. 2008) which allowed for the evaluation of ecosistemic impacts as induced by the initiation of scallop aquaculture in the year 2003.

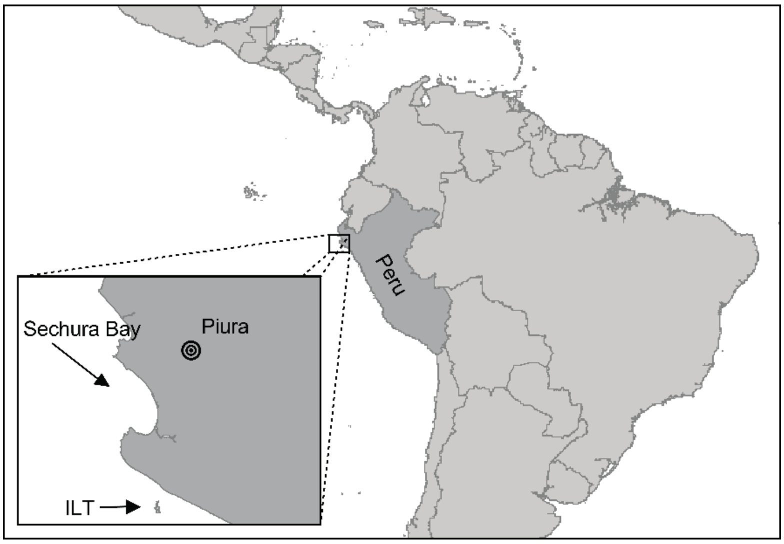


Figure 1.6. *Location of Sechura Bay in South America.*

1.2.2 Species of interest

The Peruvian bay scallop *Argopecten purpuratus* (Lamarck, 1819) represents the commercially most important mollusc bivalve species along the Pacific coast of South America. Its distribution ranges from Paita, Peru (5 °S) to Valparaíso, Chile (33 °S) (Sanzana 1978, Alamo & Valdivieso 1987; both cited in Peña 2001) on sand-bottoms in depths of 5-30 m (Wolff et al. 2007). As a member of the family Pectinidae, it has an almost circular appearance, with two ears (auricles) projecting from the umbo (Gosling 2003). Its colours range from black-white to orange and pink-fuchsia (Figure 1.7). The two shells are held together along the hinge line by a rubbery internal ligament, and the single, centrally placed adductor muscle (Gosling 2003). Several ribs radiate from the hinge, and distinct circular annual rings are usually visible on the shell's surface, allowing for a comparatively easy determination of age.

As other bivalves, the species feeds on phytoplankton and detritus that is filtered from the water with the two gills. It is hermaphrodite with a planktonic larval phase of 16-22 days (Bellolio et al. 1993, 1994, both cited in Mendo et al. 2011), comprising a ciliated trochophore stage, a D-veliger and pediveliger larvae phase (Mendo et al. 2011). After this, the adult individuals live on the bottom surface, without being attached with byssal strings. They may actively move by performing swimming-like movements. For this, the rapid contraction of the adductor muscle causes the repeated closure of the two valves, and the backward ejection of water on either side of the hinge results in a forward movement of the scallop in small dashes (Gosling 2003). In contrast to other bivalves, scallops are harvested for their large adductor muscle, sometimes in combination with the orange-white roe (with the orange part representing the female gonad, and the white part the male gonad). Due to its high growth rates, shell heights of 60 mm can be reached within 6 months (in Sechura, Mendo et al. 2011).

This species has a long fishing history, being targeted along the Peruvian and Chilean coastline in different bays. In Peru, this scallop species was harvested since the 1950s in an open-access fishing regime, with a major fishing area located around Pisco (14 °S). The fishery has experienced several booms, in particular during the strong El Niños of 1983/84 and 1997/98, always followed by a strong reduction in catches (Wolff & Mendo 2000). Since 2009, production levels have reached historically high records, and remained high ever since. The reason for this can be found in the recent transformation of the open-access scallop fisheries in Sechura Bay into many small-scale aquaculture operations that by now account for up to 80 % of annual Peruvian scallop production (in 2013, Mendo et al. 2016).

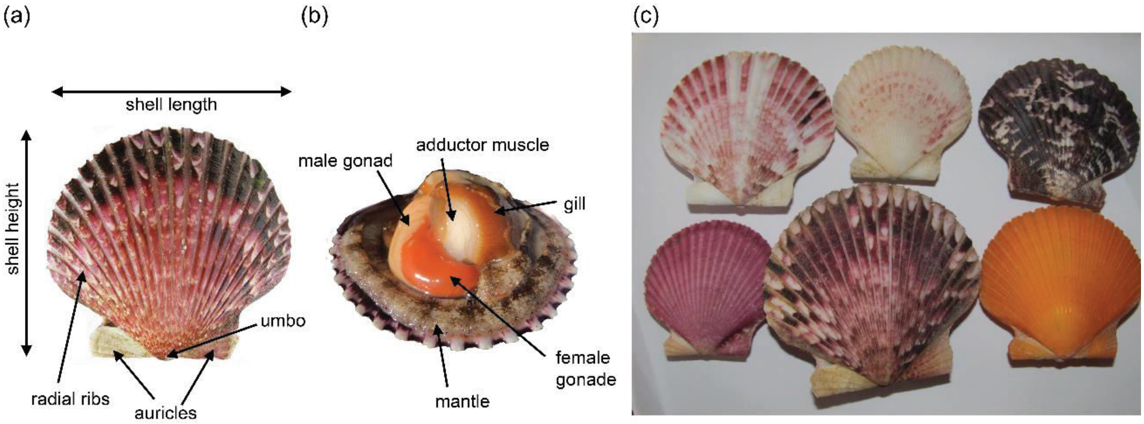


Figure 1.7. *Overview of the (a) external and (b) internal anatomy (after Mendo et al. 2011), as well as the (c) exemplary variability of colours of the Pectinidae* Argopecten purpuratus *(Photos: LC Kluger).*

Scallop cultures in Sechura are conducted on-bottom, mainly without the use of larger net structures. Artisanal fishermen associations obtain scallop seed (recruited individuals) from natural banks within the bay or from the island Isla Lobos de Tierra (see Figure 1.6), or to a lesser extend from hatcheries and transfer them into given culture areas that are distributed over the entire bay's area. This culture type, also called sea ranching, is only allowed for artisanal fishermen associations (Mendo et al. 2016) that may apply to manage a certain area (concession), by that obtaining quasi-property rights.

Scallops are harvested by divers, operating from small wooden boats (of approximately 10 m length), hand-collecting individuals of marketable sizes (65 mm) from the grow-out areas on the seafloor (Figure 1.8a). Individuals are collected in nets (called mallas), containing two to three manojos (96 individuals each), which represents the historic unit of selling (Figure 1.8b). The product is then collectively transported to the land in slightly bigger boats (called madrina, Figure 1.8c) that nowadays are the only boats allowed to land scallops at the largest landing site in the bay of Sechura (Parachique). At the landing site, the translocation of scallop nets is assumed by contracted workers (called vestidores, Figure 1.8d) who transfer the product into refrigerator trucks (Figure 1.8e). By now, scallops are processed in plants within the same region of Sechura, i.e. within 20-30 minutes ride from the landing site. In the plants, contracted workers shuck the scallop meat (Figure 1.8f), wash and sort them (Figure 1.8g), and freeze the final product. While some plants only accomplish primary processing (i.e. completing the aforementioned steps) and sell their product thereafter, other plants finalize the processing as to the final product for end consumers (e.g. 500 g bags, single scallops presented in a shell (Figure 1.8h)). It was estimated that the entire processing chain provides work to 5000 artisanal fishermen and 20000 people involved in the scallop processing chain (J. Proleon pers. comm.). Depending on the demands of the end consumer, scallops are either commercialized as adductor muscle alone or in combination with the roe. The obtained prices depend on the number of individuals (as muscle or muscle-roe) comprising one pound. The majority of the final product is exported, mainly to France (60%), the USA (22%), and Belgium (5%) (in 2011, PRODUCE 2011), with annual export values of about US$158 million (in 2013; ADEX 2014).

Figure 1.8. *Simplified description of scallop culture-related activities in Sechura: (a) Diving fishermen, setting out for scallop harvest; (b) fishermen preparing nets (mallas) on board that are (c) transported via larger boats (madrinas) to the landing site (Parachique). There, (d) the product is transferred by contracted workers (estivadores) to (e) the refrigerator trucks, which transport the product to the processing plants, where (f) scallops are shucked, (g) washed and sorted, and (h) eventually processed as required by the end consumer. All pictures from LC Kluger.*

1.3 OBJECTIVES OF THESIS AND RESEARCH APPROACH

The overall objective of this thesis is to develop a holistic approach for the theoretical exploration of bivalve (scallop) aquaculture impact (Figure 1.9) and the estimation of maximum sustainable production limits for a case study in Peru. Sechura Bay. As a first step, the thesis investigates how an intense bottom culture of the Peruvian scallop changes benthic community structures and energy flows within the bay's system by applying a combination of community ecology (multivariate statistics) and trophic modelling (Ecopath with Ecosim) approaches (Chapter 2). As a second step, the bay's ecological carrying capacity for bivalve (scallop) aquaculture is estimated, for which a novel approach based on trophic modelling was developed (Chapter 3). The impact of culture expansion on ecosystem structure and functioning – in particular ecosystem resilience – is further analysed by a second approach developed in the course of the thesis (Chapter 4). For a holistic evaluation of the system's potential for long-term sustainable aquaculture socio-ecological approach is used (Chapter 5). Based on scallop production trajectories of the last years it was hypothesized that current culture levels have already imposed a change to benthic community structure and ecosystem functioning, and that the system is close to its ecological carrying capacity.

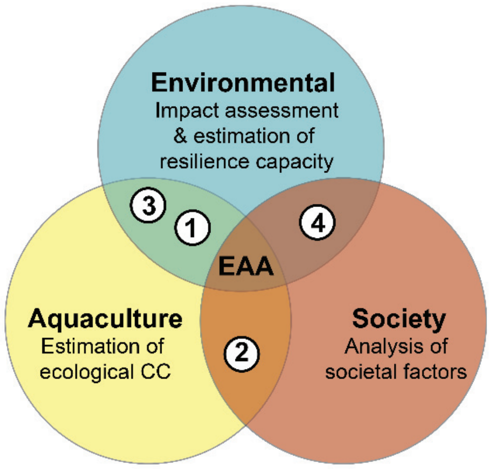


Figure 1.9. *Overview of the ecosystem approach to bivalve aquaculture as suggested by the presented thesis. Small numbers (1-4) represent the individual studies that represent Chapters 2-5. The assessment of bivalve aquaculture impact on the benthic community ((1) Chapter 2) and ecosystem functioning and resilience ((3) Chapter 4), acts on the interface of aquaculture and environmental considerations, while the estimation of the system's ecological carrying capacity is defined by management decisions with respect to culture scenarios ((2) Chapter 3). Social-ecological considerations for long-term sustainability are identified at the interface between society and the environment ((4) Chapter 5). The integration of all different steps allows for an ecosystem approach to aquaculture (following Ross et al (2013, see Figure 1.5), though aspects of site selection were not covered by the presented thesis, since aquaculture operations were already in place.*

1.3.1 Research questions

For the here presented thesis, the following research questions were developed, and will individually be addressed in the different chapters (manuscripts) subsequently presented.

(I) How can multi-variate statistics and trophic modelling be combined for the holistic impact assessment of bivalve culture? How has the introduction of intense bottom culture of the Peruvian scallop into the bay's system changed its community structure and energy flows?

> *Manuscript 1*: Kluger LC, Taylor MH, Barriga Rivera E, Torres Silva E, Wolff M (2016b). Assessing the ecosystem impact of scallop bottom culture through a community analysis and trophic modelling approach *Marine Ecology Progress Series* 547:121-135.

(II) How can the ecological carrying capacity of coastal systems for bivalve culture be assessed using a truly ecosystem-based approach? What is Sechura B ay's ecological (long-term) carrying capacity for scallop culture?

> *Manuscript 2*: Kluger LC, Taylor MH, Tam J, Mendo J, Wolff M (2016a). Carrying capacity simulations as a tool for ecosystem-based management of a scallop aquaculture system. *Ecological Modelling* 331: 44-55.

(III) How can the ecological resilience of coastal systems exposed to bivalve aquaculture be estimated with a trophic modelling approach? What is the limit to culture expansion in Sechura Bay based on considerations of resilience?

> *Manuscript 3*: Kluger LC, Filgueira R, Wolff M (in preparation). Integrating the concept of resilience into the ecosystem-based approach for bivalve aquaculture management. Manuscript in preparation for submission to *Ecosystems*

(IV) Which are the main factors driving the success of Sechura Bay as a major Latin American center for scallop production? How can long-term sustainability of scallop production in Sechura Bay be achieved?

> *Manuscript 4*: Kluger LC, Taylor MH, Wolff M, Mendo J (in preparation) The rise of Sechura Bay as the centre for scallop culture in Latin America – a socio-ecological analysis. Manuscript in preparation for submission to *Ecology & Society*

1.3.2 Thesis outline

This thesis is structured into six chapters, with an introductory section and a general discussion framing four scientific publications that address the different research questions as formulated in section 1.3.1. While all individual studies represent separate approaches to different questions arising from bivalve (scallop) aquaculture, they all form part of a bigger strategy the development of which was the greater aim of this thesis.

In the opening section (*Chapter one*), all important information related to bivalve aquaculture is revised, including recent production trends, a synthesis of potential interactions of bivalve aquaculture with its environment, as well as approaches for the evaluation of long-term sustainability focusing on the concept of ecological carrying capacity in the context of ecosystem-based management for bivalve aquaculture. I further present the case study location and study organism (the Peruvian bay scallop *Argopecten purpuratus*) as used for the development of the approaches presented in the subsequent chapters.

In the *second chapter* (manuscript 1) a combination of different methodologies (i.e. multivariate statistics, community analysis, trophic modelling) is applied for the holistic impact assessment of bivalve (scallop) aquaculture on the community and ecosystem level. Comparing two system states representing pre-culture and (current) culture conditions, the ecological consequences of the initiation of cultures in Sechura Bay is analyzed.

The *third chapter* (manuscript 2) presents a novel approach to ecological carrying capacity estimation for bivalve aquaculture systems. The expansion of culture is simulated starting from a trophic (Ecopath) model for the Sechura Bay system. Ecological thresholds are suggested and the possibility to apply the approach to other systems is discussed.

The *fourth chapter* (manuscript 3) develops an ecosystem approach to bivalve aquaculture, i.e. for the estimation of ecological carrying capacity in combination with ecological resilience. Based on the methodology as presented in the preceding chapter 3 (manuscript 2), changes in ecosystem functioning when exposed to different bivalve (scallop) aquaculture scenarios is explored through a trophic modelling approach. A new way of estimating resilience and functional diversity is presented, and applied to the case study of Sechura Bay. Resilience-based management options are developed and the potential for the application of the approach to other bivalve aquaculture systems is discoursed.

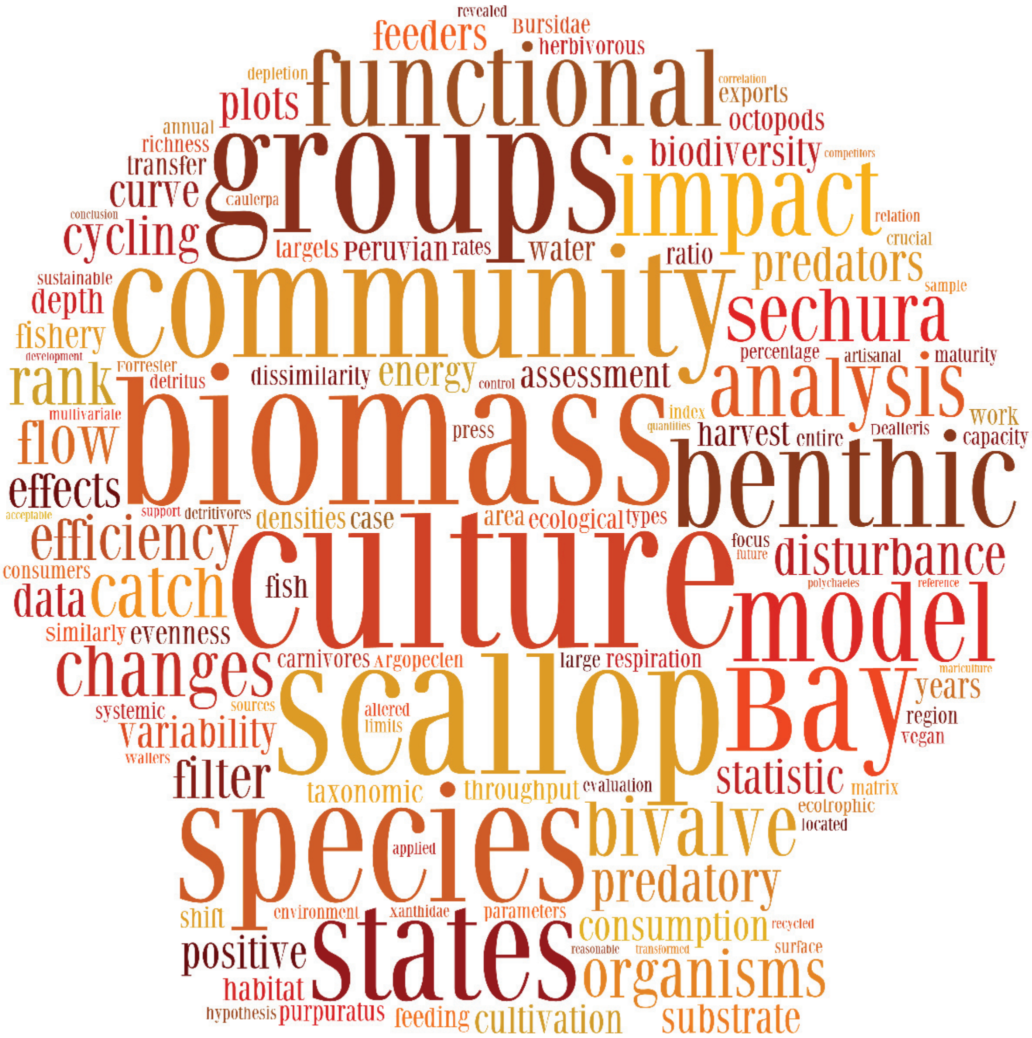
In the *fifth chapter* (manuscript IV) the analysis of various environmental, ecological, and socio-economic factors is combined to tackle the question how the case study (Sechura Bay) could develop into a major center for scallop production in Latin America. Factors driving its long-term success are identified, the potential for Sechura to maintain its production on a long-term sustainable level as well as the possible consequences for other systems exposed to bivalve culture are discussed.

The *sixth chapter* represents a concluding discussion of the combined ecosystem approach to bivalve aquaculture as presented by this thesis. Key findings and their significance is discussed, and the approach is critically assessed. It further discusses some future management considerations for the Sechura Bay system, including the potential for aquaculture certification, and integrates these thoughts into the wider context of general bivalve aquaculture management.

In addition to the development of individual scientific manuscripts, the different stages of the thesis work have been presented at different international scientific conferences in the course of this PhD. An overview of respective presentations can be found in Annex I (Supplemental Table S1.3).

CHAPTER 2

– Assessing the ecosystem impact of scallop bottom –



CHAPTER 2.
Assessing the ecosystem impact of scallop bottom culture through a community analysis and trophic modelling approach

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Lotta C. Kluger, Marc H. Taylor, Edward Barriga Rivera, Elky Torres Silva, Matthias Wolff

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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.

Keywords: Bivalve culture, aquaculture impact, community analysis, trophic modelling

2.1 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 bio-deposition (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 epibiontic 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. 2016a), it was hypothesized 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 hypothesized 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. 2016a) focussing on the ecological carrying capacity of Sechura Bay under different cultivation scenarios.

2.2 METHODS

2.2.1 Study area

Sechura Bay (5.6 ° S, 80.9 °W; Figure 2.1) is located at the northern edge of the Humboldt Current upwelling system, characterised by almost continuous up-welling of cold and nutrient-rich water to surface layers (Tarazona & Arntz 2001). The bay extends over 400 km^2, and is characterised by sandy substrates and shallow depths (<30 m) (Taylor et al. 2008d). 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 (Figure 2.1).

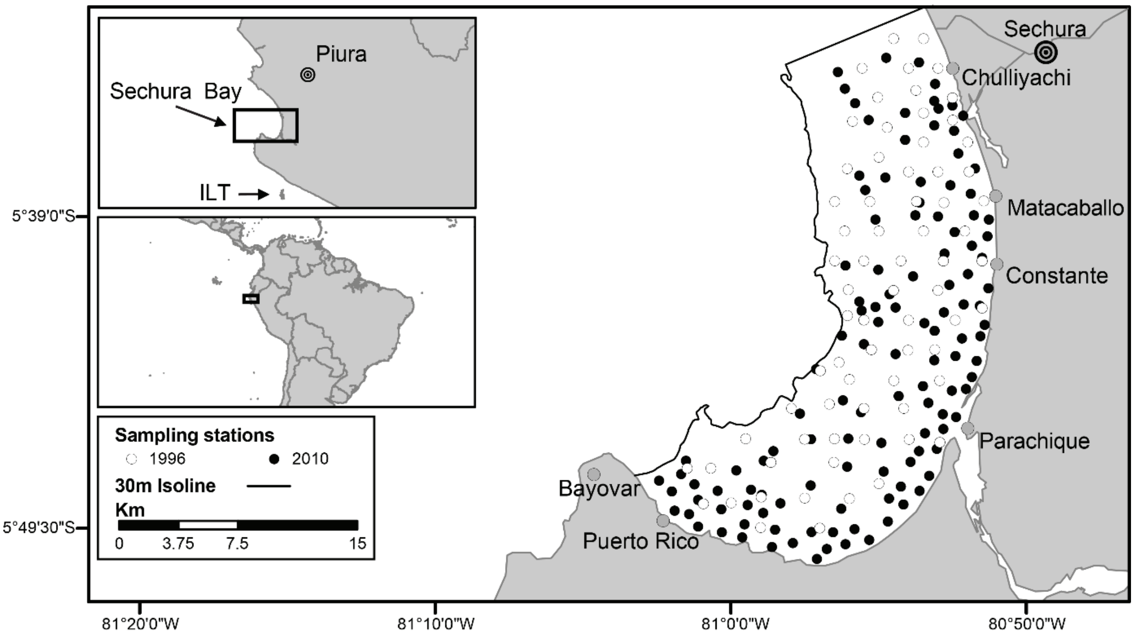

Figure 2.1. *Location of the study system Sechura Bay in northern Peru. Coastal villages, the isoline of 30 m depth and locations of the benthic evaluation in 1996 (N = 71) and 2010 (N = 124) are indicated. ILT = Isla Lobos de Tierra.*

2.2.2 Analysis of community changes

Changes in benthic community composition were analyzed 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 (Figure 2.1). Sampling of epiflora (macroalgae), epifauna (excluding mobile octopods) and infauna was conducted by divers using replicated 1 m^2 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. 2008d).

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 community (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 = 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.

2.2.3 Trophic modelling comparison

2.2.3.1 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 2004a), 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 2004a, Christensen et al. 2005), with the first equation defining the individual components of the production term:

Production = catch + predation + net migration + biomass accumulation + other mortality

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

Consumption = production + respiration + 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 2004a). The program further requires information on diet compositions for all groups, as well as exports from the system into fishery or aquaculture harvest.

2.2.3.2 Model structure

Both models were based on a previous model of Sechura Bay constructed by Taylor et al. (2008d). The model area was defined to cover an area of 400 km^2, including all depths <30 m (Figure 2.1, Taylor et al. 2008d). 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. (2008d) 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. 2008b, c). Supplemental Table S2.1 (www.int-res.com/articles /suppl/m547p121_supp.pdf) contains a complete list of species contributing to the different functional groups.

2.2.3.3 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 2.1) (after Taylor et al. 2008d). Values for production/ biomass *(P/B)*, consumption/biomass *(Q/B)* and conversion efficiency *(GE)* were based on former estimates of Taylor et al. (2008d). 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− 5.89 °S, 80.798−81.25 °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. 2008d). 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°−6 °S, <82 °W, n = 60, after Taylor et al. 2008d) 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. 2008d). 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. 2008d).

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 2.1).

The construction of diet matrices followed Taylor et al. (2008d) (Table 2.2). 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.

2.2.3.4 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 cycling, transfer efficiency) (Christensen et al. 2005, Heymans et al. 2014). In addition, the index of keystoneness 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).

Table 2.1. *Input–output parameters for the 2 balanced steady-state models for Sechura Bay (1996 and 2010). TL = Trophic level; Bi = biomass; Pi/Bi = production rate; Qi/Bi = consumption rate; EEi = ecotrophic efficiency; Pi/Qi = conversion efficiency; P/R = production/respiration ratio; R/A = respiration/assimilation ratio; Fi = fishing mortality; MOi = non-predatory natural mortality; M2i = predation mortality. All parameters calculated by EwE are shown in* ***bold***

rey \ predator	Year	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/R	R/A	Catch (t year^{-1})	F_i	MO_i (year^{-1})	$M2_i$ (year^{-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	160.66	**0.789**	**0.201**	**0.335**	**0.749**	-	-	**6.803**	**25.465**
	2010	**2.177**	25.886	35.4948	160.66	**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**	111.45	**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. Herb. 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**	**0.672**	-	-	**0.016**	**1.123**
8. Benth. 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. Misc. 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. Pred. 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**							

Table 2.2. *Diet matrices for steady-state models of Sechura Bay for 1996 (from Taylor et al. 2008d) 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. Herb. gastropods	1996								0.090	0.090	0.070	0.090
	2010								0.000	0.072	0.066	0.083
8. Benth. detritivores	1996								0.180	0.180	0.140	0.163
	2010								0.028	0.233	0.127	0.158
9. Misc. filter feeders	1996								0.070	0.070	0.060	0.079
	2010								0.029	0.045	0.029	0.096
10. Pred. 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	

2.3 RESULTS

2.3.1 Changes in benthic species community composition and biodiversity

2.3.1.1 Comparison of benthic species composition

Rank-log abundance analysis revealed differences in the abundance dominance pattern between the 2 system states (Figure 2.2, Supplemental Table S2.2 (www.int-res.com /articles/suppl/m547p121_supp.pdf)). In 1996, the families Majidae, Columbellidae 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 Lottidae (HG), Pinnotheridae (BD) and Hiatellidae (miscellaneous filter feeders, MF) (abundance rank positions 5, 8 and 10, respectively). In contrast, 11 families were only present in 2010, e.g. Calyptraediae (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 (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 (Figure 2.3, Supplemental Table S2.3).

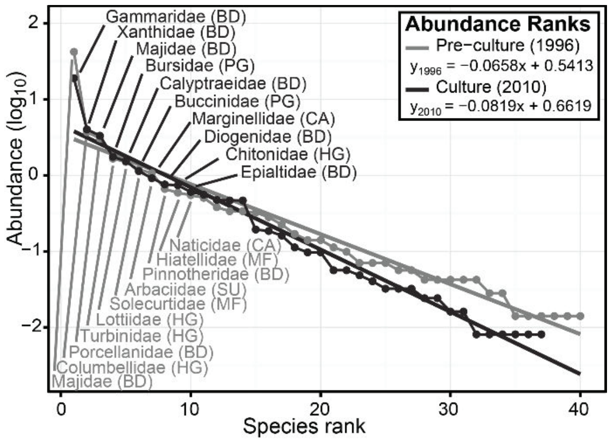

Figure 2.2. *Rank-log abundance plots for family-based benthic communities of Sechura Bay for 1996 and 2010. Functional groups as used for the EwE model are given: sea urchins (SU), herbivorous gastropods (HG), benthic detritivores (BD), miscellaneous filter feeders (MF), predatory gastropods (PG), small carnivores (CA) and predatory crabs (PC). Supplemental Table S2.3 contains a complete list of taxonomic groups, abundance and biomass values, and respective ranks.*

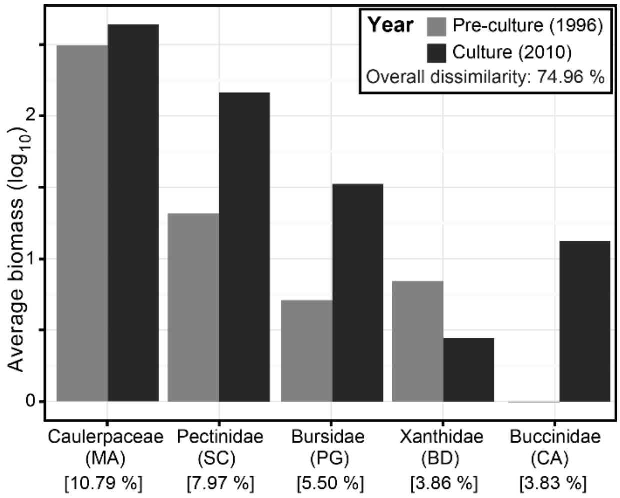

Figure 2.3. *Results of the SIMPER analysis considering year as a factor. Biomass of the 5 most important families (contributing most to overall dissimilarity) is compared between 1996 (grey) and 2010 (black), standardized per m² by dividing by the number of sampling stations. The individual contribution 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). Supplemental Table S2.3 contains a complete list of the SIMPER results.*

2.3.1.2 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 (Figure 2.4). 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.

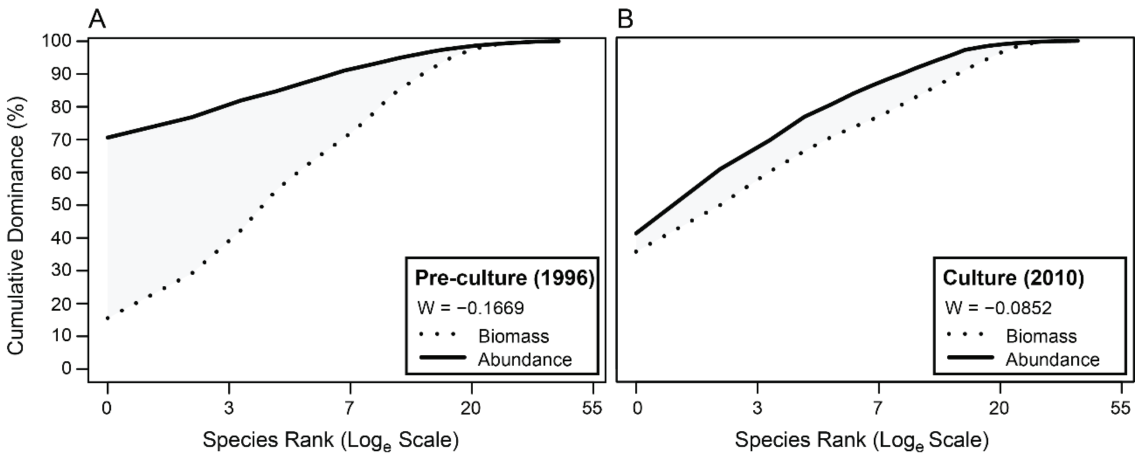

Figure 2.4. *Abundance−biomass comparison plots and Clarke's* W *statistic for the family-based benthic communities of Sechura Bay for (A) 1996 and (B) 2010. Supplemental Table S2.2 contains a complete list of taxonomic groups, abundance and biomass values, and respective ranks.*

2.3.1.3 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 2.3). 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, $p < 0.001$).

Table 2.3. *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
Caulerpa 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 x Depth	1	1.338	1.3378	4.5804	0.001
Residuals	171	49.945	0.2921		
Total	176	62.814			

2.3.2 Comparison of system states using the EwE approach

2.3.2.1 General aspects

System size (total throughput, T) increased by 16.0 % from the pre-culture to culture state (Table 2.4), 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.

2.3.2.2 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 2.4). 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.

2.3.2.3 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 2.4), 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.

Table 2.4. *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) (t km^{-2} year^{-1})	35870.34	41600.80	+ 15.98
Sum of all consumption (t km^{-2} year^{-1})	5583.78 (15.57 %)	6994.04 (16.81 %)	+ 25.26
Sum of all exports (t km^{-2} year^{-1})	12980.83 (36.19 %)	14619.74 (35.14 %)	+ 12.63
Sum of all respiratory flows (t km^{-2} year^{-1})	3350.98 (9.34 %)	4214.60 (10.13 %)	+ 25.77
Sum of all flows into detritus (t km^{-2} year^{-1})	13954.76 (38.90 %)	15772.43 (37.91 %)	+ 13.03
Total net primary production (t km^{-2} year^{-1})	16346.19	18834.34	+ 15.22
Total biomass (excl. detritus) (t km^{-2} year^{-1})	615.63	905.23	+ 47.04
Mean transfer efficiency (%)	5.5	4.3	- 21.82
Fishery indicators			
Total catches (TC) (t km^{-2} year^{-1})	2.898	114.471	+ 3850.02
Mean trophic level of the catch (TLc)	2.16	2.02	- 6.22
Gross efficiency (catch/net PP)	0.0002	0.0061	+ 3328.20
Primary Production (PP) required / 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 / TST (B/TST) (year^{-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

2.3.2.4 Analysing changes in trophic flow structure

The flow diagram shows the prominent role of scallops within the trophic structure of Sechura Bay (Figure 2.5), 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 t km^{-2} 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 (Figure 2.5). 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 2.1).

2.3.2.5 Keystoneness

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 2.5). For both system states, macroalgae represented a dominant functional group (as described by $KDi \geq -0.7$) due to its high biomass and overall impact.

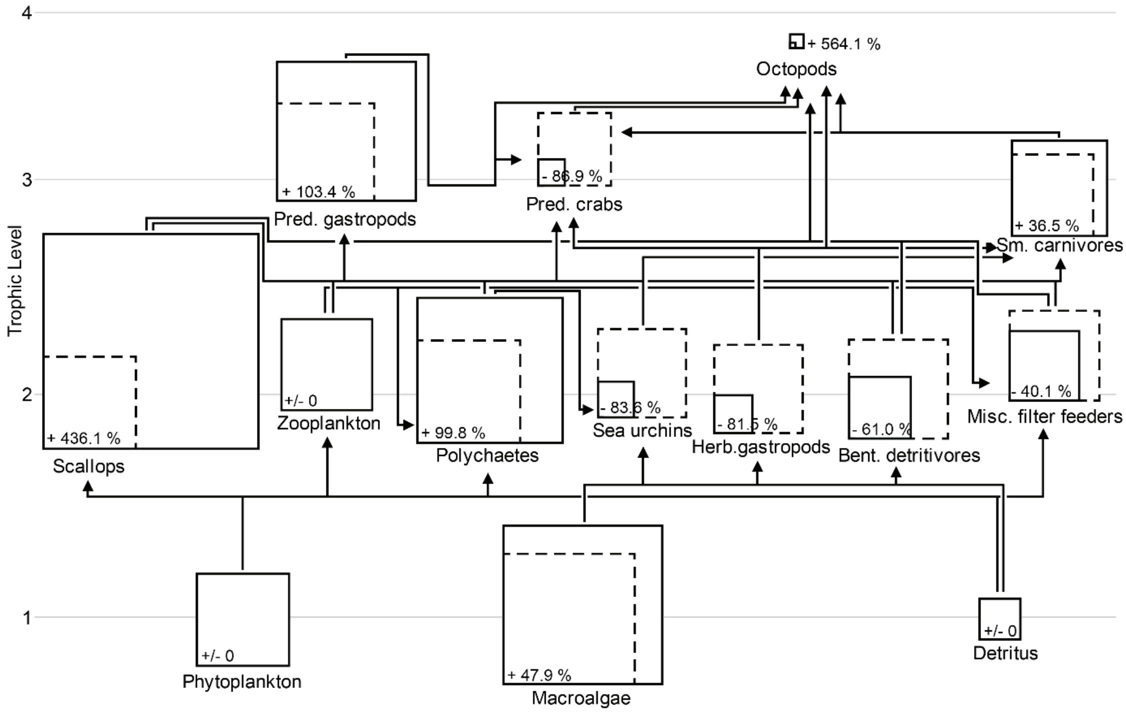

Figure 2.5. *Trophic flow diagram of the Sechura Bay ecosystem in pre-culture (1996, dashed lines) and culture (2010, solid lines) system states, demonstrating the percentage change in functional group biomass between both states. Actual biomass values and trophic levels as calculated by EwE are given in Table 2.1.*

Table 2. 5. *Results of the calculation of the keystone index #1 (after Libralato et al. 2006), and the species dominance index (after Heymans et al. 2014) for all functional groups of the pre-culture (1996) and culture (2010) system states. Keystone groups with KS ≥ 0, dominant (structural) groups with KD ≥ -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. Polychates	- 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. Herb. gastropods	- 0.5260	- 0.5899	- 10.81	- 1.9751	- 2.9518	- 33.09
8. Benth. detritiv.	- 0.5276	- 0.2780	89.79	- 1.6788	- 2.0275	- 17.20
9. Misc. filter feeder	- 1.0150	- 1.0618	- 4.41	- 2.4383	- 2.8844	- 15.47
10. Pred. 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

2.4 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 2.3), including a decrease in benthic biodiversity and species evenness in the culture period (rank plots, Figure 2.2), and shifts in dominant species. Scallops, macroalgae Caulerpaceae and predatory gastropods Bursidae contributed most to the overall dissimilarity between system states (SIMPER analysis, Figure 2.3), 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. 2006a, D'Amours et al. 2008) and a general shift in the relative dominance of 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 Calyptraediae, 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 (Figure 2.3, Supplemental Table S2.3).

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 Dealteris 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. (2016a). 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. 2006a). 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. 2016a).

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. (2016a), 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 & Christensen (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. 2008a), 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 (Ecopath 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 assessment 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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CHAPTER 3

– Simulations of the ecological carrying capacity –

CHAPTER 3
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 thePeruvian 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 com-bined with critical environmental changes may cause mass mortalities and severe consequences for theecosystem. 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 causeother 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.

Keywords: Ecological carrying capacity, Bivalve bottom culture, Ecosystem-based management, Trophic modeling

3.1 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 over-exploiting 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 focused 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. 2006a), with physical carrying capacity being the area geo-graphically 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. 2006a). Modeling approaches to carrying capacity have so far often dealt with hydrodynamics, food availability and production, as well aswith bivalve feeding physiology (Inglis et al. 2000, McKindsey et al. 2006a, 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 & Prins 1998), the production of ammonia (Gillibrand & Turrell 1997) or bio-deposits (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 & Mallet 1990) or depleting available oxygen (Uribe & 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 h olistic 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 & 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. 2006a). 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. 2011b). 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 & Gibbs 2005, Byron et al. 2011b, 2011c). 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 ecosistemic 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.

3.2 METHODS

3.2.1. 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 km^2, 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 the1950s, 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 - Ministery 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 Figure 3.1).

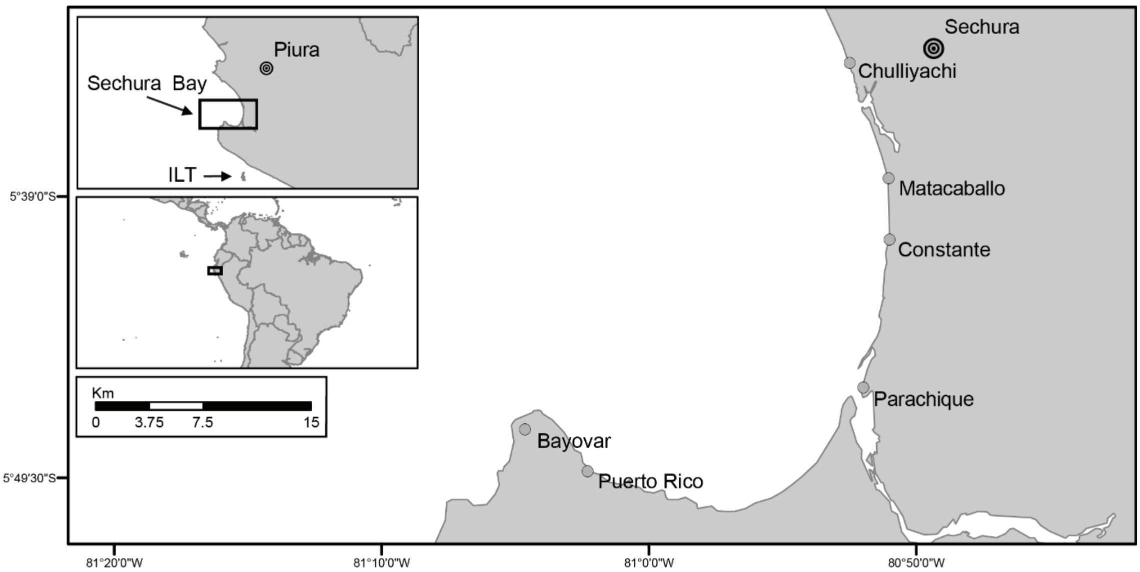

Figure 3.1. *Location of the study system Sechura Bay in North Peru, with the indication of coastal villages. ILT = Isla Lobos de Tierra, the island where scallop seed is collected.*

3.2.2. Model description and data input

A trophic model of Sechura Bay was constructed using the soft-ware Ecopath with Ecosim (EwE) 6.4.3 (Christensen & Walters 2004a), and was based on a previous model by Taylor et al. (2008d), 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 (Figure 3.2).

Input parameters for the different functional groups were obtained from various sources including regional catch statistics, empirical relationships shown in other fishermen in order to determine catches coming from within the bay (Table 3.2). Catch Values for production/biomass (P/B), consumption rate (Q) and conversion efficiency (GE) were based on former estimates of Taylor et al. (2008d).

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. (2002; Chl a : Carbon - 1:40) and 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 m^2 basis, assuming a well-mixed water column (after Taylor et al. 2008d). 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. 2008d) 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 m^2 each. Abundance and 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. 2008d). 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 under-sampling (after Taylor et al. 2008d). 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. (2008d), 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. 2008d). 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 3.2). 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. (2008d, Table 3.3). 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. 2008d), assuming a base percentage of detritus feeding (10-20 %).

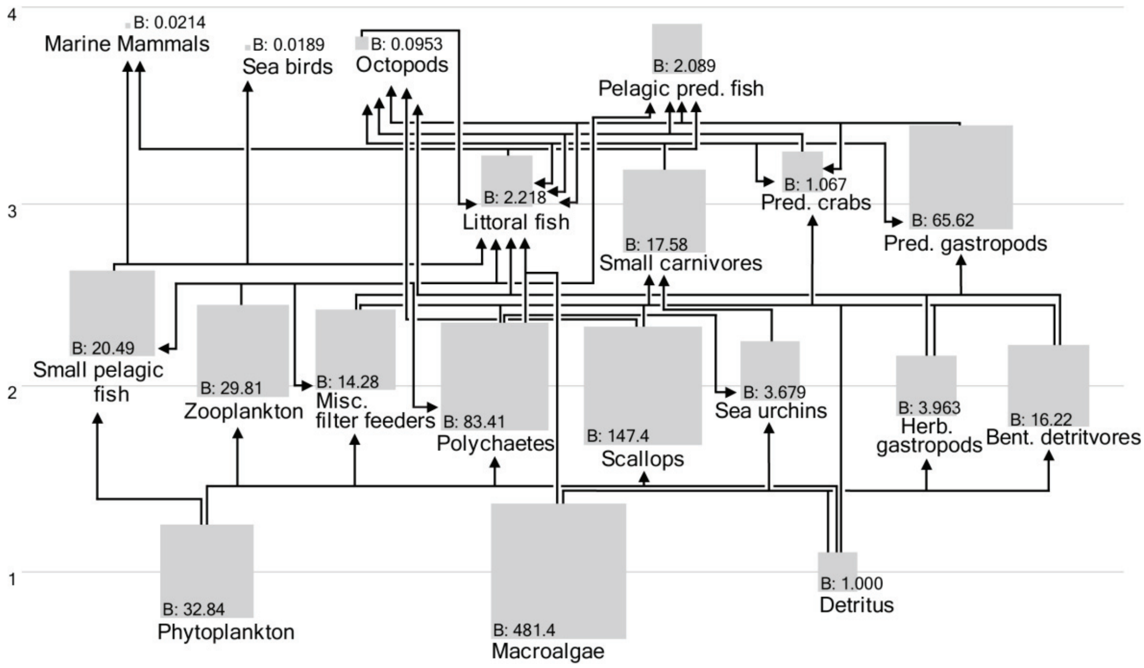

Figure 3.2. *Flow diagram of the trophic structure of the Sechura Bay ecosystem for the initial steady-state model. Each box represents one functional group scaled proportionalto its biomass. Y-axis shows the calculated trophic level (TL) of each functional group. Please consider Table 3.4 for a list of system statistics and flow indices of the Sechura Bay model.*

Table 3.1. *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 efficieny; 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**	-	-	-	-	-	-	-

Table 3.2. *Species comprising the different model compartments for the steady-state model of Sechura Bay.*

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

Table 3.3. *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		0.000			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 3.4. *System statistics and flow indices of the Sechura Bay steady-state model.*

Parameter	Value
Trophic indicators	
Sum of all consumption (t km^{-2} year^{-1})	7335.11 (17.5 %)
Sum of all exports (t km^{-2} year^{-1})	14592.82 (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})	15673.13 (37.5 %)
Total system throughput (TST) (t km^{-2} year^{-1})	41850.65
Fishing	
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
Community energetics	
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
Network indicators	
Finn's cycling index (FCI) (% of TST)	3.15
Ascendency (%)	39.6

3.2.3. 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 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 3.4):

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

Here, $B_{culture}$ represented the scallop biomass for within culture as described above (i.e. 900, 1800, 2700, 3600 t km^{-2} for scenarios1−4, respectively), and $B_{non\text{-}culture}$ was maintained at 147.4 t km^{-2} as for the initial EwE model. $A_{culture}$ and $A_{non\text{-}culture}$ represented the proportion of culture (165/400 km^2) and non-culture (235/400 km^2) areas, respectively. Accordingly, for the four scenarios B_{final} = 458, 829, 1200, and 1572 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 exceedthese levels. The vulnerabilities (υ) in Ecosim, describing the flowsand type of trophic control (bottom-up, intermediate, or top-down) between predator and prey, were set to be proportional to thetrophic level of the functional group (following Cheung et al. 2002, Buchary et al. 2003, Chen et al. 2008):

$$V_i = 0.1515 \times TL_i + 0.0485 \qquad (1)$$

where TL_i represents the trophic level of a functional group as calculated by Ecopath. Vulnerability settings as proposed by the abovementioned 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 & Walters 2004a). A linear conversion was therefore applied to derive at values for υ ranging from 1-Inf (as used for the EwE version 6.4.3, Table 3.5):

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

Result of the individual scenario simulations (including biomasses and ecological network analysis indicators, see Table 3.6) were downloaded from Ecosim and via the Ecosim network analysis form in Ecopath. The development of ecological network analysisindicators over simulation time was compared with initial values.

Table 3.5. *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

Result of the individual scenario simulations (including biomasses and ecological network analysis indicators, see Table 3.6) 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. 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 lowabundance, recruitment of a population may be severely limited (Worm et al. 2009).

Table 3.6. 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 organisation 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 & Taylor 1976, Christensen & Walters 2004b), expressing both species richness and evenness (Ainsworth & 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 & Walters 2004a), in this context the mean TE for TL>2 is used.

3.3 RESULTS

3.3.1. 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 (Figure 3.3). However, 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 eveness, 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 (Figure 3.3), 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.

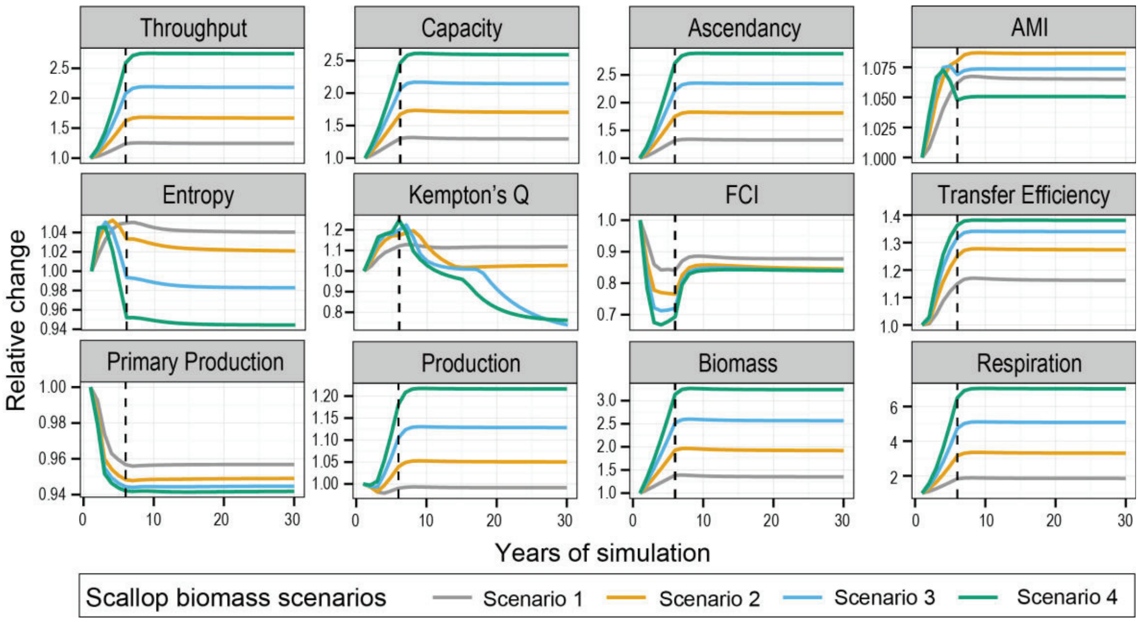

Figure 3.3. *Relative changes in ecological network analysis indices for the scenarios 1 to 4 (increasing scallop biomasses to 458, 829, 1200, and 1572 t km⁻², respectively) when compared with the initial balanced EwE model. The vertical dashed black line indicates the point in time after which scallop biomass levels were held constant (i.e. year 6). AMI = Average mutual information, FCI = Finn's cycling index, PP = Primary Production.*

3.3.2. Effects on other functional groups

The further expansion of scallop culture generally caused total system biomass to increase (Figure 3.4), 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, Figure 3.4, Figure 3.5), 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 (Figure 3.4, Figure 3.5), 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.

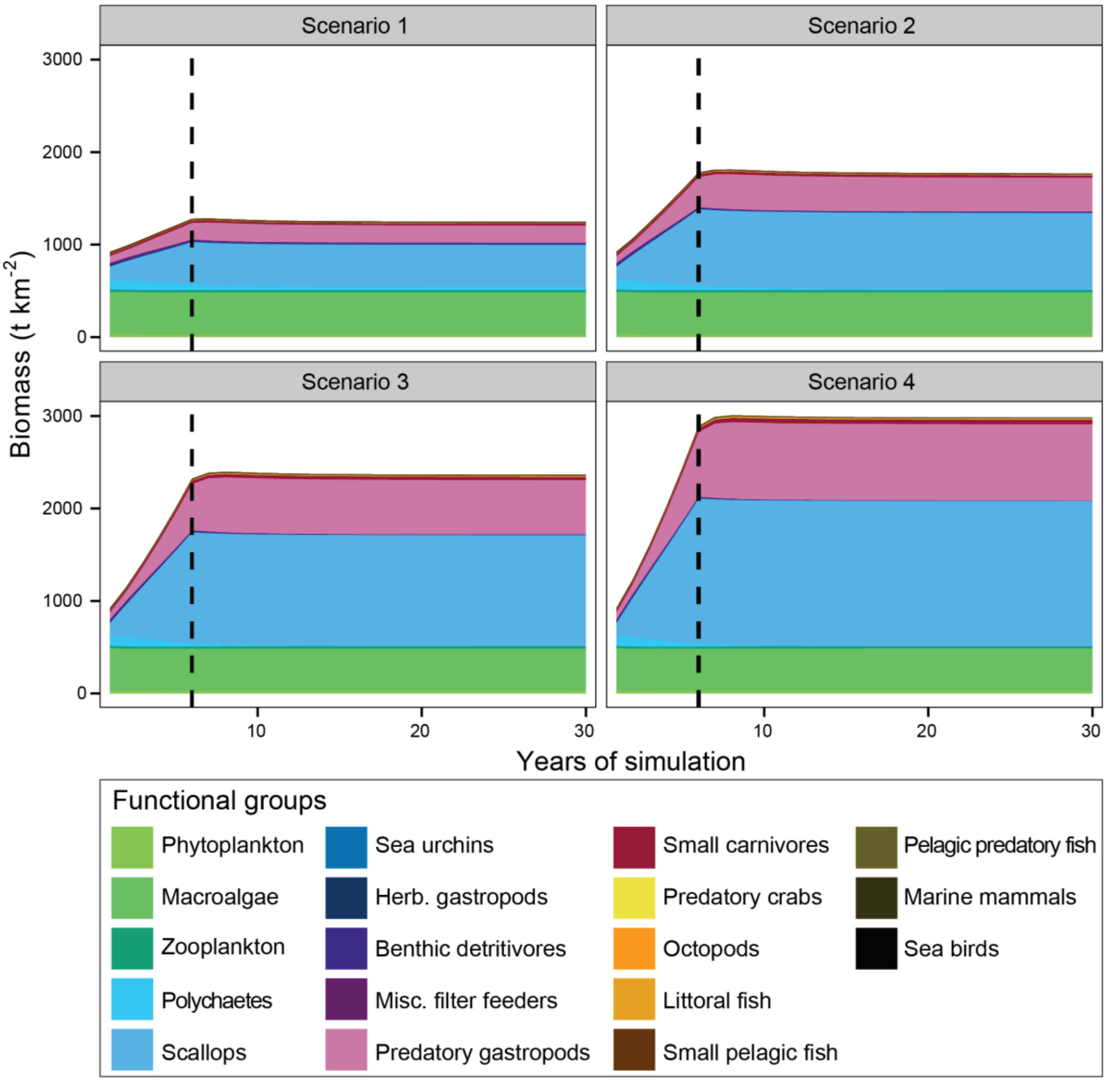

Figure 3.4. *Biomass contribution of each functional group to overall system biomass during simulation time for the scenarios 1 to 4 (increasing scallop biomasses to 458, 829, 1200, and 1572 t km^{-2}, respectively). The vertical dashed black line indicates the point in time after which scallop biomass level was held constant (i.e. year 6).*

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 % (Figure 3.5). 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.

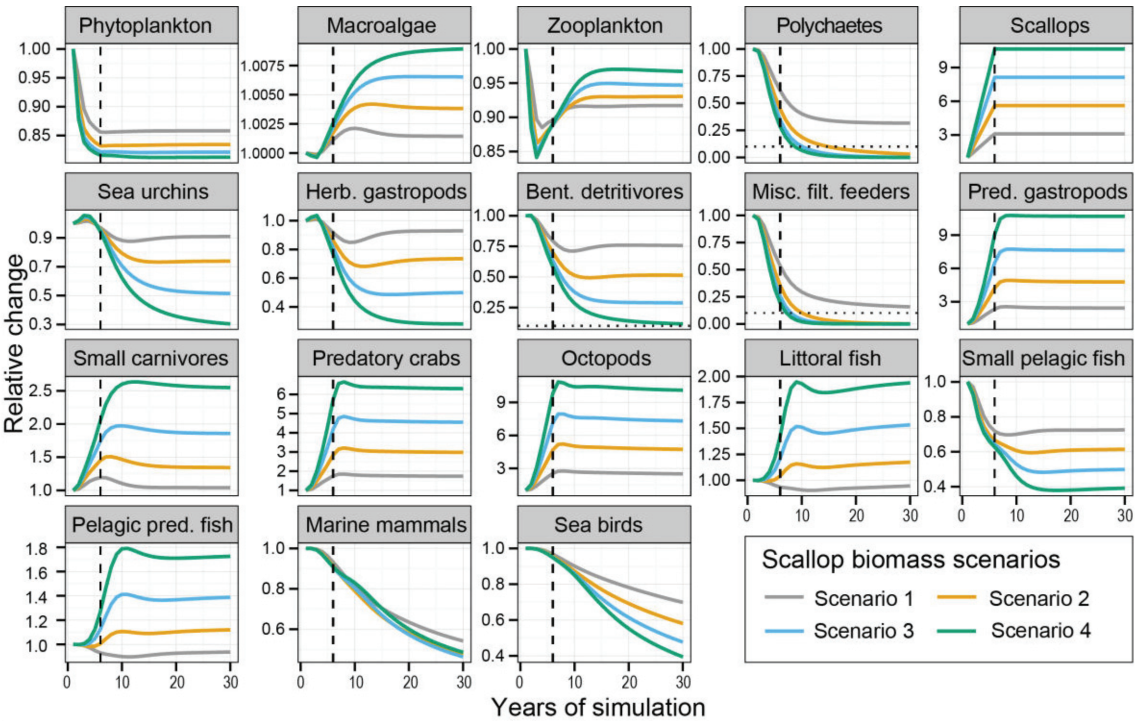

Figure 3.5. *Relative changes in biomass of all functional groups for the scenarios 1 to 4 (increasing scallop biomasses to 458, 829, 1200, and 1572 t km^{-2}, respectively) when compared with the initial balanced EwE model. The vertical dashed black line indicates the point in time after which scallop biomass level was held constant (i.e. year 6).The horizontal dotted line represents the 10 % threshold of initial biomass stocks.*

3.4 DISCUSSION

3.4.1. 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, ascendency, 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 & 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 below 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 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 3.1), 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 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 & Gibbs 2005, Byron et al. 2011b), 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.

3.4.2. 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 3.5), 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 & Gibbs 2005, Byron et al. 2011b). 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. 3.2 and Table 3.3), 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 out-compete 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 pro-viding settling structure, thus habitat, to other organism (Filgueira & Grant 2009), which may increase biodiversity (Dealteris et al. 2004, Tallman & 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. 2006a, 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 & Iglesias 1979), and that the diet of various fish (López-Jamar et al. 1984) as well as crab (Freire & 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.

3.4.3. 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, cur-rent 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., 2016a). 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 10^6 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 & Gibbs 2005, Byron et al. 2011b). 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 & Gibbs 2005, Byron et al. 2011b, 2011c). 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 transferrable 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 ecosistemic 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).

3.4.4. 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 practiced, personal observation), and limiting the scallop grow-out densities to 30 ind. m^{-2}. As a next step towards 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 & Costa-Pierce 2013). As SCC may be an important driver for management (Byron et al. 2011a) it will therefore be addressed in a future publication aiming at the holistic guidance of decision-making in Sechura Bay.

3.4.5. Conclusions

The use of Ecosim proved to be a useful tool for the estimation of ecological carrying capacity (ECC) and ecosystem-based thresh-olds 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 inter-specific 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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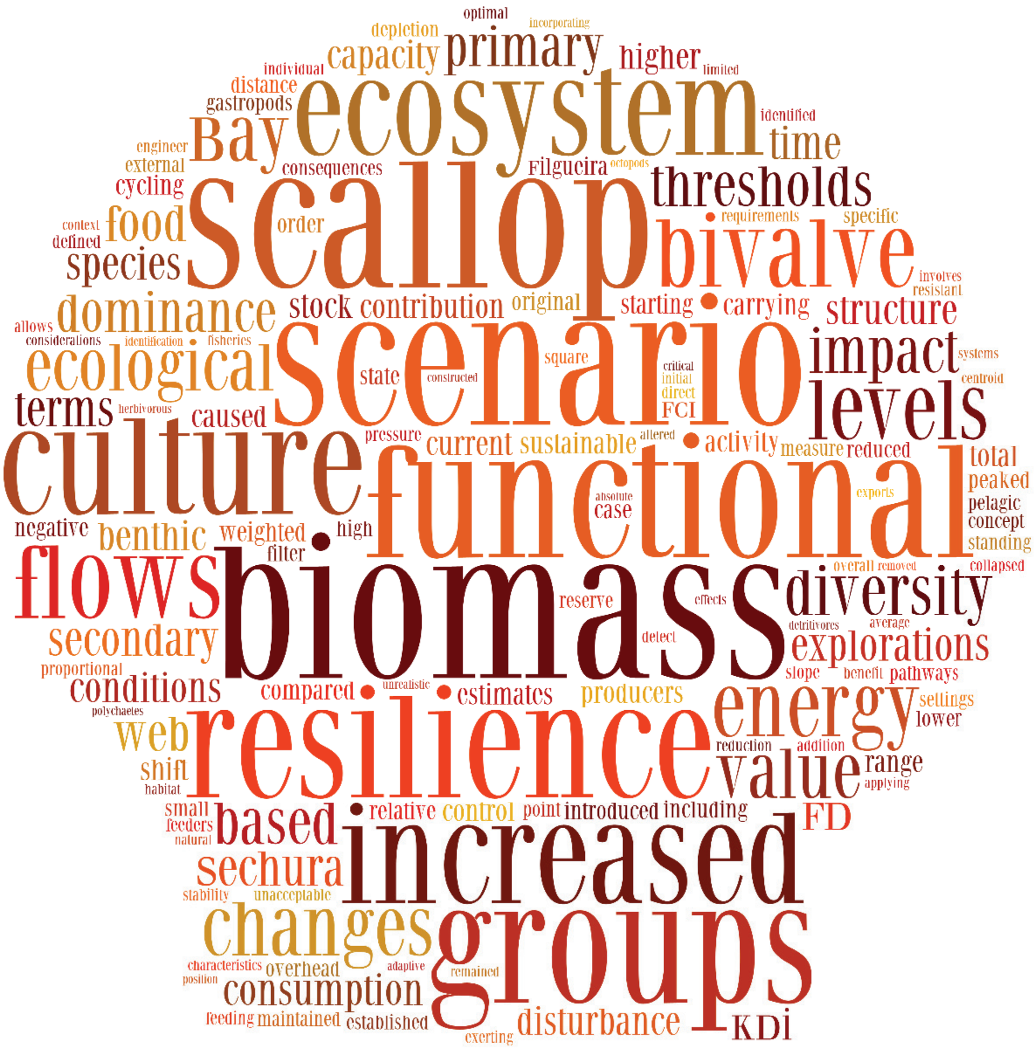
CHAPTER 4

– Adding a resilience measure to an ecosystem approach –



CHAPTER 4
Integrating the concept of resilience into an ecosystem approach to bivalve aquaculture management

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ABSTRACT

Bivalve aquaculture has become increasingly important for marine protein production, alternative to exploiting natural resources. Its further and sustainable development should follow an ecosystem approach, to allow maintaining both biodiversity and ecosystem functioning. The identification of critical thresholds to development remains difficult. The present work aims at combining the calculation of the system's ecological carrying capacity (ECC) with the ecosistemic view of resilience for a bay system exposed to bivalve (scallop) aquaculture. Using a trophic food web model, a step-wise further expansion of culture activities was simulated and the impact on the system was evaluated two-fold: Firstly, a recently developed approach to estimating ECC was used, and secondly, a resilience indicator was calculated which is based on the distribution of consumption flows within the trophic network (sensu Arreguín-Sanchez 2014). Results suggest that a culture expansion beyond present day scale would (a) cause a shift in community composition towards a system dominated by secondary consumers, (b) lead to the loss of system compartments, affecting ecosystem functioning, and (c) result in a decrease in resilience, emphasizing the need to regulate aquaculture activities. The applicability and potential of the here presented method in the context of an ecosystem-based approach to aquaculture is discussed. This work aims at adding to the on-going discussion on sustainable bivalve aquaculture and is expected to help guide aquaculture management.

Keywords: Bivalve aquaculture, resilience, ecological carrying capacity, functional diversity, ecosystem functioning, ecosystem approach to aquaculture, ecosystem-based management

4.1 INTRODUCTION

Bivalves represent important marine resources that have been targeted worldwide for a long time. During the last decades, their production in aquaculture has continuously increased (FAO 2014). Since no external feed input is required, bivalve culture is considered of less impact to the ecosystem than other aquaculture types (e.g. Cranford et al. 2003, Dumbauld et al. 2009), while providing important ecosystem services to humans (Petersen et al. 2015). Bivalves and additionally introduced culture facilities can nevertheless function as "ecosystem engineers" (Jones et al. 1994) by significantly altering environmental conditions such as flows of energy and matter (Dowd 2003, Cranford et al. 2012), depleting phytoplankton standing stocks (Dame and Prins 1998, Newell 2004, Huang et al. 2008, Petersen et al. 2008), or by increasing habitat complexity, providing settlement substrate to other organisms (Inglis et al. 2000, Powers et al. 2007, Ysebaert et al. 2009, Filgueira et al. 2015) and increasing predator densities (Inglis & Gust 2000, D'Amours et al. 2008). Consequently, extensive cultures may lead to changes in ecosystem structure and function, loss of benthic biodiversity, disease outbreaks or even mass mortalities due to oxygen depletion in the benthic layer (e.g. Inglis et al. 2000, Ferreira et al. 2013). In order to avoid these negative ecosystem effects while maintaining sustainable aquaculture production, an ecosystem approach to aquaculture (EAA) should be followed. This approach aims at integrating the aquaculture activity into the wider ecosystem context by promoting its sustainable development in ecological and socio-economic terms (i.e. equity and resilience of the interlinked social and ecological systems) (Soto et al. 2008a). In the context of sustainable development of bivalve aquaculture, the concept of carrying capacity (CC) – defined as the maximum standing stock of the culture species that not yet imposes "unacceptable" impacts in terms of physical, production, ecological, and social considerations – is increasingly important (Inglis et al. 2000, McKindsey et al. 2006a). Many models have been developed to address CC for bivalve culture, ranging from simple index models, farm models, and full ecological (food web) models (Filgueira et al. 2015). The definition of related thresholds depends, however, on individual system characteristics (Cranford et al. 2012), as well as on judgements on what represents an "unacceptable" change (McKindsey 2013). Especially the development of approaches to address ecological and social carrying capacity is still in its infancy (Byron et al. 2011a, Byron & Costa-Pierce 2013), and there are still no common criteria or thresholds, potentially hindering the application of the approach to management (Filgueira et al. 2015). In order to identify unacceptable ecological impacts in accordance with EAA goals, the identification of tipping points of ecological resilience may be recommendable (Filgueira et al. 2015). This requires means for a quantitative measurement of resilience in order to operationalize the concept for management purposes (Standish et al. 2014).

Ecosystem resilience represents the capacity of a system to persist or maintain its function in the presence of exogenous disturbance (Holling 1973, Walker et al. 2004). Measuring and quantifying resilience remains difficult (Standish et al. 2014), and proposed approaches are based on a diverse range of individually defined "stability concepts" that depend on site-specific ecological characteristics (Grimm & Wissel

1997). Accordingly developed indices either use functional diversity as a proxy to resilience (Standish et al. 2014), or are based on the calculation of the energy in reserve of an ecosystem (Arreguín-Sanchez 2014, after Ulanowciz 1986) that may be used to cope with an external disturbance. The definition of acceptable thresholds to changes in resilience nevertheless is crucial, especially for aquaculture systems, in order to ensure long-term sustainable development of the activity without compromising ecosystem health.

The aim of this work is therefore to develop an ecosystem approach to estimating ecological carrying capacity by combining food web structure analysis with ecological resilience for the definition of thresholds for bivalve culture. This will be done for a case study system (Sechura Bay, North Peru), by exploring the behavior of the ecosystem as represented by a mass-balanced trophic model when exposed to intense bivalve (i.e. scallop) aquaculture under different management scenarios (i.e. different bivalve biomasses). Hereby, special emphasis is given to the exploration of thresholds for carrying capacity and resilience of the system. The method as developed for this work and the outcome of these first explorations are expected to advance the on-going research on the important topic of ecological carrying capacity for bivalve culture and to be applicable to similar settings. By providing an ecosystem-based approach for the quantification of resilience, this work substantially contributed to the further development of EAA.

4.2 METHODS

4.2.1 Description of study site

Sechura Bay in the North of Peru (5.6 °S, 80.9 °W) is a relatively large (400 km^2) and shallow bay (with depths <30 m) (Taylor et al. 2008d), located at the northern edge of the Humboldt Current Upwelling system. In the region, artisanal fisheries provide livelihoods to most coastal villagers, and several fish species as well as benthic invertebrates such as the Peruvian bay scallop (*Argopecten purpuratus*) are targeted. Since 2003, the bay has developed into the South American centre for the cultivation of the latter species, with 78.6 % of the country's production originating here, and an export value of about 158 million US$ (in 2013, ADEX 2014). Culture involves ca. 5000 artisanal fishermen that work in cooperatives using delimited bottom areas of the bay. They transfer scallop seed from natural banks into culture areas, with no need for larger net structures or cages. In addition, 20000 persons are further involved in the scallop processing chain, making scallop culture the most important socio-economic activity of the region. Since culture activities have continued to expand ever since 2003, concerns about the long-term sustainability of this activity have driven several studies on culture impact (Kluger et al. 2016b, I. Vivar unpublished data) and the bay's ecological carrying capacity (Kluger et al. 2016a).

4.2.2 Model description

The model of Sechura Bay used for this work was taken from Kluger et al. (2016a, originally based on Taylor et al. 2008d) and describes the present system state (i.e. the year 2010). It is a steady-state food-web model (established via Ecopath with Ecosim (EwE), Christensen & Walters 2004a) comprised of 19 functional groups that are interconnected by trophic links, representing both the benthic and pelagic part of the trophic network: 3 primary producers (including detritus, trophic level (TL) 1), 6 primary consumers (TL 2.0-2.5), 4 secondary consumers (TL 2.6-3.5), and 4 top predators (TL>3.5) (Figure 4.1). 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 (Taylor et al. 2008d, Kluger et al. 2016a).

4.2.3 Scenario simulations using Ecosim

The ecosystem response to scallop bottom culture was explored by analysing 14 different culture scenarios (i.e. different scallop biomasses), the definition of which will for any study system depend on site-specific management considerations. For this, differing amounts of scallop biomasses were introduced over five annual steps and was then held constant until the end of the simulation time of 100 years, i.e. to ensure that the system reached equilibrium in all scenarios (following the approach of Kluger et al. 2016a). The introduced biomasses ranged from pre-culture levels (below present biomass) to the simulation of culture expansion (Table 4.1), with scenario 6 representing current culture levels (i.e. zero change induced). 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 proportional to the trophic level of the functional group (following Cheung et al. 2002, Buchary et al. 2003, Chen et al. 2008, for details see Kluger et al. 2016a).

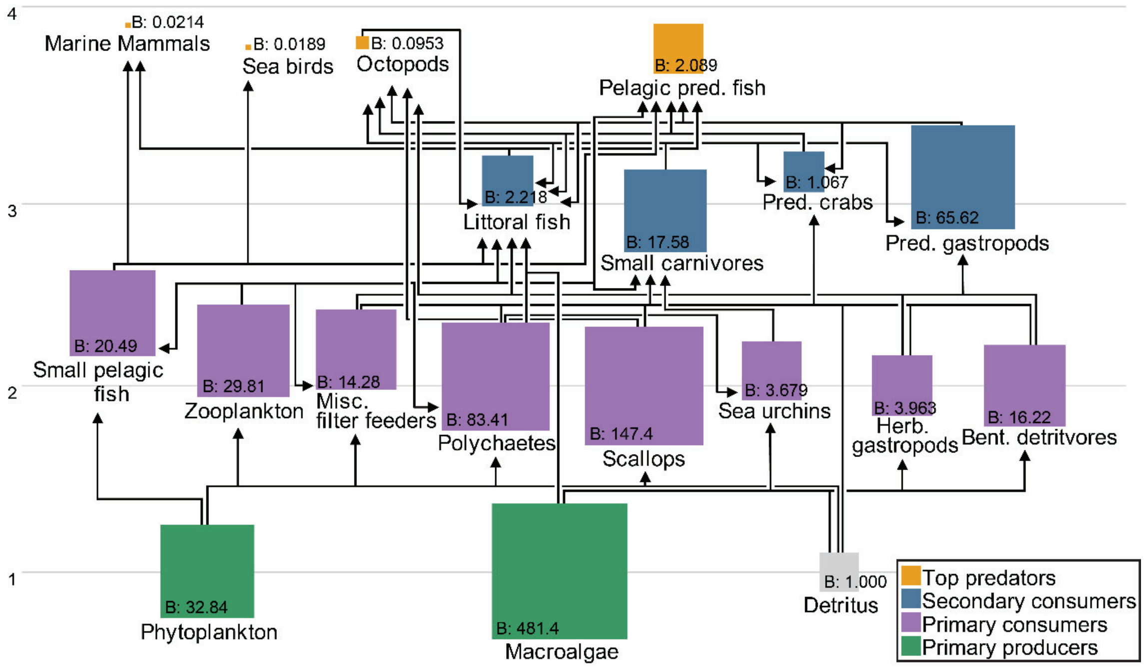

Figure 4.1. *Trophic flow structure of the Sechura Bay model as represented by its 19 functional groups. The area of functional group's boxes are proportional to the group's biomass (B) and the y-axis describes the trophic level (TL) as calculated by the Ecopath with Ecosim (EwE) software. Colours describe trophic groups: primary producers (TL=1.0), primary consumers (TL 2.0-2.5), secondary consumers (TL 2.6-3.5), and top predators (TL>3.5). Please note that this Figure is based on Figure 2 in Kluger et al. (2016a) and describes the original Ecopath model (from Kluger et al. 2016a) that is exposed to different culture scenarios in Ecosim as described in section 2.3 of this work.*

Table 4.1. *Scallop aquaculture scenarios used for the simulations, with number of the scenario (N°), the respectively introduced scallop biomass in t km^{-2} (B), and the reasoning for scenarios used (explanation).*

N°	B	Explanation
1	28	B value from Taylor et al. (2008d) representing pre-culture conditions
2	37	- 75% of present state (=Scenario 6) scallop biomass
3	74	- 50% of present state (=Scenario 6) scallop biomass
4	111	- 25% of present state (=Scenario 6) scallop biomass
5	133.6	B value for which optimum resilience was calculated (see Figure 8) *
6	147	B value of balanced steady-state model representing present state conditions (i.e. the initial steady state model)
7	185	+ 25% of present state (=Scenario 6) scallop biomass
8	222	+ 50% of present state (=Scenario 6) scallop biomass
9	258	+ 75% of present state (=Scenario 6) scallop biomass
10	458	ECC scenario 1 (after Kluger et al. 2016a)
11	829	ECC scenario 2 (after Kluger et al. 2016a)
12	1200	ECC scenario 3 (after Kluger et al. 2016a)
13	1572	ECC scenario 4 (after Kluger et al. 2016a)
14	7369	50x of present (=Scenario 6) scallop biomass

* The scallop biomass resulting in an optimum resilience indicator was identified by forcing the system to scallop biomasses that differed by 0.1 t km^{-2} steps.

4.2.4 Evaluation of systemic impact

<u>4.2.4.1 Shift in species dominance and network indicators</u>

The development of all functional group's biomasses was compared over time. A group was considered extinct, if its biomass felt below 10% of its original standing stock. This threshold was suggested by Kluger et al. (2016a) and follows the definition of a "collapsed stock" in fisheries science (representing a point at which recruitment of a population may be severely limited, Worm et al. 2009). The impact of differing scallop biomasses on the ecosystem was evaluated at year 100 (i.e. when the system had reached equilibrium in all scenarios), comparing the community composition of the trophic web in terms of relative and total biomass contribution of different trophic groups to total system biomass (TSB). In addition, the index of species dominance (KD_i) was calculated for each functional group following Heymans et al. (2014). KD_i helps in identifying dominant functional groups (or structural groups), resulting in high values for groups that have both high biomass proportions and high overall trophic impact (i.e. KD $\geq$ -0.7, Heymans et al. 2014). For all scenarios, the sum of consumption flows on primary producers, scallops, and secondary producers (i.e. all groups with TL > 2.0) was contrasted at year 100, in order to detect changes in the relative importance of primary production to the total consumption flows. In addition, scenarios were compared at year 100 using several ecological network analysis indicators (as presented in Table 4.2) that can be calculated from the trophic flow structure of a Ecopath food web model.

Table 4.2. *Description and explanation of ecological network indicators used for the evaluation of systemic impact resulting from the different simulated scenarios as described in Table 1.*

Indicator	**Description**
Total system throughput (TST)	Sum of all flows in a system (Christensen et al. 2005)
Development capacity (C)	Limit of growth in the system, representing the upper limit to the ascendency (Heymans et al. 2007), scaling the TST to a measure of the information carried by flows (Heymans et al. 2014). C is divided into ascendency and overhead both of which are split up into exports, dissipation, and internal flows (Ulanowicz 2000)
Relative ascendency (A/C)	Organization (maturity) of a food web, being a product of both the growth (TST) and development (AMI) of the system (Ulanowicz 1980, 2004)
Overhead (O/C=1-A/C)	Describing system stability (Christensen 1995), and its strength in reserve to cope with disturbances (Ulanowicz 1986, Heymans et al. 2014)
Internal flow overhead (IFO) /C	Redundancy of the system, measuring the uncertainty associated with the multiplicity of pathways through which biomass may be exchanged within the system (Ulanowicz 1980), or the distribution of energy flow among the pathways within the system (Ulanowicz 2004). Will be high if flows are not concentrated in one or two main pathways but channelled along many alternative pathways for energy (Heymans et al. 2007)
Average mutual information (AMI)	Organization of flows among components (Mageau et al. 1998), with a rise in AMI representing the system to develop further constraints to channel flows along more specific pathways (Ulanowicz & Abarca-Arenas 1997)
Finn's cycling index (FCI)	Percentage of the ecosystem throughput that is recycled, serves as an indicator of stress and structural differences (Finn 1976)

<u>4.2.4.2 Using supply-demand matrices for estimating resilience</u>

The ecosystem response to differing scallop culture biomasses was also explored in terms of its resilience following the approach described in Arreguín-Sanchez (2014). The author proposed to calculate the resilience as an equivalent to the elasticity of cost-benefit analysis (e.g. Hursh 1980) from the consumption matrix in EwE, providing details on all individual trophic flows between the different functional groups. For each functional group, its “demand of energy” is described by the sum of all consumption flows on other functional groups and the “supply of energy” is depicted by the sum of all predation on the functional group itself (Arreguín-Sanchez 2014). The slope of the linear regression from the log–log plot then represents an indicator for redundancy of internal flows, reflecting the energy in reserve of the ecosystem, a concept defined as resilience of the overall system (Ulanowicz 1986, Arreguín-Sanchez 2014). The slope of the regression will be negative, with increasingly negative values for systems with a low resilience. We used the approach presented by Arreguín-Sanchez (2014) for the resilience calculation for our case study and scenarios, but propose to obtain the respective resilience value from a weighted least square regression instead (Figure 4.2A, 4.2B). Using the *lm()* function of the R environment (R version 3.1.2, R Core Team 2014), we applied a weighted least square regression to calculate the slope, incorporating the functional group’s biomasses. The weight – for our case the percentage biomass contribution of each functional group to total system biomass –, determined how much each observation in the data set influenced the final parameter estimates (Guthrie et al. 2012). This allows to give more importance to those groups dominating the system in terms of biomass (Figure 4.2B) and this was done because functional group’s biomass differed widely for the initial EwE model (between 1 and <300 t km^{-2}), with increasing divergences for rising scallop biomasses introduced for the different scenarios. Accordingly, the results of the linear regression differed greatly from the approach applying the weighted least sum of squares regression (Figure 4.2B).

The functional group’s dispersion on the demand-supply plot may be closely aggregated, or widely spread, depending on changes in consumption flows within the ecological network. The distance of functional groups to the food web’s centroid (i.e. the average position of the trophic web) was therefore used here as an indicator of Functional Diversity (FD) of trophic flows. Average Euclidean distances to the food web’s centroid ($Dist_{centr}$) were calculated for all scenarios at year 100 and FD computed as FD = 1 / (1+ $Dist_{centr}$) (Figure 4.2C). For a balanced (i.e. resilient) system, functional groups would always be close together, $Dist_{centr}$ will tend to zero and FD will accordingly approach 1. The higher the functional group’s dispersion, the larger the $Dist_{centr}$ value and consequently the lower the FD indicator. If a species (or functional group) gets reduced (in terms of its biomass) as a result of inter-specific effects (i.e. predation), its position on the supply-demand plot will shift towards the left side. This generates an un-balanced system in which certain trophic groups will be more dominant than others, resulting in an increase of $Dist_{centr}$, reduction of FD, and a decrease in system resilience. The FD indicator is therefore directly proportional to trophic diversity.

The Euclidean distance of any functional group i to the -1 slope was considered as an indicator of how much energy the group has available for metabolism, growth, and reproduction (Figure 4.2D). The value will be 0 if a functional group is demanding as much from the system as it’s supplying and will be positive if it is above the line, and negative if below. If the distances <0, the group would provide more energy to the system than receives from the system (i.e. supply > demand). This unrealistic situation could only be maintained with externalities, e.g. the constant biomass input of this group into the system.

All Figures were constructed using the *ggplot2()* (Wickham 2009) of the R environment (R Core Team 2014).

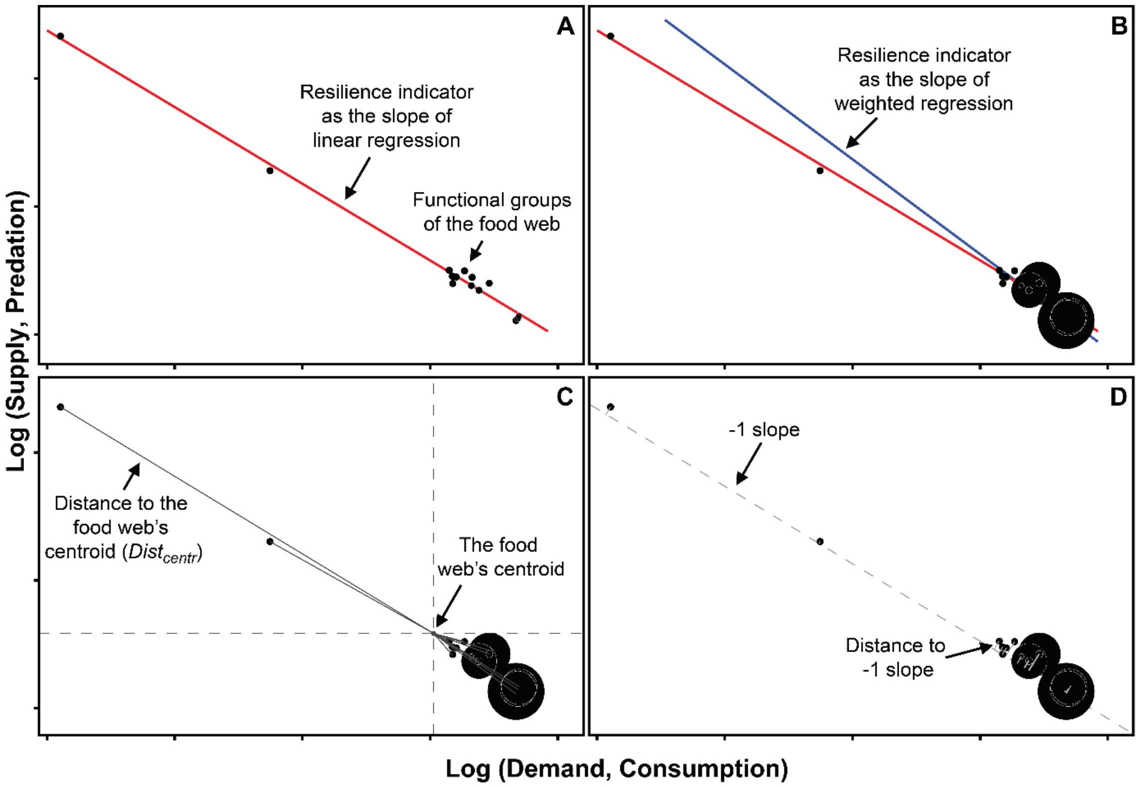

Figure 4.2. *Schematic calculation of the indicators as proposed in this work, using a theoretical system state for which the functional groups (black points) are projected onto the log(supply)-log(demand)-plot: Depicted is the calculation of the resilience indicator as the slope* ***(A)*** *of linear regression (sensu Arreguín-Sanchez 2014) (red line) and* ***(B)*** *weighted least sum of square regression (blue line), where the size of each functional group is scaled proportional to its biomass.* ***(C)*** *The functional diversity (FD) of the food web is calculated as FD = 1 / 1 + ($Dist_{centr}$), with $Dist_{centr}$ representing the average euclidean distance of functional groups to the food web's centroid.* ***(D)*** *The distance of a functional group to the -1 slope describes the energy the has available for metabolism, growth, and reproduction.*

4.3 RESULTS

4.3.1 Trophic web and community composition under aquaculture scenarios

The analysis of the trophic web over simulation time of the different scenarios revealed the important role scallops exert within the Sechura Bay ecosystem. Whenever scallop biomass was increased (i.e. for scenarios 7-14), the bottom-up effect of scallop on its predators (e.g. *predatory gastropods* and *octopods*) became evident, as depicted by a biomass increase of those groups (Figure 4.3). Simultaneously, other primary consumers such as *miscellaneous filter feeders*, *polychaetes*, *herbivorous gastropods*, and *benthic detritivores* decreased in biomass, likely a result of (1) increased predation pressure exerted by secondary consumers benefiting from scallop culture expansion, and (2) inter-specific competition with scallops in the case of *misc. filter feeders*. The decrease in phytoplankton biomass reflects the top-down control scallops impose on their food source. In addition, the propagation of scallop's impact through the food web via indirect trophic links became apparent by the biomass increase in *pelagic predatory fish* due to an increase in respective prey availability (mainly different secondary consumers), while the opposite hold true for the groups of *marine mammals* and *sea birds* (which mainly feed on the small pelagic plankton feeders which are food limited and therefore reduced).

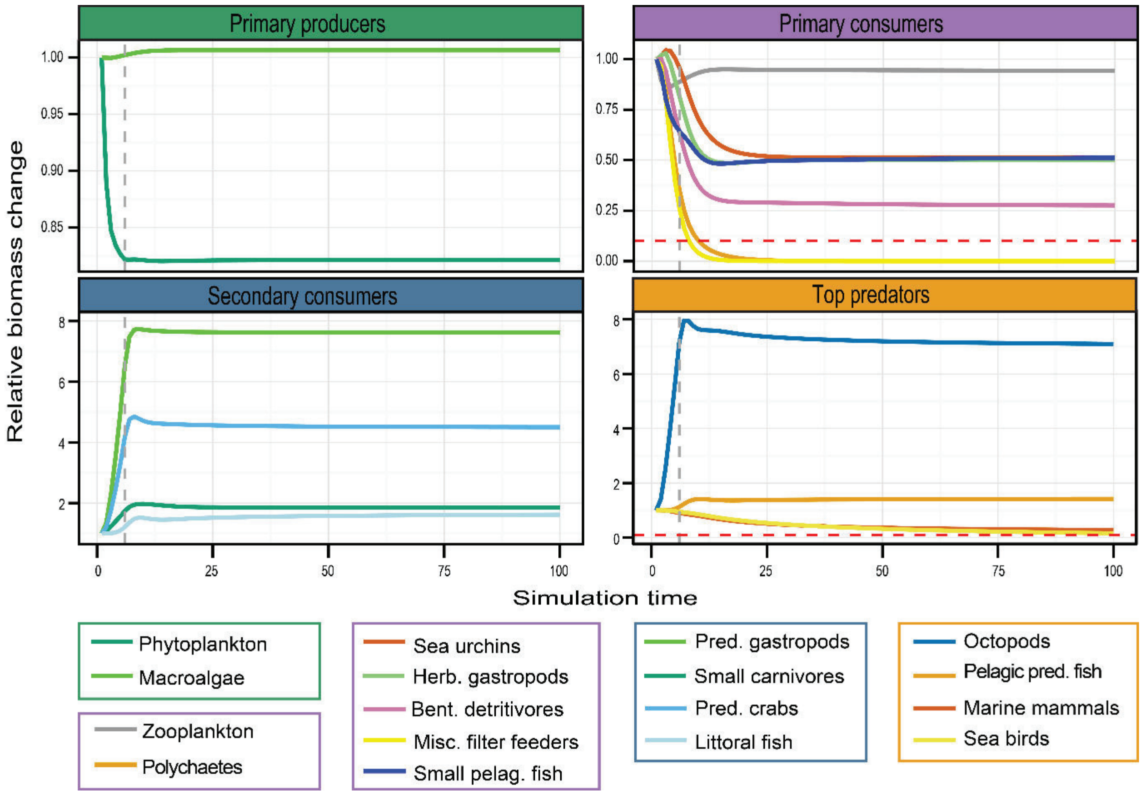

Figure 4.3. *Biomass development of all functional groups (except scallops) over simulation time of 100 years, here shown for scenario 12 (scallop biomass introduced: B=1200 t km*$^{-2}$*), for which lowest resilience was identified (see Figure 4.8A). The vertical dashed line indicates the point in time (i.e. year 6) after which the scallop biomass was held constant. The horizontal red dashed line represents the 10% biomass extinction threshold of initial standing stocks for ecological carrying capacity (ECC) as suggested by Kluger et al. (2016a).*

The expansion of scallop culture to biomasses beyond 458 (i.e. starting from scenario 11) caused several functional groups to fall below 10% of its original standing stock: *polychaetes* and *misc. filter feeders* (both primary consumers (PC)) starting from scenario 11 (in the years 15 and 11, respectively), *benthic detritivores* and *sea birds* (PC and top predators (TP), respectively) in scenario 13 (years 58 and 97, respectively), and *sea urchins*, *herbivorous gastropods*, and *small pelagic fishes* (all PC) in scenario 14 (years 12, 9, and 10, respectively).

The analysis of the biomass contribution of trophic groups at year 100 revealed a shift in community composition, with an increased dominance of secondary consumers (and scallops) when culture expands (Figure 4.4A). Primary producers decreased their percentage contribution to overall system biomass, but their absolute biomass remained stable (Figure 4.4B). Scallops as well as secondary consumers increased in biomass, both in relative and absolute terms (Figure 4A, 4B), causing total system biomass to increase by 15.6 times (comparing scenario 1 and 14; Figure 4.4B). Other primary consumers decreased in biomass, most likely a result of increased predator biomasses. Accordingly, the group of top predators benefitted from the increased prey availability as a result of aquaculture expansion, though their relative contribution to total system's biomass remained low (Figure 4.4A).

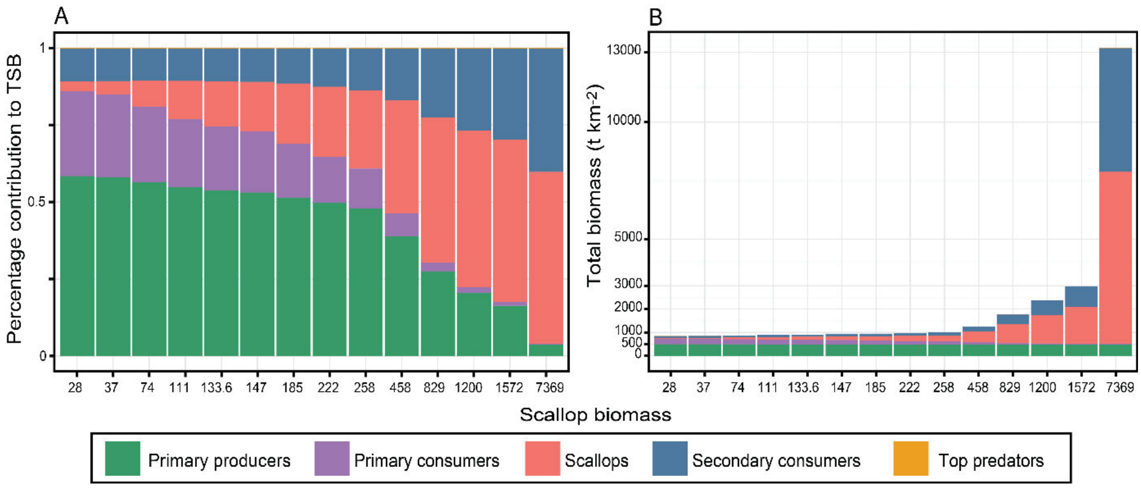

Figure 4.4. *Community composition of systems at year 100 for all scallop biomass scenarios, demonstrating the relative (A) and total (B) biomass contribution of trophic groups to total system biomass (TSB). Colours describe trophic groups: primary producers (TL=1.0), primary consumers (TL 2.0-2.5), secondary consumers (TL 2.6-3.5), and top predators (TL>3.5). Please note that the trophic groups are assemblages of different functional groups of the model as described in Figure 4.1.*

The shift in community composition with increasing scallop biomass was also apparent from the analysis of the group's dominance index KD_i (Figure 4.5). The group of *macroalgae*, representing a dominant functional group (with $KD_i \geq -0.7$) up to a scallop biomass of 829 t km^{-2} (i.e. for scenarios 1 to 11), was of decreasing importance with increasing culture pressure. At the same time, all primary consumers decreased in their KD_i value. Scallops, on the contrary, increased in importance, with KD_i values of $\geq$ -0.7 starting from B=458 t km^{-2} (scenario 10). Those secondary consumers directly preying on scallops (i.e. *predatory gastropods* and *predatory crabs*) increased in KD_i, with *pred. gastropods* passing the threshold of -0.7 at a scallop biomass of

7369 t km^{-2} (in scenario 14). All top predators decreased in KD$_i$, except for octopods, likely a result of the direct trophic link of this group to scallops.

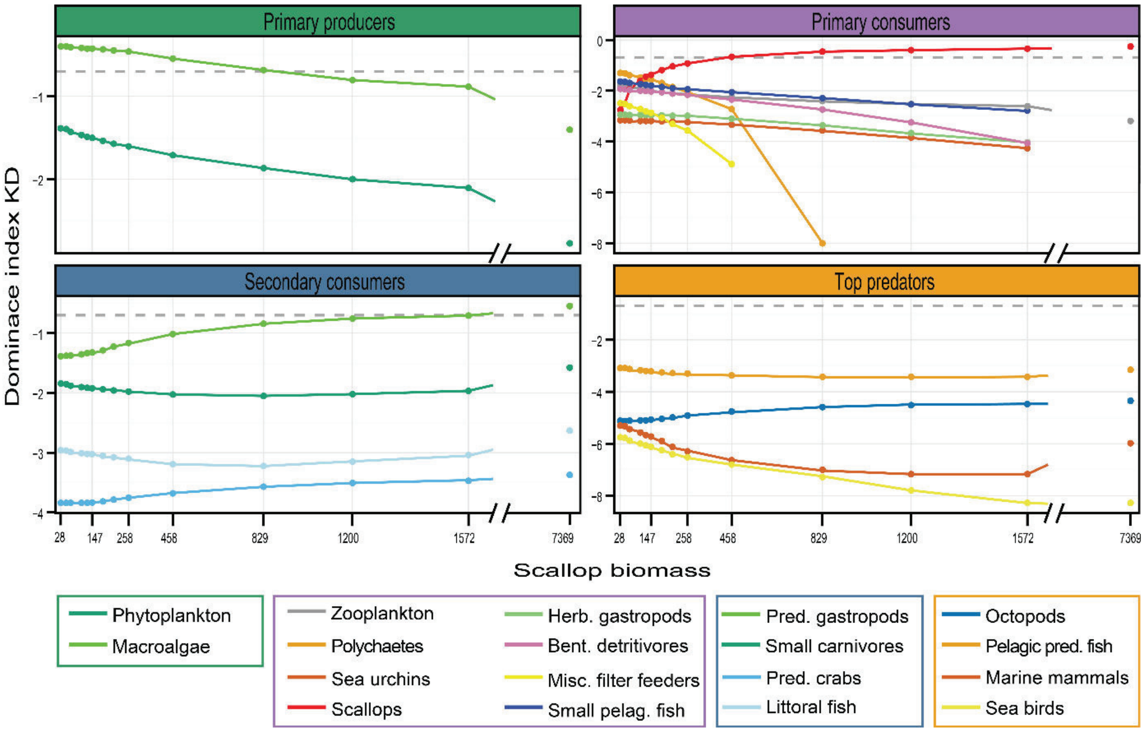

Figure 4.5. *Index of dominance of species (KD$_i$) for all functional groups in the different scallop biomass scenarios at year 100. The dashed grey line represents the -0.7 threshold that defines a dominant functional group (i.e. groups with both high biomass proportions and high overall trophic impact, after Heymans et al. 2014).*

The changes in community composition were also reflected in a change of dominant flows within the network. Consumption on primary producers (i.e. on functional groups of TL 1) was about 86-87 % of total consumption for scenarios with a scallop biomass of up to 258 t km^{-2} (i.e. for scenarios 1-9), but decreased thereafter (Figure 4.6A). Simultaneously, the relative contribution of secondary consumption (i.e. on groups of TL > 2.0, including consumption on scallops) increased starting from a scallop biomass of 458 t km^{-2} (scenario 10), likely reflecting the increasing dominance of scallops (as indicated by the increased KD$_i$ valu, Figure 4.5).

The reduction of cycling within the system as indicated by a decrease in the Finn's cycling index (FCI) suggested the system to become more stressed and less resistant with increasing scallop biomasses (Figure 4.6B). Decreasing scallop biomass to below current levels (scenarios 1-5) resulted in higher FCI values, while the simulation of culture expansion (scenarios 6-14) caused the indicator to decrease. The FCI value decreased from 3.26 % at scallop biomass of 28 t km^{-2} (scenario 1) to 2.29 % at B=7369 t km^{-2} (scenario 14), with current conditions (B=147 t km^{-2}, scenario 6) at 2.9 %.

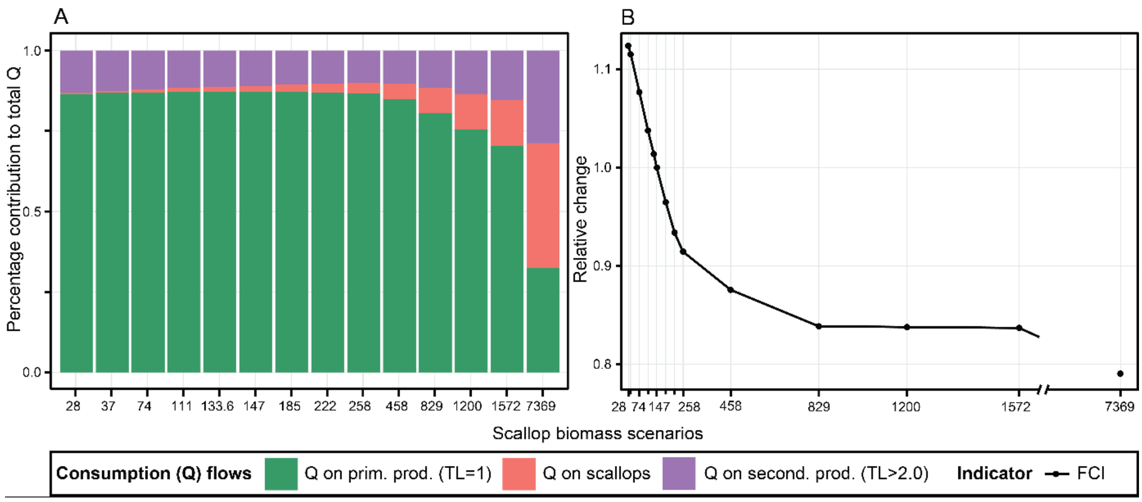

FIgure 4.6. *(A) Composition of consumption flows for all scallop biomass scenarios at year 100, describing the relative consumption of the system compartments on primary producers, scallops, and secondary producers, respectively. Please note that - in contrast to Figure 1 - secondary producers include here all functional groups with TL > 2.0. (B) Relative change of the Finn's cycling index (FCI) for all culture scenarios at year 100.*

4.3.2 Resilience estimates

An example for the development of resilience over simulation time is displayed in Figure 4.7. Table 4.3 summarizes resilience calculations using the weighted least square regression approach. Please consider the supplementary material for a complete list of all supply-demand information used for resilience calculations (Supplemental Table S4.1), the results of resilience calculation from linear and weighted least square (weighted) regression (Suppl. Table S4.2), the latter being plotted for all culture scenarios in Supplemental Figure S4.1.

Table 4.3. *Model output estimating the resilience calculated using the here proposed approach (i.e. with weighted least sum of square regression), indicating the scenario number (N°), the respectively introduced scallop biomass (B, in t km^{-2}), the slope (representing resilience), intercept, adjusted sums of squares (Adj. R^2), the F-value, and the p-value. For a description of scenarios please consider Table 4.1. A comparison of resilience calculation from linear and weighted least square regression can be found in the supplementary material (Supplemental Table S4.2).*

Scenario	B	slope/resilience	intercept	Adj. R^2	F	p
1	28	-0.825	0.130	0.474	12.73	0.0039
2	37	-0.775	0.035	0.424	10.58	0.0069
3	74	-0.607	-0.303	0.310	6.839	0.0226
4	111	-0.530	-0.468	0.306	6.722	0.0235
5	133.6	-0.519	-0.496	0.342	7.76	0.0165
6	147	-0.522	-0.493	0.373	8.745	0.0120
7	185	-0.558	-0.430	0.487	13.36	0.0033
8	222	-0.621	-0.310	0.611	21.39	0.0006
9	258	-0.680	-0.195	0.693	30.36	0.0001
10	458	-0.861	0.170	0.839	68.61	< 0.0001
11	829	-1.165	0.916	0.921	152.7	< 0.0001
12	1200	-1.241	1.040	0.848	73.7	< 0.0001
13	1572	-1.101	0.481	0.635	23.64	0.0004
14	7369	-0.062	-3.824	-0.075	0.088	0.7714

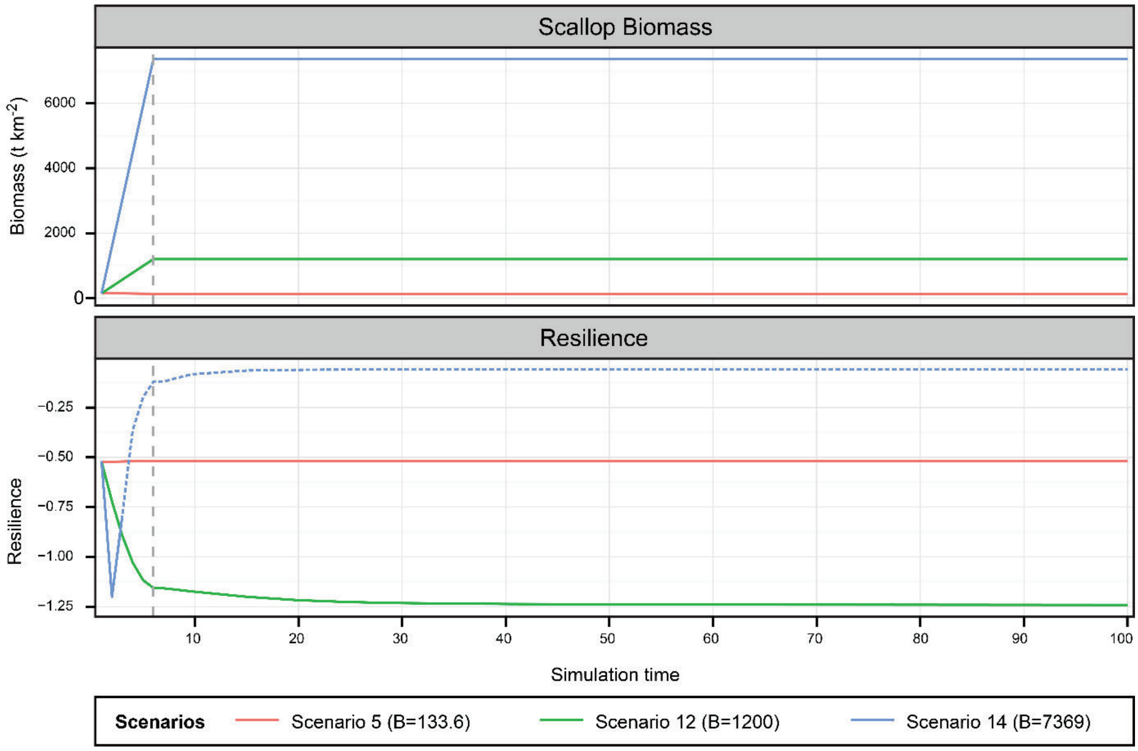

Figure 4.7. *Development of scallop biomass (as introduced into the system) and resilience (obtained from the slope of the weighted least sum of squares regression) over simulation time of 100 years, exemplary displayed for scenarios 5, 12, and 14 (introduced scallop biomass 133.6, 1200, and 7369 t km^{-2}, respectively). The vertical dashed grey line represents the point after which scallop biomass was maintained at the same level (i.e. year 6). For scenario 14, the resilience calculation was not statistically significant (p>0.05) starting from year 4, indicated by a dashed line in the graph (compare Table 4.3).*

The point of optimum resilience was identified by applying small scale scallop biomass changes (see small panel in Figure 4.8A): B=133.6 t km^{-2}, representing 91% of current scallop biomass in the system (i.e. of scenario 6). Scenarios introducing lower and higher scallop biomass (scenarios 1-4 and 6-13, respectively) resulted in lower resilience values when compared to this peak. Only for a scallop biomass of 7369 t km^{-2} (scenario 14), resilience was higher than for the scenario of optimum resilience, but the regression calculation ceased to be significant (p=0.77) starting in year 4 of the simulation (Table 4.3, Figure 4.7), shedding doubt on whether this approach is useful for a skewed situation like this, i.e. of unrealistic amounts of scallop biomass that would never be observed under natural conditions. Consequently, this scenario was excluded from further discussions, but nevertheless, the fact that the method identified this scenarios as a potential outlier (p > 0.05) serves as an argument for the usefulness of the method presented in this work.

The overhead (O/C) of the ecosystem, reflecting the ecosystem's strength in reserve to cope with disturbances (Ulanowicz 1986), peaked at a scallop biomass level of 185 t km^{-2} (scenario 7) and decreased thereafter (Figure 4.8B). The internal flow overhead (IFO, redundancy) gradually decreased with culture expansion. These results suggested a change in system structure, with a decreasing number of pathways being available for energy to be channelled from primary producers to top predators (Heymans et al. 2014), reflecting the increasing dominance of scallops (and its predators) in the system.

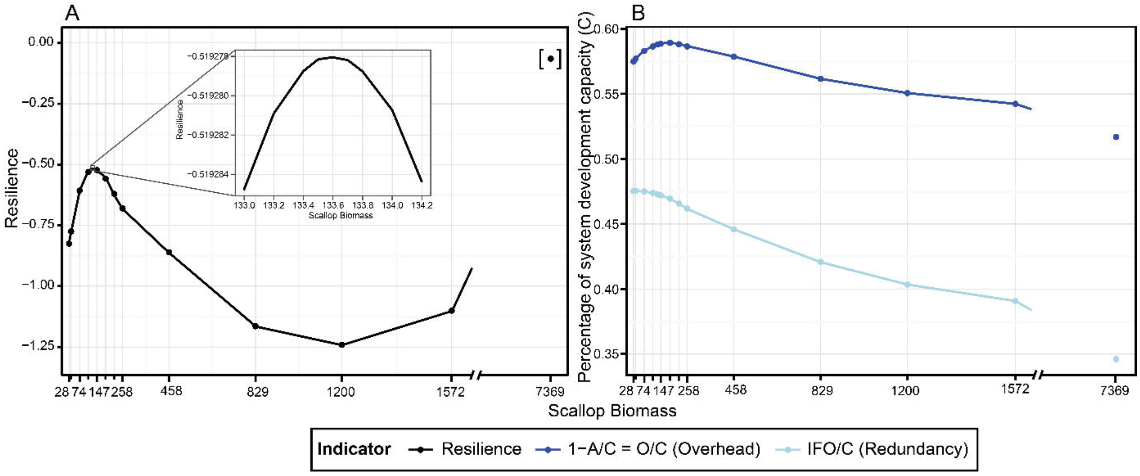

Figure 4.8. *Resilience as calculated from the slope of log(Supply)-log(Demand) plots (see Figure 2 for a description) using weighted least sum of squares regression (A), and overhead (O/C) and redundancy (IFO/C) of flows (B) for the different scallop biomass scenarios at year 100 of simulation.*

Functional Diversity (FD) of trophic flows (calculated based on the average distance of functional groups to the trophic web's centroid) was highest for a scallop biomass of 185 t km^{-2} (scenario 7) and decreased thereafter (Figure 4.9A). The distance to the -1 slope (representing the amount of energy available for growth and reproduction) decreased for scallops with increased culture pressure until reaching negative values at B=1572 t km^{-2} (scenario 13) (Figure 4.9B), likely a result of increased predation pressure by other functional groups. The Q/B value of scallops (describing the consumption per unit biomass, Figure 4.9B) decreased, reflecting a decrease in feeding rates due to increased scallop biomasses and decreased food availability.

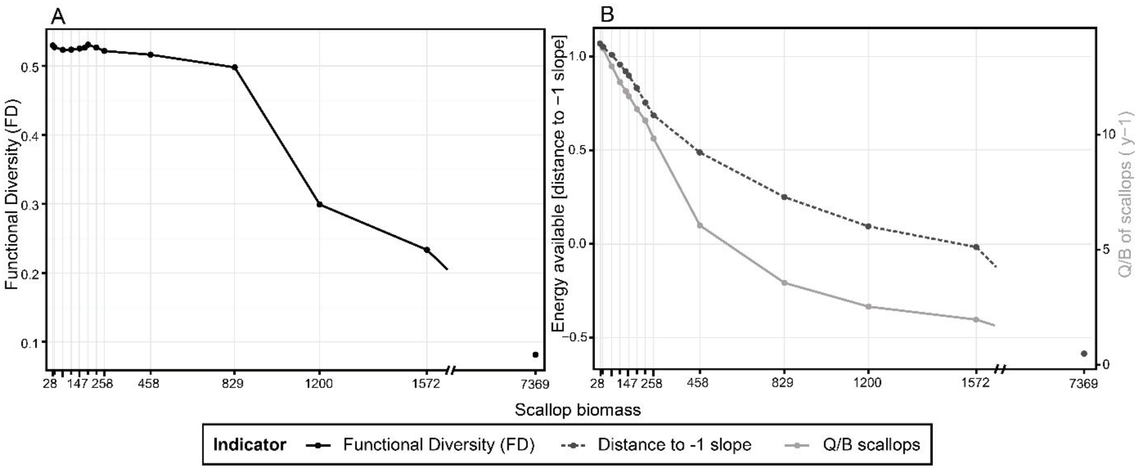

Figure 4.9. *(A) Indicator of Functional Diversity (FD), calculated as FD = 1 / (1+Dist$_{centr}$), with Dist$_{centr}$ as the Euclidean distances to the food web's centroid; (B) scallop distance to -1 slope (describing the energy available for metabolism, growth, and reproduction), and Q/B values (representing the consumption per unit biomass) for scallops for the different culture scenarios at year 100 of simulation.*

4.4 DISCUSSION

The aim of this work was to develop a measure for a holistic ecological carrying capacity estimate for bivalve aquaculture, which also takes into account system resilience. Sechura Bay, which recently developed into the centre of Latin American scallop production, served here as a case study, for which pertinent estimates are timely since the pressure for further enhancement of the culture activities are high. The results indicate that the approach be useful for other (bivalve) aquaculture settings.

4.4.1 Community changes under aquaculture scenarios

With a further culture expansion scallops increasingly control the energy fluxes from lower to higher trophic levels by exerting a top-down control on phytoplankton and a bottom-up impact on its predators. Our simulations suggest secondary consumers to increasingly dominate system biomass and energy flow if current culture levels were to be increased. Accordingly, the KD_i increases for scallops and its direct predators (such as *predatory gastropods* and *octopods*), while it declines for other primary consumers including *misc. filter feeders* and *benthic detritivores*. Beyond scallop biomass levels of 458 t km^{-2} (scenario 10), several groups are expected to collapse (i.e. fall below 10% of original biomass), indicating the potential threat of bivalve aquaculture to biodiversity and ecosystem functioning of the Sechura Bay ecosystem. Bivalve culture has been described to enhance biodiversity (e.g. Dealteris et al. 2004, Tallman & Forrester 2007) by providing habitat and settling substrate, thus functioning as ecosystem engineer (after Jones et al. 1994), but may also negatively impact a community if the introduced ecosystem engineer threatens niches within the ecosystem (Jones et al. 1997), e.g. by outcompeting other bivalve species and filter feeding organisms such as zooplankton (Gibbs 2004, Newell 2004). The potential loss in biodiversity is important, since it is known to correlate with ecosystem functioning and resilience, as well as the generation of ecosystem services (Chapin et al. 1997, Duffy 2002). Functional groups of an ecosystem usually behave differently in the face of environmental change, and species that initially may seem redundant or unnecessary for the community may become critical for the regeneration and re-organization of the system after a disturbance or disruption (Bellwood et al. 2004, Folke 2006). The maintenance of biodiversity thus allows enhancing the system's adaptive capacity in the event of an external disturbance. For the Sechura Bay system, bottom-reared scallops are predicted to out-compete other benthic primary consumers (such as other bivalves) with as yet unforeseeable consequences on the ecosystem level. With aquaculture reducing this species pool, the system is therefore expected to become less resilient, which is confirmed by our theoretical explorations.

An aquaculture-induced change in species composition and trophic flow structure is likely to lead to altered ecosystem functions, eventually causing a decrease in ecosystem resilience. A measure of system resilience is therefore imperative when aiming at the sustainable development of aquaculture in the context of an ecosystem-based approach to aquaculture (after Soto et al. 2008a). Under conditions of high diversity of trophic interactions, many alternative pathways of energy are possible, potentially adding to ecosystem stability (MacArthur 1955, Johnson et al. 1996) and resilience. This is where the here proposed indicator of functional diversity may be included for further analysis. As shown in the present work, the introduction of bivalve biomass and culture facilities modifies trophic flow structures within the system, and induces a shift from pelagic to benthic consumers, as has also been found in other bivalve culture settings (Leguerrier et al. 2004). Under conditions of a further scallop culture expansion the system's trophic pathways are altered, with secondary producers becoming increasingly important (Figure 4.6A). The observed decrease in the internal flow overhead (Figure 4.8B) reflects a decrease in the number of pathways available for the transfer of energy from lower to higher trophic levels, likely a result of the biomass increase of scallops and their predators, and the decrease in biodiversity. This shift may represent a potential threat for system stability/resilience since this secondary production is maintained only through the external input of scallop seed into the system, and an interruption of this supply (for whatever reason) would thus greatly destabilize the system.

4.4.2 Functional changes under aquaculture scenarios

A shift in community composition as a result of culture expansion also induces changes in ecosystem functioning, as revealed by the ecological network analysis indicators.

System cycling continuously decreases with culture expansion (Figure 6B), suggesting the system to become more stressed and less mature (Odum 1969). This result agrees with the study of Díaz López (2011), who described the establishment of a fin-fish aquaculture to result in a reduced system cycling (i.e. reduced FCI value). Similarly, Kluger et al. (2016a) compared two system states of Sechura Bay (representing pre-culture and culture conditions, respectively), and proved that the introduction of scallop culture caused a decrease in system cycling. These results may (partly) be explained by the continuously increasing biomass removal through harvest that is considered as exports in Ecopath (Christensen et al. 2005), reducing the biomass available for recycling. Since system cycling represents an important feedback mechanism contributing to system stability (Odum 1969) and the resistance towards perturbations (DeAngelis et al. 1978, DeAngelis 1980, DeAngelis et al. 1989), its reduction reflects a direct impact of aquaculture on system's functioning.

Similarly to the FCI, the internal flow overhead (IFO), describing the distribution of energy flow among pathways within the system (Ulanowicz 2004), continuously decreases with scallop expansion (Figure 4.8B), reflecting a decrease in ecosystem resilience (Heymans 2003) and suggesting the flows to be increasingly concentrated in a smaller number of pathways (Heymans et al. 2007). This goes in line with the increasing dominance of scallops (Figure 4.5), controlling the energy flow from the first to higher trophic levels by exerting a top-down control on their prey while enhancing its predators' biomass. At the same time, IFO decreases in its proportion to O/C (Supplemental Table S4.3) which is – similar to the development of the FCI indicator as described above – likely due to an increasing proportion of system biomass that is removed via harvest rates (considered as exports in Ecopath).

While FCI and IFO continuously decrease with culture expansion, the system's overhead (O/C), reflecting the ecosystems strength in reserve (Ulanowicz 1986; Heymans et al. 2014) to cope with disturbances (Ulanowicz, 2004), peaked at a scallop biomass of 185 t km^{-2} (scenario 7), but decreased thereafter (Figure 4.8B). This matches the development of the functional diversity (FD), which also peaked at this biomass (scenario 7, Figure 4.9A), and decreased subsequently. The results of FD development suggest an increasing group dispersion with increasing scallop biomasses, reflecting the shift in dominance of functional (and trophic) groups. The depletion of functional groups (starting from a scallop biomass of 829 t km^{-2}, i.e. scenario 11) resulted in a further drop in FD, demonstrating the potential of this indicator to detect changes in overall biodiversity. This is important, as diversity of functional groups is crucial for maintaining ecosystem resilience (Walker 1992, Walker et al. 1999), and the likelihood of a regime shift may be increased if functional groups were removed from the system (Folke et al. 2004).

Our explorations for Sechura Bay may suggest that the system state of scenario 7 (B=185 t km^{-2}) is the most resistant (i.e. less likely to be changed) towards any further disturbance such as natural environmental variability or anthropogenic stressors, making it an attractive scenario for management considerations. At the same time, it is evident that a further aquaculture expansion would lead to the reduction of available energy to potentially cope with a future disturbance.

In contrast to the other indicators, the resilience measure as developed for this work peaked at a scallop biomass of 133.6 t km^{-2} (scenario 5), which is close but still below the value of 147 t km^{-2}, which represents current culture conditions (i.e. scenario 6, Figure 4.8A). This suggests that current biomasses may have already passed optimal levels in terms of resilience. At even higher biomass levels, resilience decreases further, with an increasing number of functional groups getting depleted when scallop biomass exceeds 458 t km^{-2} (i.e. starting from scenario 11, B=829 t km^{-2}). This is in accordance with literature describing resilience to be inversely related to biodiversity (e.g. Chapin et al. 1997).

Interestingly, our results suggest that the introduction of bivalve (scallop) biomass into pre-culture conditions (scenario 1) triggers a concomitant increase in resilience until the maximum is observed (scenario 5, Figure 4.8A). Accordingly, ecosystem services associated to bivalve culture may not only include eutrophication control through nutrient uptake during water filtering (e.g. Petersen et al. 2014), habitat provision (Inglis et al. 2000, Powers et al. 2007, Ysebaert et al. 2009, Filgueira et al. 2015), delivery of food to higher trophic level organisms and humans (D'Amours et al. 2008, Petersen et al. 2014) – bivalve culture may also enhance ecosystem resilience (this work).

While our explorations reveal that the Sechura Bay system has a narrow range of optimum resilience (considering the small differences found in optimal culture densities for the different indicators calculated), the trophic structure does not disintegrate immediately if a culture scenario differs from this optimum range. In fact, as mentioned above, functional diversity may still be increased surpassing optimum resilience. This suggests that a slight increase in scallop biomass from the present reference level (i.e. scenario 6) would still benefit the system, likely due to the increase in total biomass (providing the system with energy in the reserve, i.e. increasing O/C). At this point (B=185 t km^{-2}, scenario 7), the community composition (respectively functional group's biomasses) changed only to a small extend, i.e. by less than 10 % when compared to biomass values of the initial EwE model (as represented by scenario 6). A further increase in scallop biomass, however, would lead to drastic consequences in terms of community composition, energy cycling, and the system's availability to cope with future disturbances.

4.4.3 Using supply-demand matrices for an ecosystem-based approach to aquaculture management

The here proposed indicators proved useful in detecting changes as induced by culture expansion on the ecosystem level. In a recent study, Kluger et al. (2016a) established 458 t km^{-2} (scenario 10) as the critical threshold for aquaculture expansion in Sechura Bay. This level represents the maximum biomass that not yet causes any other (functional) group to fall below 10 % of its original standing stock, a concept which is based on the definition of a "collapsed" stock from fisheries science (after Worm et al. 2009). The results of the present study, however, propose to manage the system at a significantly lower scallop biomass since the system's overhead and the functional diversity indicator both peaked at 185 t km^{-2} (scenario 7) and the optimum for the resilience indicator peaked at 133.6 t km^{-2} (scenario 5). The EEC threshold and the functional diversity and resilience *optima* allow the definition of a "safe operating space" (Tett et al. 2011). Threshold and *optima* can be combined to construct a simple risk analysis to guide aquaculture management (Figure 4.10). For this case study, management may use, for example, the range of scenarios between pre-culture conditions (28 t km^{-2}, scenario 1) and optimum resilience (133.6 t km^{-2}, scenario 5) without major risks. Risk would increase with stocking biomass from this *optimum* onwards until the system collapses when the ECC threshold is reached. Since present state (i.e. 147.4 t km^{-2}, scenario 6) is between resilience and functional diversity *optima*, the simulations do not suggest significant impacts on the functioning of Sechura Bay. A further increase of aquaculture activities would not cause direct impacts either, however, the risk of aquaculture impact on the system level, e.g. with respect to the system's resistance towards future perturbations such as the climate phenomena El Niño-Southern Oscillation (ENSO), would increase.

The definition of precautionary thresholds for tipping points of resilience is of high importance in order to optimize ecosystem functioning (Filgueira et al. 2015), and resilience-based management should consider resilience across different scales, incorporating intra- and interspecific diversity (Cavers & Cottrell 2015). Based on the explorations presented in this work, we propose the following step-wise ecosystem approach towards sustainable bivalve aquaculture: (1) establish a steady-state food web model representing all important functional groups of the system of concern; (2) define potential culture scenarios based on individual site specific characteristics and management requirements, and estimate ECC as the maximum culture intensity that does not yet cause other functional groups to get depleted (following Kluger et al. 2016a); (3) explore ecosystem functioning through estimates of resilience and functional diversity (based on supply-demand matrices) as done in this work for the different culture scenarios and establish a range of optimal management options.

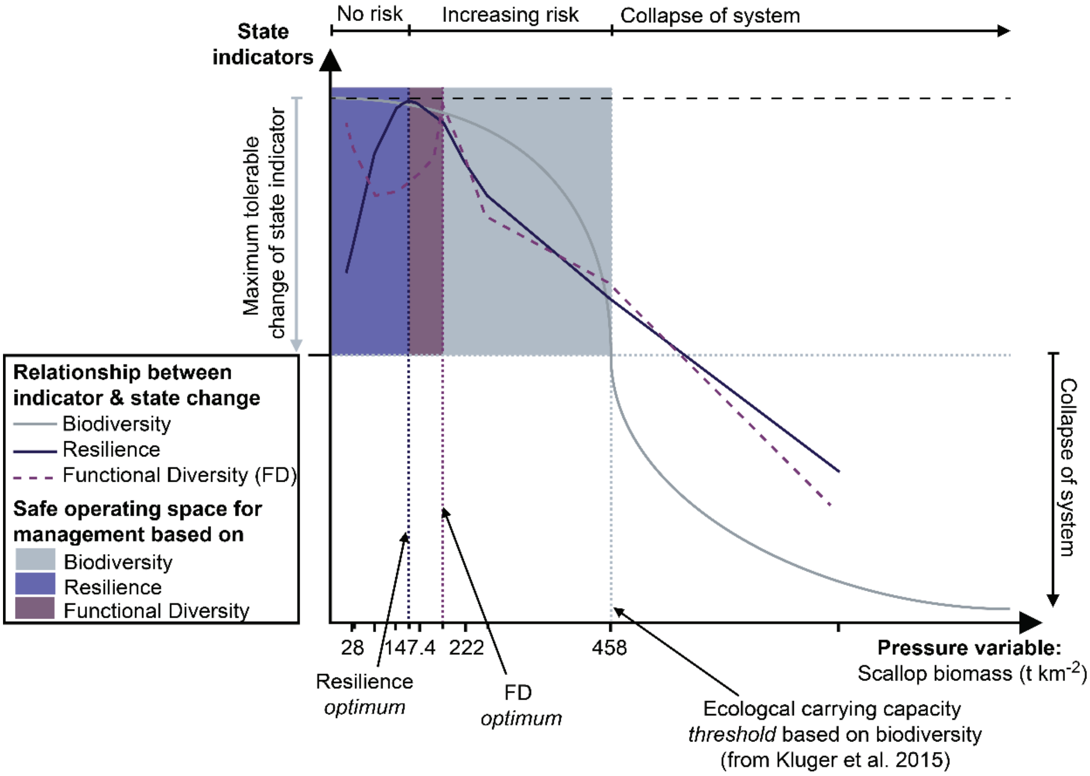

FIgure 4.10. Conceptual framework of carrying capacity (CC, following Figure 1 in Tett et al. (2011), originally based on McKindsey et al. (2006a)), describing the behavior of any state indicator in relation to the pressure variable (i.e. bivalve biomass). The CC is defined as the maximum level of the pressure variable not yet causing the state variable to exceed the maximum tolerable change. This range has to be defined for any state variable on a site-specific, but objective basis. Using measurable state indicators, e.g. based on biodiversity (Kluger et al. 2016a), resilience and functional diversity of trophic flows (this work), a safe operating space for management of scallop aquaculture levels may be established considering optimum ranges of all state indicators.

While the ECC as proposed by Kluger et al. (2016a) allows for the identification of "unacceptable" limits to the maintenance of the system's species pool, the proposed resilience indicator based on the supply-demand matrix summarizes all trophic flows, providing an integrated ecosystem-based view that is absolutely critical for ecosystem-based management. The step-wise approach outlined above needs to go hand in hand with an adaptive management that involves a continuous monitoring of the system to detect changes and that should be flexible enough to adapt both methods and respective thresholds.

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CHAPTER 5

– A socio-ecological analysis of scallop aquaculture in Sechura –

CHAPTER 5
The rise of Sechura Bay (Peru) as the centre for scallop aquaculture in Latin America – a socio-ecological analysis

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ABSTRACT

The present study describes the development of scallop aquaculture in Latin American over the past three decades, particularly focusing on the Peruvian scallop *Argopecten purpuratus*, which has been harvested along the Peruvian and Chilean coastline for more than 60 years. Following the strong El Niño event of 1983/84, both countries experienced a boom in scallop fisheries, but catches dropped as soon as the environmental conditions normalized. In Peru, bottom culture activities were first designed to sustain catches, while Chilean aquaculture followed technologies developed in Japan based on suspended scallop culture and the production of scallop seed in hatcheries. Aquaculture production took off in Chile, dominating the Latin American scallop market in the 1990's, with Peruvian production remaining small until the early 2000's. Since then, Peruvian production has dramatically increased, with one particular location being responsible for the majority of production: Sechura Bay located in Northern Peru. This work represents an analysis of the ecological and socio-economic factors that have allowed this shift in production to take place and describes the unique factors that have resulted in Sechura Bay's dominance. Discussing the obstacles to achieve long-term sustainability of aquaculture operations in this particular bay, we also consider transferrable lessons learned for other coastal settings exposed to bivalve aquaculture.

Keywords: Socio-ecological analysis, sustainable resource use, bivalve aquaculture, Peruvian bay scallop *Argopecten purpuratus*

5.1 INTRODUCTION

5.1.1 Historical trends of scallop production worldwide and in Latin America

Bivalves have been of importance to coastal human livelihoods for almost two centuries and until today continue to sustain socio-economically important fisheries worldwide. Representing high-value species, pectinid scallops – in particular the genera *Pecten*, *Placopecten*, *Patinopecten*, *Aequipecten*, *Argopecten*, and *Chlamys* – have been intensively exploited in the last decades (Medina et al. 2007). In the course of time, many fisheries experienced an intensification of effort due to favourable market prices, followed by a collapse due to over-exploitation and the lack of a regulatory framework (e.g. *Argopecten purpuratus* in Chile (Stotz 2000); *A. ventricosus* in Mexico (Félix-Pico et al. 1997) and Panama (Medina et al. 2007); *Aequipecten techuelchus* in Argentina (Ciocco et al. 2006); *Euvola ziczac* in Brazil (Pezzuto & Borzone 2004); *Placopecten magellanicus*, east coast of USA (Murawski et al. 2000); *Patinopecten caurinus*, west coast of USA (Kruse et al. 2005)). In some cases, successfully implemented management strategies, such as temporal area closures (*P. magellanicus*, east coast of USA (Hart & Rago 2006), *Patinopecten yessoensis* in Japan (Uki 2006)), catch quotas (*Pecten fumatus* in Australia (Dredge 2006)) and stock enhancement /sea ranching (*P. yessoensis* in Japan (Uki 2006) allowed for the recovery of natural populations, but in many places, aquaculture has overtaken wild fisheries in terms of production.

World scallop production increased 7-fold from 370,150 tons in 1980 to 2,600,000 tons in 2013 (FAO 2016, Figure 5.1a). A steadily increasing proportion of production originates from aquaculture (71.1 % in 2013, FAO 2016), with China, Japan, and Peru representing the most important aquaculture producers (contributing 86.9 %, 9.1 %, and 3.7 %, respectively, FAO 2016). First attempts of suspended (hanging) culture of *P. yessoensis* and *Chlamys farreri* date back to the late 1960's in Japan (Uki 2006) and 1970's in China (Xiao et al. 2005), respectively, and was also first used for *A. purpuratus* culture in Chile in the 1980's (Disalvo et al. 1984).

In Latin America, three scallop species are currently of commercial importance (Figure 5.2): Along the Atlantic coast, the Patagonian scallop *Zygochlamys patagonica* occurs from Uruguay to Argentina and is mainly harvested in Argentina (FAO 2016). Along the Pacific coast, the Pacific calico scallop *Argopecten ventricosus* (occurring from Mexico to Ecuador) and the Peruvian bay scallop *A. purpuratus* (from Peru to Chile) are the main target species, with the first species currently being exclusively produced in Mexico. The latter species *A. purpuratus* is found on sandy bottoms in shallow bays (with depth <30 m, Wolff et al. 2007) from Paita (5° S) in North Peru to Valparaíso (33 °S) in Chile (Sanzana 1978, Alamo and Valdivieso 1987, both cited in Peña 2001), and this species' production currently accounts for 68.4 % of total scallop production from Latin America (in 2013, FAO 2016, Figure 5.2). Peru and Chile both are bordering the Humboldt Current System (HCS), characterized by almost continuous up-welling of cold and nutrient-rich water to surface layers (Tarazona & Arntz 2001), creating a highly productive system. As filter-feeding organisms, scallops mainly feed on phytoplankton and therefore benefit from the high food availability. In both countries, a diving scallop fishery has been an open access activity since the 1950s, and international export (mainly to France and the USA) was launched in the 1980s, following the great natural increase in scallop population caused by the El Niño event 1983/84 (Wolff 1987, Stotz 2000). More recently, the extractive fishery has been almost entirely replaced by aquaculture, with Chile dominating the market (of this species) in the 1990's (Figure 5.1b). But, while Chilean production stagnated in the 2000's and recently decreased (Figure 5.1b), scallop production in Peru has steadily increased in the last two decades, establishing itself as the third most important scallop aquaculture producer worldwide (in 2013, FAO 2016). Of particular importance to Peruvian production is Sechura Bay, located in the north of the country. At present, 80 % of Peruvian production originates from Sechura (in 2013, Mendo et al. 2016), implying that 50 % of total Latin American scallop production is obtained from this bay alone.

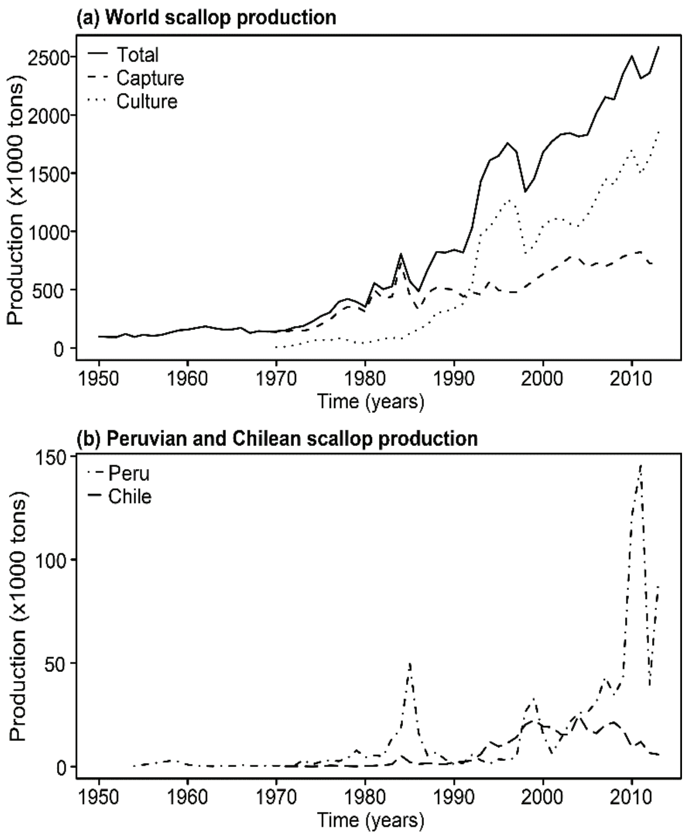

Figure 5.1. *(a) Annual world scallop production for the period of 1950 to 2013, demonstrating production from fisheries ("Capture"), aquaculture ("Culture), and the sum of both ("Total"). (b) Annual scallop production for Peru and Chile for the same period, showing the sum of aquaculture and capture production. Source of data: FAO 2016.*

5.1.2 Context and focus of study

The analysis presented here was conducted as part of the bilateral SASCA project ("Sustainability Analysis of Scallop Culture in Sechura bay (Peru)", www.sascaperu.wordpress.com), which aimed at (i) evaluating the impact of scallop bottom culture in Sechura Bay on benthic communities and energy flow structure (Meyer 2014, Kluger et al. 2016b, I. Vivar, unpublished data), (ii) estimating the bay's long-term ecological carrying capacity for scallop production (Kluger et al. 2016a); and (iii) analyzing the socio-economic conditions for its sustainability (Bossier 2015, L. Sanchez & L.C. Kluger, unpublished data; this work).

The work is an analysis of the factors that allowed scallop *A. purpuratus* production in Sechura Bay (5 °S) to expand, while in other regions – particularly Chile – production decreased. For this, the historical background of scallop production in the region is revised to provide a complete picture of respective developments (section 3). Special emphasis is given to the comparison of Sechura Bay to the historically most important bays for scallop production in Chile (Tongoy Bay, 30 °S) and Peru (Independence Bay, Pisco, 14 °S) (see Figure 5.2 for exact locations). As a second step, ecological, socio-economic, and societal conditions of the two countries (i.e. the aforementioned bays) are analyzed and contrasted in order to understand differences in development (section 4). The potential of Sechura Bay to maintain long-term sustainable scallop production, as well as the transferability of the development to other locations is discussed (section 5). It is hypothesized that Sechura Bay benefits from the combination of favourable environmental conditions with socio-economic aspects related to the type of aquaculture used, as well as societal factors providing a unique setting for the successful development.

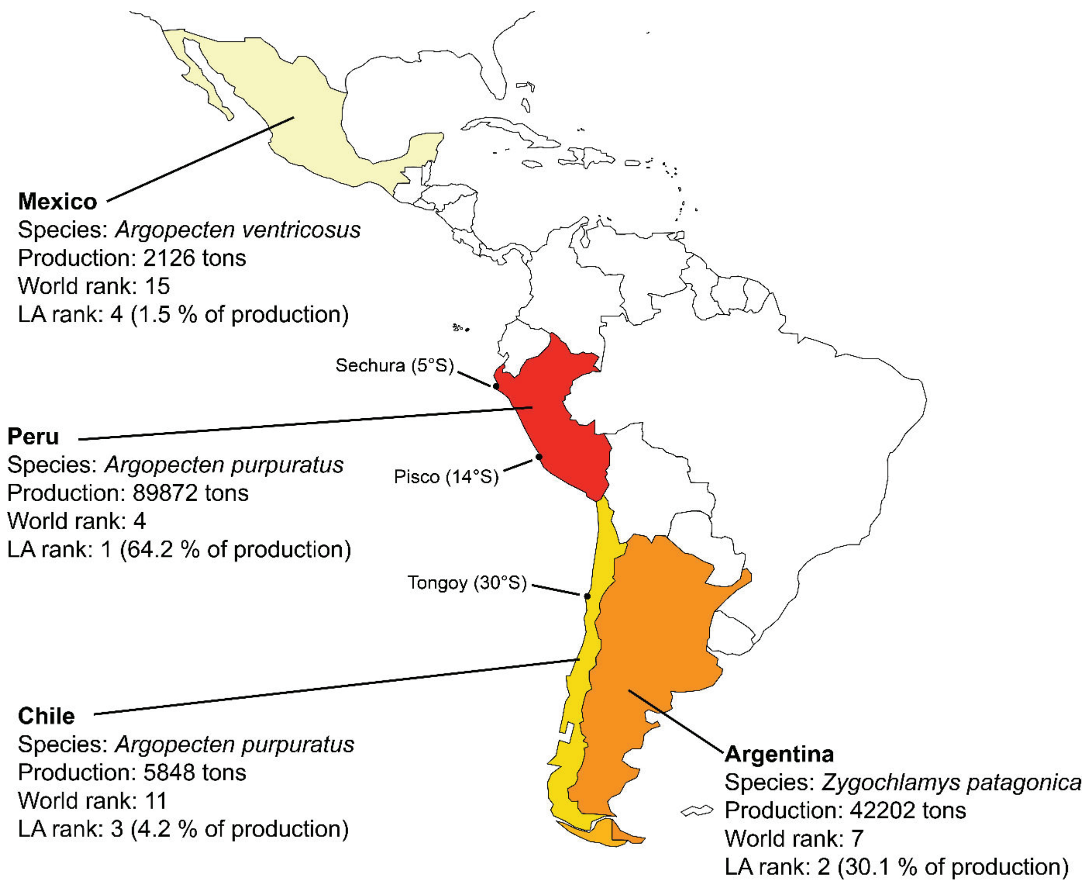

Figure 5.2. *Latin American scallop producing countries in 2013. The rank of each country considering total world ("World rank") and total Latin American scallop production ("LA rank") is given, as well as the percentage contribution of each country to total Latin American production. Specific locations of importance for historical* A. purpuratus *production are also indicated (Sechura, Pisco, and Tongoy). Source of data: FAO 2016 (sum of aquaculture and capture production).*

5.2 METHODOLOGICAL APPROACH

All available literature, including peer-reviewed and grey-literature publications, were reviewed for the description of the historical development of scallop culture in Latin America, focusing on the species *A. purpuratus* produced in the region of Peru and Chile (section 3). Environmental and socio-economic conditions of the different locations were compared basd on available literature and data as obtained in the SASCA project.

5.2.1 Analysis of societal factors using social network analysis (SNA)

The analysis of societal factors was based on a stakeholder analysis that was conducted in Sechura Bay from April to July 2013. This involved the conduction of semi-structured, open-ended surveys and structured interviews with different groups involved in the scallop production chain, as well as participatory observations of activities (L. Sanchez & L.C. Kluger, unpublished data) with the aim to identify the different groups involved, as well as their interactions. In this context, stakeholder were defined as all "interested" actors (i.e. (groups of) persons or organizations) (Schmeer 1999) directly or indirectly (monetarily) involved in the scallop cultures and associated activities (e.g. processing, transport). For the Chilean case, stakeholder mapping was based on literature (e.g. Brand et al. 2016) and expert knowledge (W. Stotz, pers. comm.).

Then, social network analysis (SNA) was applied to visualize and analyze patterns of the relationships and interactions in the social system (Prell 2012). For this analytical approach all relevant actors (either discrete individuals, corporate, or collective social units) are integrated as *nodes* and their respective interactions are described as linkages (defining channels for the transfer of resources) as *edges* (Wasserman & Faust 1994). Based on the stakeholder analysis, interviews, and literature research as mentioned above, a qualitative social network was constructed for the Sechura and Tongoy Bay case studies. The network boundary was chosen to include all actors (nodes) holding functional roles for the scallop aquaculture business. Qualitative links (edges) were established as to represent a flow of money or resource (i.e. scallop biomass), with the arrow head indicating the direction of flow: The unidirectional flow from actor A to B is described as A → B, and the bidirectional exchange of energy (scallop biomass) for money between actor C and D is depicted as C ↔ D (Figure 5.4). Analysis was conducted with the software Gephi (version 0.8, https://gephi.org). For both networks, the nodal degree was calculated for each actor, defined as the total number of adjacent (i.e. incoming and outgoing) links (Wasserman & Faust 1994). Though easy to compute, the nodal degree represents a highly informative indicator, describing the "activity" of individual actors in a network (Wasserman & Faust 1994), and is used here to identify important social actors in the network. Average nodal degree was used to compare the two networks.

5.3 HISTORICAL CONTEXT OF SCALLOP PRODUCTION – FROM AN OPEN-ACCESS FISHERY TO A REGULATED AQUACULTURE ACTIVITY

This section describes the development of *A. purpuratus* production in Chile and Peru that mainly took off after the strong El Niño (EN) 1983/84. The market was initially dominated by Chile, producing *Argopecten purpuratus* in suspended culture, while Peruvian production was low. In the early 2000's, a shift in dominance occurred, following the discovery of important scallop banks in the Peruvian North (Sechura Bay). Since then, scallop bottom cultures (i.e. sea ranching) have successfully established in this location, with production volumes currently dominating the market of this species.

5.3.1 The rise of suspended scallop culture in Chile

In Chile, the Peruvian bay scallop *A. purpuratus* was traditionally targeted by extractive artisanal fisheries, hand-collecting individuals while using hookah diving (Brand et al. 2016) have been targeted since 1945. Until 1980, catches remained at relatively low levels (< 500 tons year^{-1}), being destined only for the national market (Stotz 2000), with scallop populations being several times fished to such low levels that the fishery had to be closed (Brand et al. 2016). The development of an active policy to supply international markets with fishery products in the late 1970's caused a sharp increase in production after 1981 (Avendaño & Cantillánez 1996, Stotz 2000), additionally favoured by a good recruitment event in 1983 caused by the EN phenomena 1983/84 (Stotz 2000). During EN years, the intensity of upwelling along the Pacific coastline decreases, and water temperatures increase by almost 10 °C (for the 1983 event, Tarazona & Arntz 2001). This affects scallop population dynamics by increased recruitment rates (Wolff 1988), increased growth rate of juveniles (Wolff 1985), and accelerated maturation (Wolff 1988, Wolff et al. 2007). Landings peaked in 1984 (Figure 5.1b), but decreased afterwards despite effort regulations (Avendaño 1993, as cited in Cantillánez et al. 2007). The Chilean scallop fishery was completely closed in 1988, after different fisheries management regulations (e.g. minimum sizes of capture, closed fisheries seasons) failed to be successfully implemented (Stotz 2000). Still, natural banks did not show recovery thereafter, which was partially attributed to on-going (illegal) harvesting of the resource due to its high value (Stotz & González 1997). Among bay scallop species, *A. purpuratus* is somewhat exceptional for its relative large size and fast growth rate (Wolff 1987, Wolff & Mendo 2000), obtaining higher international prices (10.1 US\$ kg^{-1}) when compared to other scallop species such as *Pecten maximus* (6.9 US\$ kg^{-1}) or *Patinopecten yessoensis* (1.5 US\$ kg^{-1}) (all values for 2013, FAO 2016). The combination of higher international demands and decreasing national scallop production in the post-EN-period has created a great incentive for the advancement of culture possibilities of the species (Stotz 2000).

Chilean researchers were the first to complete the larval cycle of *A. purpuratus* in laboratory (Disalvo et al. 1984) and managed to develop suspended scallop culture using Japanese technology and expertise in Tongoy Bay (30 °S) in the 1980s (e.g. Disalvo et al. 1984, Parada 2010, Brand et al. 2016). Suspended culture involved the use of seed scallops collected from the environment (through the use of artificial seed collectors) or produced in hatcheries and their grow-out in pearl nets and lantern nets (for sizes >10 mm) deployed near the water surface. Since the fisheries ban in 1988, scallop production in Chile was primarily based on aquaculture (SUBPESCA 1995a, as cited in Avendaño & Cantillánez 1997). However, in the early years scallop seed was extracted from natural banks, illegally depleting natural populations (Wolff & Alarcón 1993, Avendaño & Cantillánez 1996). This practice nevertheless allowed the development of the scallop industry, since high initial investment costs would otherwise have slowed down its development (Stotz 2000). A dozen small companies were formed including former scallop fishers seeking an alternative to their previous – now restricted – activity. Total aquaculture production of *A. purpuratus* developed rapidly, with Tongoy Bay being the main producer (in 1991, Stotz & González 1997). Until the mid-1990s, the sector kept growing and Chile established itself as the third (after China and Japan) most important scallop producing country (in terms of aquaculture production) (FAO 2016). Production fluctuated, however, reaching its maximum in 2004 (Figure 5.1b), and particularly declined in the second half of the 2000's.

The industry is currently undergoing severe economic problems, and the main reason for this decline was attributed to declining international prices and the competition from countries with low production costs and massive production – such as Peru (Ulloa 2011). In addition, external factors have complicated Chilean scallop production. Since 2011, two tsunamis (March 2011, September 2015) and one big storm (August 2015) repeatedly disturbed the business, causing the loss of natural collected seed in artificial collectors (in the case of the 2011 tsunami, Brand et al. 2016) and destroying cultures (longlines, lantern nets, boats and rafts with machinery stranding and (W. Stotz, pers. comm.). These events represented the last blow to an already struggling business, forcing more and more companies to close (Brand et al. 2016, W. Stotz, pers. comm.). While at the beginning of the 2000's, 27 Chilean companies were dedicated to *A. purpuratus* production, only four are currently operating (in Tongoy, W. Stotz, pers. comm.), with some Chilean scallop producers even moving their businesses to Peru (Brand et al. 2016). From originally 12 hatcheries (in 2001, Abarca 2001, as cited in Brand et al. 2016), an increasing number was closed when the market problems arose, until the last closed in 2015 (W. Stotz, pers. comm.). In 2013, Chilean scallop (*A. purpuratus*) production resulted in only 5001 tons (FAO 2016). It remains to be observed whether the sector may be able to recover.

5.3.2 The scallop business moves northward to Peru: From an open-access fishery to a regulated aquaculture activity

<u>5.3.2.1 The start of culture activities in Pisco</u>

In Peru, *A. purpuratus* was targeted by dredge fisheries since the 19th century, a technique brought to the region by European fishermen (Murphy 1925, as cited in

Mendo et al. 2016) and used until the 1970 (Bose 1973, as cited in González-Hunt 2010). Apart from this, the diving fishery targeting *A. purpuratus* was of similar nature as in Chile, operating on a small scale since the 1950s. A main centre of fisheries was located in the area of Pisco (14 °S), while the bay of Sechura (5 °S) was initially of little interest to fisheries (Wolff 1984). Scallop populations in Pisco were - as in Chile - enormously affected by the EN event 1983/84, increasing 60-fold and causing landings to rise dramatically (Wolff 1987). From all over the country, fishermen migrated towards Pisco to join the scallop boom (Wolff 1984), and the local scallop business became a very important socio-economic activity, due to the establishment of a scallop export line and the respective involvement of not only fishermen but also other related employees, such as factory workers, middlemen, and exporters (Wolff et al. 2007).

The country started exporting, with annual production values of 50118 tons (in 1985, FAO 2016). However, this "gold rush" period ended soon with the normalization of the ecosystem and the almost depletion of the natural scallop stock, forcing the diving fishermen to target other resources (e.g. mussels, crabs, clams, octopods) besides the scallop *A. purpuratus* (Wolff et al. 2007). During subsequent years, both artisanal fishermen and businessmen attempted to maintain production by trying to grow scallops in near-shore bottom cultures (Mendo et al. 2011), similar to grow-out operations that had first been successfully established in the bay of Paracas (Pisco) back in 1982 (Wolff 1988). This stock enhancement (sea ranching) technique involves the collection of scallop seed from natural banks, which are then transferred to shallow areas of the bay where they are allowed to grow naturally on the bottom, only sometimes fenced with fishing nets (Wolff 1984). However, seed supply was often a bottleneck for the culture activities in the subsequent years, because seed from natural spatfall was often scarce and only few companies were able to produce scallop seed in hatcheries. Thus many fishermen continued to exploit natural (adult) scallop banks (Mendo et al. 2011) and – similarly to the Chilean situation – scallop production levels could not be maintained, soon reaching values as before the EN peak (Figure 1b).

During the following, similarly strong El Niño event of 1997/98, the scallop population in the region of Pisco responded as it did during the preceding event of 1983/84 (Wolff et al. 2007). Special concessions for the controlled conduction of stock enhancement were created in Paracas (Pisco) (Ministerial Resolution N° 406-97-PE, Badjeck 2008), though the number of fishermen applying overwhelmed local management authorities, who eventually decided to suspend concessions in 1998 (Ministerial Resolution N° 418-98-PE, Badjeck 2008). Total scallop landings were, in the end, lower during these years due to mismanagement (i.e. harvest at too small size, resulting in growth overfishing) of the resource when compared to the preceding EN event (Wolff & Mendo 2000, Figure 5.1b). Still, the Peruvian scallop business grew again, and the region of Sechura played an important role herein.

5.3.2.2 Moving further North: the rise of Sechura Bay

The scallop fishery in Sechura was initiated through diving fishermen who immigrated to the area from other parts of the Peruvian coast (principally from Pisco) in the beginning of the 1990's (Badjeck 2008, Mendo et al. 2008). Initially, scallop banks discovered at a near-by island (Isla Lobos de Tierra, ILT) were exploited as an open-access fishery. Between 1994 and 1997, the fishery experienced a small "boom", with up to 500 boats involved (Rubio et al. 1997), though this development was quickly interrupted by the 1997/98 El Niño (Badjeck 2008). In contrast to the South, scallop populations in the North suffer from adverse conditions, i.e. from high precipitation (diluting salinities) that were thirty times higher than in "normal" years during the 1997/98 EN event (Takahashi 2004). Sea surface temperatures reached up to 29 °C (Takahashi 2004), thus were above the optimum range of scallops and appear responsible for the decrease in scallop biomass following EN (Taylor et al. 2008d). In fact, scallop populations at ILT tended towards zero in 1998 (Tafur et al. 2000) and fishermen adapted by switching prey or migrating to the Pisco region (Badjeck 2008).

In the years following the EN 1997/98, several fishermen associations started conducting scallop bottom culture (i.e. stock enhancement/sea ranching) in the Paracas National Reserve (Pisco), though management agencies impeded the long-term authorization through controversially discussions (e.g. conservation targets vs. resource exploitation, Badjeck 2008). Scallop fishermen started moving again to the North, with the fishery experiencing a steady increase in activities through the period of 2000-06 (Badjeck 2008). This happened besides a temporal suspension of bivalve exports due to the encounter of Hepatitis A virus in 2000 (Directorial Resolution N°0327/2000/DIGESA/SA – 2000, Badjeck 2008), a period during which only the local market was supplied (Mendo et al. 2006a, as cited in Badjeck 2008). These fishermen also brought the knowledge on bottom culture, i.e. the stock enhancement (sea ranching) technique, to the region. Soon, they started to transfer small scallop seed from natural banks (i.e. from the island ILT) – representing a very cheap source of seed – into the bay of Sechura. At first, these activities informally occupied areas within the bay, while laws regulating the aquaculture operations were only formulated in 2001 (DS N°030-2001-PE, Mendo et al. 2016). Since then, those originally informal areas have been gradually allocated officially to artisanal fishermen associations (*Organizaciones sociales de Pescadores artesanales*, OSPA) for the conduction of scallop bottom culture (i.e. stock enhancement) – from initially three (in 2003) to 158 (Mendo 2015). Peruvian scallop production has been steadily growing ever since, with Sechura Bay currently producing 80 % of the countries annual production (in 2013, Mendo et al. 2016).

5.4 DIFFERENCES BETWEEN SCALLOP CULTURE SETTINGS IN CHILE AND PERU

Considering the historical background of scallop production in the region of Peru and Chile, it becomes clear that besides the apparently similar environmental settings, other factors have played a role for the specific development observed in Sechura Bay. In the following, we will take a closer look at differences in the environmental, socio-economic, and societal settings of both countries and will particularly aim at identifying drivers for the successful development in Sechura (5 °S) when compared to the historically most important bays for *A. purpuratus* production in Chile (Tongoy Bay, 30 °S) and Peru (Independent Bay, Pisco, 14 °S).

5.4.1 Environmental factors

Although located at the Humboldt Current system as do the other two bays, Sechura provides unique environmental settings for scallop cultures. To begin with, the bay represents a very large and shallow coastal embayment. While Tongoy Bay covers an area of 60 km^2 (with average water depths of 25 m, Wolff 1994), and Independence Bay 172 km^2 (with 62 % of the bay's area at depths >30 m, Taylor et al. 2008a), Sechura Bay extends over an area of 400 km^2 (with average water depths of 15 m, Taylor et al. 2008d). The large amount of suitable area represents a clear advantage of Sechura Bay with respect to producible volumes in comparison to the other regions. The differences in water depth may be even more important, as growth performance of *A. purpuratus* is inversely related to grow-out depth (e.g. Avendaño et al. 2008).

Sechura Bay is located at the northern edge of the Humboldt Current system, where colder waters from the South mix with warmer waters from the equatorial currents. While benefitting from the nutrient-rich upwelling waters as do the other two bays, water temperatures are in average higher (20 °C, Taylor et al. 2008d)) than for Independence Bay (16 °C, Taylor et al. 2008a) and Tongoy Bay (14.6 °C, Wolff 1994). As for many bivalve species, an inverse relation between temperature and growth performance (Mendo & Jurado 1993) as well as recruitment (Wolff et al. 2007) was shown for *A. purpuratus*, thus growth conditions may be favoured in Sechura when compared to the locations in the South.

Faster scallop growth in Sechura due to favourable water depths and temperatures implies a shorter grow-out cycle when compared to the other locations, and thus lower costs, while the risk of mortality events induced by spontaneously occurring environmental disturbances is lower (due to the shorter time span spend in water). In fact, growth of *A. purpuratus* varies greatly with latitude, depth, density, and environmental conditions (Mendo et al. 2016). While commercial size (90 mm shell length) may be reached in 18 months in Chile (Stotz & González 1997), marketable size (65 mm shell height) may be reached in 12-18 months in the area of Pisco (Mendo et al. 2008), and in only 7-8 months in Sechura Bay (Mendo et al. 2011). Despite several short-term mortality events (e.g. in 2007, IMARPE 2007) and 2012 (Gonzales et al. 2012), growth conditions are generally continuously beneficial in Sechura.

5.4.2 Economic factors

One mayor economic factor hampering Chilean development were the large Peruvian production volumes that were produced at comparatively lower costs. The differences in production costs are mainly found in the fact that in Chile, scallops are produced in suspended culture, while in Peru, mainly bottom cultures (i.e. sea ranching) are applied. Suspended cultures require a comparatively high initial investment for materials (e.g. nets), while bottom cultures, in contrast, can often be started off without larger costs, only requiring the purchase of seed harvested from natural banks (see Figure 5.3). In combination with the access to large, shallow areas (as discussed in the preceding section), the low initial investment costs may have facilitated the launching of the aquaculture operations in Sechura.

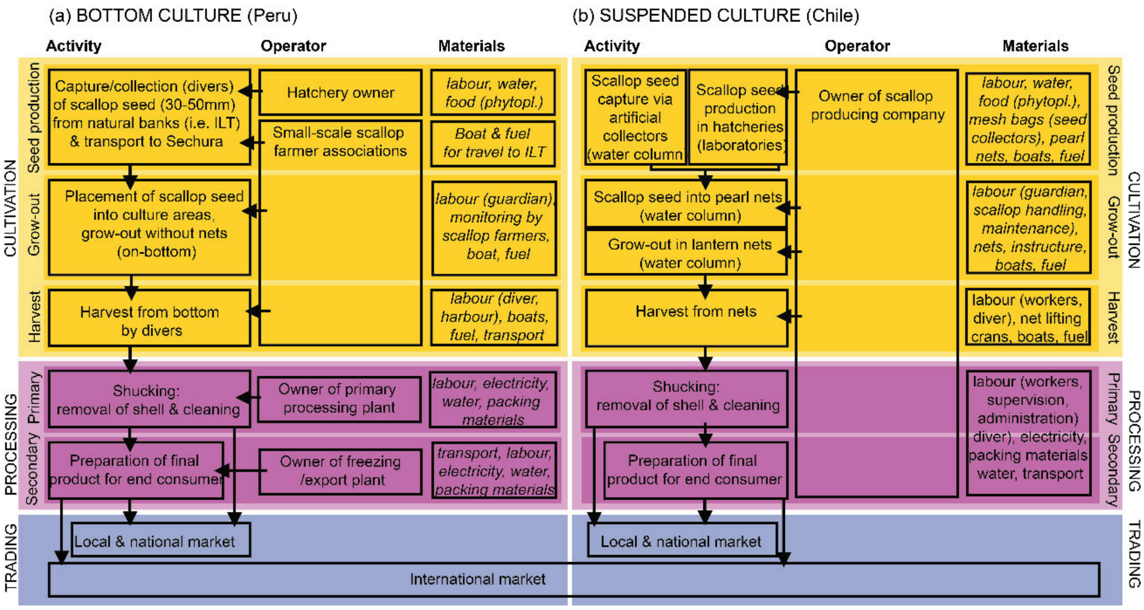

Figure 5.3. Comparison of the production flow for scallop aquaculture in Sechura, Peru (a) and Tongoy, Chile (b). For each case, the activities related to each production step (Cultivation, scallop processing trading), the operators (actor) that is leading the respective work, and the materials (and labour) contributing to total production costs are depicted.

The difference in the source of scallop seed represents a further factor influencing production costs. In Chile, extraction of scallops from the natural environment was banned in 1988 (Stotz 2000), forcing culturists to obtain seed from hatcheries or through artificial seed collectors from the natural environment. The latter technique involves the suspension of mesh bags in the upper water column providing settling substrate to scallop larvae that can be used for the grow-out to marketable sizes afterwards. In contrast, aquaculture in Sechura Bay mainly use seed collected from natural banks (i.e. at the island *Isla Lobos de Tierra*, ILT, Mendo 2015, Mendo et al. 2016). And although this then must be transported to culture areas within Sechura Bay in a 10 hour boat drive, scallop seed is still much cheaper (16 US$ /1000 seed) as compared to that produced in Chilean hatcheries (24 US$ / 1000 seed, Bossier 2015). In addition, scallop individuals from natural banks are usually collected at a relatively large size of 20-50 mm (Mendo et al. 2016), while hatchery originated seed is first cultured in small-meshed pearl nets before being transferred to grow-out cultures in lantern nets at a size of 10 mm (Mendo et al. 2016). This difference in initial sizes shortens the grow-out cycle and lowers mortality, further reducing costs as associated to maintenance or labour during the production cycle.

These salaries for external workers represent another important cost item for production costs. Although scallop farmer associations in Peru rely on external help for their bottom cultures, e.g. during harvest, the main part of the production cycle is relatively little labour-intensive. Divers monitor scallops after their placement on the sea bottom, and guardians (living on boats installed within culture areas) prevent poaching. Suspended cultures, in contrast, require much more personnel and equipment, e.g. for the cleaning, repairing and replacement of long-lines and lantern nets and the re-allocation of scallop individuals (i.e. decreasing culture densities with increasing scallop sizes) (Figure 5.3). In this context, it was hypothesized that the complicated administrative structure of scallop producing companies, i.e. the large amounts of salaries paid to administrative workers was suggested to have enhanced costs for the case of Chile (W. Stotz, pers. comm.). In addition, the increase in labor costs due to inflation of almost 8 %, the rise of prices for fuel and energy by 100 %, as well as the decrease in the exchange rate of the dollar (impeding exports) in the period 2006-2009 were important factors fostering the Chilean decline (Brand et al. 2016).

In conclusion, total production costs for suspended cultures as used in Chile are much higher than for the technique used in Peru. This has likely driven the decreased competitiveness of Chilean production entities (e.g. Molina et al. 2012), destabilizing the Chilean market since 2006 (Brand et al. 2016). After a highly profitable period (1990-2007) for Chilean producers, international prices fell (by 44.7 %, from 15 US$ kg^{-1} in 2006 to 8.3 US$ kg^{-1} in 2009, Brand et al. 2016) after countries with low production costs and high natural biomass (i.e. ensuring constant seed supply) – such as Peru – had entered the market. A bioeconomic model of Bossier (2015) confirms this by showing the main economic factors for the success of Sechura Bay to be the faster scallop growth, lower costs for scallop seed and the generally lower production costs.

5.4.3 Societal factors

First, the migration of fishermen towards the region of Sechura was likely supported by the Peruvian legislation, temporarily prohibiting scallop extraction along the entire Peruvian coast starting from 1994 (law R.M.N°275-94-PE, Rubio et al. 1996), except for the North (i.e. the states of Tumbes and Piura, the latter of which integrates Sechura) where the scallop stock seemed large enough for commercial extraction (law R.M.N°361-94-PE, Rubio et al. 1996). Traditionally, seasonal migration represented an important livelihood option for fishermen (Badjeck 2008), thus moving north was common for fishermen, once the scallop banks were detected there. Accordingly, the fishing effort in the region increased rapidly, with a simultaneous decrease in scallop population size of the natural banks at the island ILT (from 1995 to 1996, Rubio & Taipe 1996).

Secondly, the opening of the European market to Sechura via sanitary improvements (i.e. the installation of chemical toilets on guardian boats, sanitary monitoring, etc.) in 2009 caused a great increase in production (J. Proleon, pers. comm.). At the same time, a direct link from the region to international markets was established through the installation of processing plants able to do the entire processing process (including final processing for export) in Sechura. Before that, only plants for the simple shucking of scallops existed in the region, while final processing for the export had to be done in other locations, retarding export competitiveness. Still, only two companies are authorized for the export in Sechura (Mendo 2015).

A third potential success factor of importance is the way how scallop cultures were developed in Sechura. Several factors facilitated the transformation of a previously open-access fishing activity into many small-scale mariculture operations, including: The experience in bottom culture (stock enhancement /sea ranching) techniques from divers coming from Pisco, the existence of open access to large quantities of shallow waters, and comparatively low initial costs (as discussed in the previous section). In contrast to the Chilean case, where business men and companies greatly dominate the scallop activity, Peruvian scallop divers directly entered the bottom culture business themselves. No spatial planning by political authorities preceded their initiative, and the subsequent phase of growing scallop production was mainly self-organized, with an increasing number of artisanal fishermen involved. The regulatory and political framework responded in a relatively slow process, though until today, only few management regulations were formulated (e.g. minimum size limit of 65 mm shell height, Resolución Ministerial 209-2001 PE, Mendo et al. 2016).

Fourthly, the granting of quasi-property rights to fishermen (i.e. designated areas for sea ranching) also involves the transfer of direct monetary benefits and risks of the operation to the fishermen. In Chile, larger companies producing scallops in suspended culture contract technical staff, who receive a monthly salary (e.g. Molina et al. 2012), independent of profits. Some cases from the 1990's show that Chilean fishermen organized themselves to establish small-scale companies for the production of scallops, which they would subsequently run through contracted workers, while allowing themselves to continue fishing (targeting other species) (W. Stotz, pers. comm.). In contrast to this, scallop farmers associations in Sechura directly depend on the success of their aquaculture, i.e. the completion of grow-out cycles, creating a strong personal motivation and commitment to the activity. This direct connection to the individual's livelihood may create an incentive for the sustainable use of the resource (Aburto et al. 2013).

These thoughts are supported by the results of the social network analysis, which suggest the scallop farmers to hold a prominent role within the social network of Sechura (Figure 4a). From the 34 actors identified as participators of the scallop production, 18 groups were directly linked to the associations of scallop farmers. Those other actors are contracted for different services (e.g. sanitary monitoring, materials, etc.) or work (e.g. as divers during harvest or for the transport of the harvested scallops) (Figure 5.4a). Scallop farmers sell their product to the owner of processing plants, who contract workers for the primary processing (shucking and cleaning of scallops, "Plant 1"), secondary processing (presentation for final consumer, deep freezing, "Plant 2") or both ("Plant 3"). Other companies integrate secondary processing and export ("Plant 4") or the entire processing process ("Plant 5"). In addition, several actors are important for the entire production chain, e.g. supplying materials, for the service of transport, or as intermediate buyers (Figure 5.4a). At present, the scallop cultures in Sechura involve about 5000 artisanal fishermen (in scallop farmer associations), while the activity creates income for ca. 20000 additional personnel, working in the scallop processing chain and associated businesses (J. Proleon, pers. comm.). In the Chilean case, in contrast, the social network appears less complex, with the owners of scallop producing companies dominating all production-related processes by contracting personnel for the different production steps at land and sea, as well as the export (Figure 5.4b). 18 actors were identified for the Tongoy case, all of which (except for taxi drivers) were directly linked to the company owners (i.e. receiving salary). At present, one fishermen association is producing scallop seed via artificial collectors in Tongoy, selling their product to the owner of companies. Though the production process in Chile is more complex (in terms of materials and workers needed), the entire control lays in the hand of a single person. In Sechura, in contrast, the scallop production in Sechura strongly depends on the actions of small-scale scallop farmer associations.

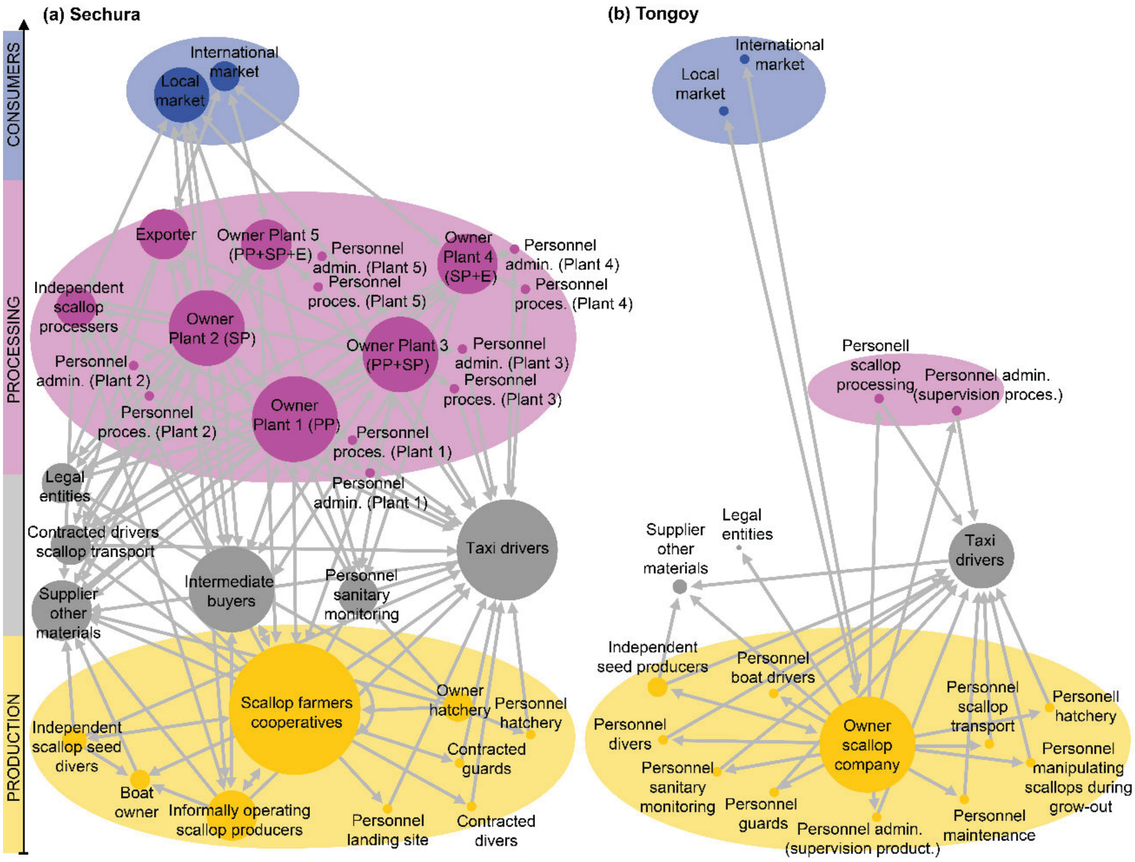

Figure 5.4. *Qualitative social network analysis applied to the case of (a) Sechura Bay (Peru) and (b) Tongoy Bay (Chile). The size of nodes (actors) is proportionally to its nodal degree (i.e. to the sum of incoming and outgoing linkages). Arrows describe a qualitative link between two actors of the network, indicating the flow of energy or money from one actor (source) to the other (target). Average nodal degree resulted in 3.79 for Sechura and 1.71 for Tongoy. Colours represent actors involved in scallop cultures (yellow), scallop processing (magenta), other entities with functional roles in the business (grey), and representing end consumers (blue). A complete list of actors (nodes) (including the results of nodal degree calculation) can be found in the supplementary material (Supplemental Table S5.1, S5.2).*

5.5 DISCUSSION: A POSSIBLE FUTURE OF SCALLOP PRODUCTION

5.5.1 Identifying drivers for long-term sustainability

Considering all these different factors, the historical development can be explained and the reasons why Sechura Bay has developed so successfully into a Latin American hotspot for scallop production emerges. Though understanding the historical context is important, the questions arise whether these factors will also help Sechura Bay to maintain its success - and what would be factors driving its long-term sustainability?

5.5.1.1 Seed supply

A constant and sustainable seed supply is crucial for the long-term success of the business in Sechura (as well as for any other aquaculture). But even though scallop seed collection from the natural environment is currently – with only few exceptions – prohibited by law (DF N°030-2001-PE, RM N°293-2006-PRODUCE, Mendo et al. 2016), most *A. purpuratus* production is nevertheless based on seed collected from natural banks at the island ILT (Mendo et al. 2008, Mendo et al. 2016). Although this source has been constant over the last 15 years, the reasons for that are not entirely understood, indicating the activity’s vulnerability towards any disturbance disrupting recruitment processes of natural scallop populations. It is therefore of high importance to increase the knowledge on scallop meta-populations and larval connectivity and to determine drivers of population dynamics controlling these beds (Mendo et al. 2016). In the end, it may be recommendable to decrease the dependency on natural banks, i.e. to diversify the sources of scallop seed. In fact, the government has authorized the use of 10 % of each concession area for the use of seed collectors (RD 202-2014 Gobierno Regional Piura-DR, Mendo et al. 2016), and has released a regulation for each association to maintain 30000 scallop adult individuals in their areas as to enhance larvae production within the bay (DIREPRO 2015).

Only recently, 4 hatcheries have been established in the region of Sechura in the last years. Nevertheless, hatchery output is not necessarily constant and may result in unintended consequences for the population (e.g. genetic impoverishment), inhibiting sustainability. As long as natural banks continue to represent a distinctively cheaper source of seed, scallop farmers may not change their approach. It may therefore be recommendable to promote hatchery production (aiming at reducing associated costs) in order to reduce dependencies from the natural environment. Otherwise, overall production costs may be enhanced, potentially decreasing profitability and competiveness of Peruvian scallop producers.

5.5.1.2 Management of wild scallop populations

At the same time, the management of wild scallop stocks that are linked with wild scallop populations through larval flows, seed supply, and spill-over effects from culture areas is of high importance for long-term sustainability. At the moment, the main regulation issues the minimum size limit of 65 mm shell height (Resolución Ministerial 209-2001 PE, Mendo et al. 2016), and monitoring of the scallop fishery only consists of recording landings by the Ministry of Production (Mendo et al. 2016).

Fishing effort, however, is not controlled, and the fishery remains (apart from the culture activities in certain bays) an open-access activity (Mendo et al. 2016). In theory, this means that fishermen are still free to migrate to the bays where the scallops are most abundant (Badjeck et al. 2009), potentially altering local fishing effort without being monitored.

Controlling and – if required – limiting the access to (parts of) natural scallop populations is could, for example, be achieved through the implementation (and enforcement) of spatial refugia (i.e. marine protected areas, MPAs) within the bay. An alternative to permanent area closures may be to shift culture areas within the bay in a rotational way. This could e.g. result in temporal area closures that are open only for a certain period of time, allowing scallop populations to proliferate without fishing pressure when closed. This concept has been successfully implemented to the fishery of the Atlantic sea scallop (*Placopecten magellanicus*) off the northeastern coast of the USA (Georges Bank, Hart 2003), but may be difficult to implement in a spatially organized situation as in Sechura.

A further management recommendation includes the limitation of the bay's total scallop production as well as on ecological considerations with respect to limits of culture expansion, i.e. the system's carrying capacity (CC). This is especially important since the production is currently stagnating, indicating the reaching of natural limits. Kluger et al. (2016a) have calculated the ecological carrying capacity of Sechura Bay – defined as the amount of bivalve (scallop) biomass that not yet causes other organisms to get extinct – and suggested to not exceed scallop biomass levels of 458 t km^{-2}. From this maximum biomass value a total allowable catch for the bay may be calculated that could further be translated into individual catch quota (i.e. total allowable catch, TAC) for single farmer cooperatives. A further means to control aquaculture production may be to implement density limits of scallops during the grow-out phase which may be easier to control in practice. For this, it may be recommendable to not exceed a density of 30 scallop individuals m^{-2}, since otherwise scallop growth may negatively be impacted and ECC reached (e.g. Mendo et al. 2011, Kluger et al. 2016a).

5.5.1.3 Ownership

While in open-access fishery situations, resource over-exploitation has often occurred where control was lacking, resulting in a so-called "tragedy of the common" situation (Hardin 1968), granting property rights in fisheries assumes to provide incentives for sustainable resource exploitation (Aburto et al. 2013), passing the costs of enforcement to those who benefit from the sensible management of the resource (Stotz 2000). The transfer of quasi-property rights to fishermen (scallop farmers) via legal concessions for sea ranching and the fact that it is the owner of these concessions (fishermen) themselves that conduct the cultures are therefore considered a major driver for long-term sustainability of the activity in Sechura. In practice, however, the specific aquaculture strategies of scallop farmers (i.e. densities, length of grow-out cycles, etc.) are based on long-term experiences (if they migrated to the region from Pisco) or trial-and-error experimentation (if they switched to cultures from other fishing activities). While they hold the decision-making power within their allocated

areas, little to no guidance (e.g. with respect to biological reference points of the species, Mendo et al. 2016) is provided by authorities as to set production limits.
International market demands for large scallop individuals (i.e. large adductor muscles) have driven the increase in production in Sechura, assigning highest market prices to the largest scallop individuals. This trend may have indirectly ensured harvest of individuals at a size above maturity (25 mm shell height, Mendo et al. 1989), which has incentivized sustainable harvest practices (J. Mendo, pers. comm.). In addition, the pressure of international markets to comply with international sanitary production standards has caused – to some extend – a self-regulated system in Sechura. If, for example, bacteria (e.g. E. *coli*) are detected in any product originating from Sechura the entire bay – or a part of it – is temporarily closed, causing financial damage to not only the cooperative in whose product bacteria were encountered, but to all others involved. This creates an inter-dependency of scallop farmer associations, depending on each other's compliance to market-based requirements. In this context, scallop farmers were seen to report on other associations harvesting scallops in a closed area (with the catch presumably being declared as originating from a different area of the bay, thus eluding the ban), ultimately forcing each other to comply with the rules – for the sake of all. The compliance with international sanitary production standards and traceability aspects as required e.g. by the European Union, may still be improved, but will be of major importance for the enduring access to international markets, in turn an important driving factor for all scallop-related businesses in Sechura.

5.5.1.4 Maintaining profitability in international markets

One factor that likely allowed the prospering of Sechura was the cost-effective and profitable operations in the context of international competition. At current market prices, the Chilean case is not profitable, and may only be able to compete with Peru if international market prices increased (i.e. above 10 US$ kg^{-1}, J. Alcazar, pers. comm.).

According to our analysis, a major factor preventing the re-entrance of Chilean operations into the market is the high costs of seed. Thus, Chile had a chance to re-enter the market if for Peru, costs for scallop seed increased. This may occur if seed collection from natural bank were to be effectively prohibited or the abundance of naturally occurring seed decreased, forcing scallop farmers to obtain seed from hatcheries. This would cause production costs to increase and changing the profitability of producers, i.e. potentially open a commercial window for Chile. Obtaining scallop seed from similar sources as in Chile would additionally favour Chilean because the technology for the cultivation of small scallop sizes in hanging culture is already well established in Chile (while it would have to be initiated in Peru).

With respect to Chilean competition it may therefore be concluded that unless Peru drops out of the market – either entirely or for a long enough time –, Chilean producers would have a hard time re-entering the market. A mass mortality event in Sechura that happened in 2012 caused Peruvian production to cease by 73 %, but Chilean production continued to decrease (Figure 5.1b), indicating that Chilean producers were not able to react fast enough. It is very important to mention, however, that the very recent EN 2015/2016 may have changed the situation. High precipitation and low recruitment has caused scallop production in Sechura to come to a halt, with the members of scallop farmer associations migrating to other regions in the search for work (J. Alcazar, pers. comm.). At the same time, Chilean producers have encountered a new, i.e. high value market and started selling scallops in one valve – a product that is sold mainly to Belgium and the USA at prices of 34-38 US\$ kg^{-1} (but note that half of this weight is made up by the shell already; W. Stotz, pers. comm.). At these prices, production became attractive again, and in fact, the still existing companies are currently investing and expanding. Production for the year 2016 is expected to triple (W. Stotz, pers. comm.), and with the Peruvian production being potentially disturbed for some years, it remains to be observed whether Chilean producers are about to re-establish themselves on the international market again.

5.5.2 Future projections of scallop cultures in Sechura

Recently, great effort is allocated in the certification of aquaculture production following internationally recognized standards, e.g. through the Aquaculture Stewardship Council (ASC). These certification schemes reward responsible aquaculture practices with a consumer label that connects the producers with the international market (ASC 2012). This may enhance sustainability through the participation in niche markets and increased profitability (through higher market prices). Respective certification schemes are, however, time and resource costly, and require a high degree of internal organization and cooperation, i.e. among the fishermen associations, in order to apply for the process. Until now, the world's only two scallop cultures certified by ASC are two farms of the Peruvian company Aquapesca group that possess farms with some of the few suspended scallop cultures south of Sechura Bay. More farms from larger scaled producers are in preparation for certification (J. Alcaczar, pers. comm.). It will have to be monitored, whether or these recent changes may lead to competition between small- and large-scale producers in Sechura, for example with respect to market conditions and access. Obtaining large-scale certification (i.e. for all artisanal scallop farmer associatons) is, however, as yet unrealistic, since the source of seed basically remains that of an unregulated fishery of natural banks (which is not certifiable, ASC 2012).

To obtain long-term sustainability, not only the management of the target species (i.e. scallops) is required, but also the ecosystem-based consideration of aquaculture consequences is of importance. After all, the introduction of large amounts of cultured bivalve individuals into the bay has the potential to alter benthic community structures, e.g. by providing settling substrate to hard-bottom associated organisms in an otherwise soft-bottom habitat (i.e. functioning as ecosystem engineers, Jones et al. 1994). Several recent studies indicate that scallop bottom culture in Sechura has in fact altered benthic community structure, i.e. decreasing biodiversity, enhancing predator (i.e. gastropods families Buccinidae and Bursidae) biomass, and negatively impacting competitor's biomass (Kluger et al. 2016b, I. Vivar, unpublished data). Though these effects are expected to be smaller than for other, more intensive types of aquaculture, altering the system's trophic structure may nevertheless impact ecosystem functioning, e.g. by changing system size, modifying energy flows and cycling within the system (Kluger et al. 2016b), and the system's strength to withstand a future disturbance, i.e. ecosystem resilience (Walker 1992, Walker et al. 1999). This is important since Sechura Bay represents a semi open-bay system and is influenced by a variety of external anthropogenic and environmental factors such as sulphidic events and the periodically occurring climate phenomena El Niño that causes adverse environmental conditions for scallops (as mentioned earlier). The high scallop mortalities as resulting from the last strong EN 1997/98 (Tafur et al. 2000), indicate the potential risk for aquaculture activities in the face of a future EN event. In fact, scallop production in Sechura currently came to a halt due to the very recent EN 2015/2016. Low recruitment and decreased salinities have hindered grow-out cycles to be successfully initiated in this year, and currently most members of scallop farmer associations have switched to traditional fishing, or migrated to other regions (though in Pisco, this EN has not as positively impacted scallop population as it did during preceding events) to search for work. The effects for the entire socio-ecological system (SES) depending on the scallop aquaculture operations in Sechura has as yet to be investigated. In particular, the potential for the SES to return to the system state preceding this EN will be crucial. On the long run, management strategies will have to integrate the monitoring of environmental and ecological consequences as induced by the scallop cultures. More importantly, the understanding and prediction of external effects (such as EN) for the involved socio-ecological system will have to be enhanced and ultimately incorporated into management measures in order to maintain the livelihood of 25000 persons and their families.

5.6 CONCLUSION

In general, we believe that a combination of unique factors has led to the successful development of Sechura Bay into a major center for scallop production in Latin America, including the favourable environmental conditions (e.g. low water depths, higher temperatures, high natural seed supply), and several socio-economic aspects resulting in lower production costs. Certain general factors may have played a role that are also transferable to other aquaculture settings. We believe that the bottom-up initiation of aquaculture operations by small-scale producers that are in contact with their resource has likely created a personal incentive for the long-term sustainable use. This aspect should be considered when designing future management strategies – not only in Sechura but also in other locations exposed to bivalve culture.

At the same time, we identified obstacles for long-term sustainability of activities in Sechura that also hold true for other coastal settings. The aquaculture depends on natural scallop banks for seed supply, and the conduction of aquaculture reduces the space for recovery of wild scallop beds (Brand et al. 2016) within the bay. A sound understanding of larval connectivity and meaningful (and enforced) management of wild scallop stocks is crucial for preventing aquaculture collapse. The integrated analysis of environmental, socio-economic, and societal factors has helped in obtaining a complete picture of the differences in system settings. These aspects are likely to promote long-term sustainability of cultures in this particular location and added to our general understanding of consequences of human activity on the ecosystem level. In the face of future challenges, the understanding and integration of both the ecological and social dimension of the system is crucial for the designing of effective management measures.

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CHAPTER 6

- General discussion -

The principle objective of this thesis was to develop a holistic ecosystem approach to bivalve aquaculture management. The main steps of this approach integrate well into the ecosystem approach to aquaculture (EAA) as described by Soto et al. (2008a, Figure 6.1). A combination of different methodologies was applied for the assessment of culture impact on the biotic community and ecosystem level (Chapter 2), the ecological carrying capacity estimated through a novel approach (Chapter 3), critical changes in ecosystem functions identified and the system's resilience capacity analysed (Chapter 4), and the potential for long-term sustainability discussed (Chapter 5). By this, the underlying research questions (RQ) of this thesis were answered.

In the light of the main research questions for this thesis, the main results suggest the following: (1) The introduction of scallop culture into the system of Sechura Bay has altered benthic community composition and structure, and ecosystem functioning (RQ 1, *Chapter 2*). (2) Current culture levels are close to ecological carrying capacity (RQ 2, *Chapter 3*) and (3) an even more conservative approach to culture expansion should be followed when considering resilience and functional diversity (RQ 3, *Chapter 4*). Moreover, (4) a complex combination of socio-ecological factors has helped Sechura to rise as a hotspot for scallop production though future sustainable development will strongly depend on the successful tackling of certain obstacles to long-term sustainability (RQ 4, *Chapter 5*). In the following, the key findings and the significance of this thesis will be summarized (*section 6.1*), and the applicability of the individual steps of the presented approach as well as the framework as a whole debated (*section 6.2*). The results of the thesis will be used for an integrated discussion on the future of the socio-ecological system of Sechura Bay (*section 6.3.1*), the possible advantages of aquaculture certification (*Section 6.3.2*), and general requirements for management on the way to an ecosystem approach to aquaculture (*section 6.3.3*).

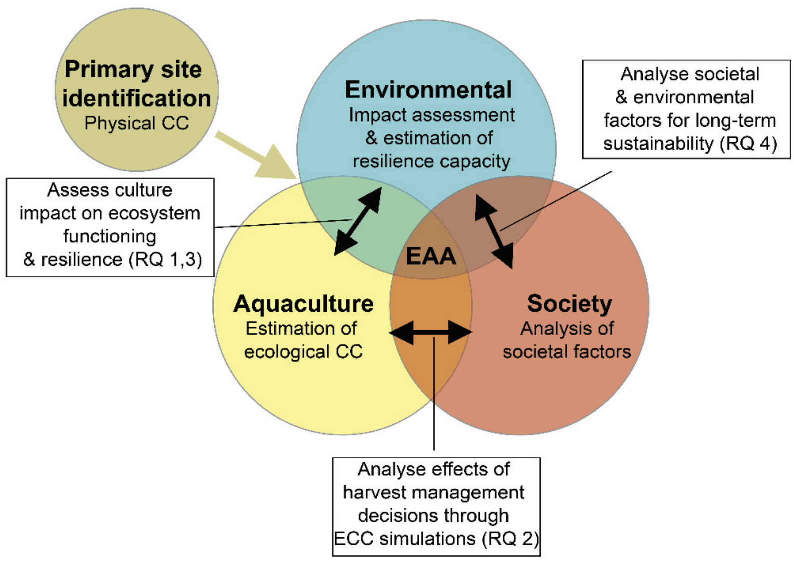

Figure 6.1. *Integration of the different aspects covered by the chapters of this thesis (demonstrated in boxes) into an ecosystem approach to (bivalve) aquaculture (EAA) that should also be applicable to other coastal settings exposed to aquaculture. Since aquaculture operations was already in place for the Sechura case, aspects of site selection were not covered by the present thesis. Management strategies seeking to newly introduce aquaculture into a given ecosystem should, however, include this as described by this figure. ECC=Ecological carrying capacity. Constructed following Figure 1 in Ross et al. (2013) and Figure 1.9 of this thesis.*

6.1 KEY FINDINGS AND SIGNIFICANCE: ECOSYSTEM RESPONSE TO BIVALVE AQUACULTURE

6.1.1 The effect of bivalve culture on the benthic community and ecosystem functioning

The results of this thesis suggest scallops to function as ecosystem engineers (after Jones et al. 1994) in Sechura Bay, interacting with the community in a complex way. The benthic community composition was significantly altered by the initiation of scallop aquaculture, causing a decrease in species diversity, and scallop predators (e.g. predatory gastropods such as Buccinidae and Bursidae, and octopods) to increase, while their filter-feeding competitors (e.g. bivalve *Tagelus dombeii*) decreased in biomass (Kluger et al. 2016b, i.e. *Chapter 2*). A shift towards hard-bottom associated species occurred, which is in accordance with the assumption that bivalvesand its culture facilities provide settling substrate to sessile organisms (Filgueira & Grant 2009), attract mobile species in the search for prey or shelter (McKindsey et al. 2006a, D'Amours et al. 2008) and to cause a shift in relative dominance of trophic groups (Cranford et al. 2012). A further culture expansion may even risk certain species to disappear (Kluger et al. 2016a, i.e. *Chapter 3*), causing a reduction in the food web's functional diversity (*Chapter 4*). A reduction in biodiversity, i.e. the loss of system compartments and altered ecosystem functioning (*Chapter 3, 4*) is important for maintaining ecosystem functioning, and ultimately ecosystem resilience (Walker 1992, Walker et al. 1999, *Chapter 4)*. The loss of species as a result of culture expansion can – from a conservation point of view – never be desirable, and may increase the likelihood of a regime shift to occur (Folke et al. 2004). Management efforts should therefore aim at the maintenance of species composition and biodiversity (or more specific the maintenance of functional groups composition) in order to allow for the enhancement of ecosystem resilience.

The simulated aquaculture expansion resulted in a change of system's flow structure and functioning as to decrease cycling within the system (*Chapter 2, 3, 4*), which is crucial for the preservation of feedback mechanisms that contribute to system stability (Odum 1969) and its resistance to perturbations (De Angelis et al. 1978, DeAngelis et al. 1989). The simulated introduction of further scallop biomass caused energy flows to be increasingly be channeled through more specific pathways (Ulanowicz & Abarca-Arenas 1997), e.g. secondary production (Kluger et al. 2016a, i.e. *Chapter 3*). Results suggested that expanding scallop aquaculture as to exceed the ECC threshold would possibly jeopardize ecosystem resilience. But when considering the development of the resilience indicator from low scallop biomass levels (i.e. 28 t km^{-2} (scenario 1) representing the pre-culture system state in *Chapter 4*) until this threshold, the step-wise increase of scallop biomass caused an initial increase in resilience (*Chapter 4*). This suggests that bivalve do not only provide ecosystem services associated to eutrophication control (e.g. Petersen et al. 2014), habitat provision (Inglis et al. 2000, Powers et al. 2007, Ysebaert et al. 2009, Filgueira et al. 2015), delivery of food to higher trophic level organisms and humans (D'Amours et al. 2008, Petersen et al. 2014) but that bivalve culture may also enhance ecosystem resilience (*Chapter 4*).

Conclusively, scallop culture introduction did impact the benthic community and ecosystem functioning in Sechura, mainly through the provision of habitat and food for higher trophic levels. This development should be monitored carefully to not risk ecosystem collapse. But in the end, the magnitude of ecosystem impact of this particular aquaculture operation shall be much smaller when compared to other types of aquaculture. Bivalve aquaculture does not require external feed input, since the organisms feed on naturally occurring phytoplankton, which also reduces the risk of eutrophication-related problems. In the Sechura case, no larger net structures are deployed as is done in most other bivalve and finfish cultures, thus the main modifying action represents the introduction of scallop individuals, the installation of guardian boats and traffic-induced disturbances. During harvest, scallops are hand-collected by diving fishermen, thus neither by-catch related issues nor the physical impact of dredging (as is the case for many scallop fisheries) destructively act upon the benthic environment.

6.1.2 Evaluating the potential for further culture expansion

The results of this thesis suggested that current culture levels in Sechura Bay are still below ecological carrying capacity (ECC), but that the respective threshold (calculated based on a model representing the year 2010) nearly matches the production levels of the year 2013 (Kluger et al. 2016a, i.e. *Chapter 3*). Thus, present day aquaculture levels should not be expanded further. Phytoplankton depletion – the most studied pelagic impact of bivalve farming (Filgueira et al. 2015) – did not represent an important limiting factor. Other inter-specific trophic interactions, i.e. the enhancement of scallop predator populations, which in turn imposed a top-down control on other benthic organisms such as herbivorous gastropods (Kluger et al. 2016a, 2016b, i.e. *Chapter 2, 3*), were more important ecological considerations.

The approach to ECC as developed in this thesis proposed to use the point at which any functional group falls below 10 % of its original standing stock as a critical threshold for the expansion of bivalve cultures. Since at this point, the species' recruitment may be severely affected, preventing to fulfill its ecological role (Worm et al. 2009), this measure allows to objectively estimate the magnitude of ecologically "tolerable" change. A food web model is, however, a simplification of nature, and the allocation of all species of a community into functional groups as used in Ecopath represents a potential source of bias (for a detailed discussion of the EwE approach please consider *section 6.2.1*). At this point, i.e. at 10 % of its original biomass, a species may already effectively be lost to the system (Kluger et al. 2016a, i.e. *Chapter 3*) because this threshold may ultimately impose very different consequences for the individual species. Species assembled into the model's functional groups are expected to generally have similar life history traits and growth characteristics. But individual species may also differ in specific dispersal rates, movement, feeding, and recruitment pattern, as well as vulnerability to predation. Thus, the here presented approach should only be considered an approximation to ECC, rather than a fixed measure. To add realism, knowledge on all species' life history traits and their potential to recover from the 10 % level (i.e. their risk to depletion) should be included, in order to define functional group-specific thresholds, and to ensure long-term survival of the species pool. Following the principles of the precautionary approach to aquaculture as suggested by the FAO (FAO 1996, Soto et al. 2008a), the respective thresholds should be set even more conservative for cases in which this ecological information is lacking.

In summary, the approach to ECC integrates the entire food web surrounding cultures, which is something most previous approaches have not done. The method's potential to detect and quantify the impact on other groups in the system and estimate ECC based on biodiversity-related considerations represents a clear step towards EAA, but could be extended to include species-specific thresholds. The Sechura Bay system is already close to ECC limits, and a further aquaculture expansion is not recommendable from an EAA-perspective.

6.1.3 Considering the economic and societal context of bivalve farming in Sechura

Chapter 5 identified and analyzed the different factors that allowed the scallop business of Sechura to thrive so successfully, while other regions' production, in particular Chile (producing the same species), ceased. The access to a cheap source of scallop seed from natural banks (at the island *Isla Lobos de Tierra*, ILT) and the low technological requirements resulting in low production costs were identified as some of the most important factors for the continuous success of Sechura. Moreover, the small-scale character of activities, i.e. the transformation of a previously open-access fishery to a property rights regime, transferring all rights and responsibilities to artisanal fishermen associations has further driven the development. In Sechura, the owner of the operations (i.e. the scallop farmers) conduct the aquaculture themselves, something that is different for the case of Chile, where businessmen contract workers that are not financially linked to the resource. This setting is likely to have set incentives for the reasonable (i.e. sustainable) use of the resource. Several management measures may be reasonable to adopt to neither over-exploit natural nor cultured scallop populations, e.g. enhancing traceability of the product, implementing production limits for single farmer associations. Their implementation should carefully be assessed and implemented by local decision makers.

The assessment of biodiversity alterations and consequences for the benthic community, as well as the determination of ecological thresholds to culture expansion is necessary for the development of meaningful management strategies in aquaculture operations. It has to be considered, however, that bivalve aquaculture is seldom the only socio-economic activity of importance in coastal ecosystems, but that fishing, tourism, agriculture, and other boat traffic also takes place. The degree to which changes in community composition and biodiversity are considered positive or negative will accordingly depend on individual stakeholder perceptions and site-specific management and conservation targets (i.e. species of interest, Dumbauld et al. 2009), as well as on the values that are used to weigh the different ecosystem components (Mckindsey et al. 2011). A decrease in biodiversity may at first not appear dramatic – and the resulting restrictions for scallop production may not be convincing – to the local human population who is likely to be more concerned with sustaining its livelihoods. This becomes reasonable when considering that 42.5 % of the inhabitants of the Piura state is considered poor (in 2010, INEI 2011). Thus, those simulation results that impact socio-economic aspects of local livelihoods will likely be of highest interest to people. For example, the increase in scallop predators such as predatory gastropods and octopods – representing target species for the artisanal fisheries – as a result of scallop farming (*Chapter 2, 3, 4*) may appear economically beneficial to local fishermen. In other settings, the decline in sea birds and marine mammals (as predicted by ECC simulations in Kluger et al. 2016a, i.e. *Chapter 3*) may be considered problematic. In Sechura, little tourism (constituting the group likely to be most concerned about biodiversity changes) and other recreational activities are taking place. Marine mammals (i.e. seals) are sometimes even considered to antagonize artisanal fishing by preying on catch, targeting nets and other fishing gears (local fishermen, pers. comm.). Loosing such species would likely not result in direct economic consequences (though in ecological ones). The effect of bivalve cultures on ecosystem functioning may cause, in contrast, an indirect impact on the involved human population, through the reduction of the system's resilience capacity (*Chapter 4*) that may ultimately threaten most socio-economic important activities in Sechura.

For the communication of environmental risks, e.g. the biodiversity loss, as resulting from bivalve aquaculture expansion and development of adequate management measures it may be advisable to estimate economic consequences of the different ecological scenarios used for the estimation of ECC. Local management should therefore aim at designing strategies as to allow for the expansion of culture without exceeding ecological limits (i.e. the ecological carrying capacity) of the system, while following economic reasoning. The culture level that causes the benefit-cost ratio of single scallop farmer associations to drop below a certain (i.e. "acceptable") level – as to be defined – may be used as an estimation of the system's social carrying capacity (SCC). At the same time, management should aim at harmonizing scallop aquacultures with other socio-economic activities such as fishing that is likely to be (further) displaced and impacted if culture were to be expanded. SCC may accordingly also be defined as the culture level that induces negative consequences for other stakeholders (e.g. after Inglis et al. 2000), a measure that will be based on stakeholder's perceptions on how much change to their activity would be "acceptable". SCC is likely the most difficult category to clearly identify (McKindsey 2013), and methodologies are still under development (Byron et al. 2011a), which the reason to not address this category in this thesis. Respective thresholds and indicators must be relevant and practical to measure (McKindsey 2013), are particularly site-specific and context dependent, and will thus require the detailed consultation of all involved stakeholders. A first step could be, for example, to define and integrate all stakeholders of the social-ecological systems (i.e. all social actors and biological populations) and their interlinkages into a network model. This allows to understand general system dynamics and predictive modelling may then be used to analyse direct and indirect consequences of aquaculture expansion, e.g. due to the depletion of functional groups that otherwise represent fisheries target species. A second step could then be the definition of stakeholder-specific ranges for the own socio-economic activity within which changes may be tolerable, e.g. based on income indicators or spatial considerations. Accordingly, a "safe operating space" for management may be defined for the social (respectively socio-economic) level which could be added to management options (see Figure 1.4, section 6.3.1, Figure 6.2).

6.2 EVALUATION AND CRITICAL ASSESSMENT OF THE THESIS' APPROACH

6.2.1 Using EwE for the development of an ecosystem approach to aquaculture

The construction of an Ecopath model is a complicate process and requires a high degree of ecological knowledge on the system. The approach was often criticized for the extended data requirements such as detailed diet composition and species biomass estimates. Besides all obstacles the EwE approach was chosen for tackling the presented research questions, since reliable biomass estimates based on standardized benthic sampling and fisheries monitoring was available. In general, this thesis integrates a number of approaches that have not as yet been combined for the impact assessment of bivalve aquaculture and shall be discussed below.

As a first step (Kluger et al. 2016b, *Chapter 2*), the ecological consequences of the introduction of bivalve (scallop) aquaculture on a coastal ecosystem was assessed through coupling multi-variate community analysis with trophic modelling (Ecopath), a rather novel combination. Allowing for the evaluation of the community level on the one side, and the trophic interactions on the ecosystem level on the other side, the approach successfully integrated different ecosystem layers to understand the effects of bivalve aquaculture.

It has to be considered, however, that this approach compares two system states that represent snap-shots of the system at certain points in time (i.e. pre-culture and culture conditions). Though differences were detected, little extrapolation can be made for the time in between system (model) states. Ideally, time series data should be explored in order to validate obtained results, and to exclude the possibility that external drivers (independent from aquaculture as pressure variable) are responsible for observed changes.

For the determination of the system's ECC for aquaculture, different culture scenarios were explored using Ecosim (Kluger et al. 2016a, *Chapter 3*). Until now, most approaches to ECC for shellfish aquaculture have been developed for and implemented at the production or farm scale, neglecting all trophic levels equal to or higher than bivalves (Byron et al. 2015). Only a small number of studies have used Ecopath for the estimation of carrying capacity (Wolff 1994, Jiang & Gibbs 2005, Byron et al. 2011b, Byron et al. 2011c) by step-wise increasing the biomass of cultivated bivalves in consecutive models until the model gets unbalanced, i.e. the cultured bivalves require more food than is available by the system (indicated by the ecotrophic efficiency EE > 1). Since all other model parameters are maintained stable, this accordingly represents an estimation based on food considerations, i.e. the production carrying capacity. Using Ecosim, in contrast, all species of a system are integrated to study the trophic consequences of aquaculture expansion at the system level. The indirect effects of aquaculture operations on other benthic organisms that may be competitors or predators of the cultured bivalves can now, with this approach, for the first time be detected. This becomes even more apparent when comparing the two approaches. Using the steady state Ecopath approach as previously used by the abovementioned authors, an ECC value of 841.6 t km^{-2} (scallop biomass) was determined (see Kluger et al. 2016a, i.e. *Chapter 3*). This level is far above the value of 458 t km^{-2} as suggested from Ecosim simulations, thus several functional groups would have already gone extinct.

Though the here presented approach to ECC represents a clear step towards an EA to bivalve aquaculture, some thoughts could be directed towards improvement of the method. Carrying capacity is expected to vary over time, since environmental parameters differ seasonally, and in particular primary productivity dynamics are strongly influenced by external factors (Forrest et al. 2009). The approach to ECC should therefore integrate seasonal primary productivity dynamics, as well as environmental parameters such as temperature, salinity, and oxygen concentrations. Ecosim allows for the incorporation of times series on primary production, nutrients (as a proxy for changes in primary productivity), salinity or temperature as forcing functions. For added realism of the entire food web's dynamics, the individual functional group's tolerances to changes in these parameters may be individually adjusted in the "group info" form in Ecosim, and seasonal variation of functional group's dynamics may be incorporated through the definition of "seasonal forcing shapes" as multiplier of individual consumption and production rate functions (Christensen & Walters 2004a).

Community composition and environmental characteristics, thus ECC thresholds, may also differ spatially. Instead of considering a system as a uniform water body of 400 km^{2} (as done for the present Ecopath/Ecosim studies), the use of Ecospace (Walters et al. 1999) – the spatial component of EwE – may be more appropriate. By employing the Ecopath/Ecosim model over a raster of grid cells, this allows to define spatially explicit habitats within the bay, incorporate species' movement pattern and account for spatially-dependent population dynamics. Aquaculture areas may be specified (at present, representing 41 % of the bay's extension, PRODUCE 2015) may be defined, as well as spatial differences in community composition (if existing) incorporated. Thus, ECC management scenarios could be used to predict spatial biomass pattern of both the focal scallop species and the entire ecological community. Moreover, the impact of aquaculture could accordingly be assessed on a finer scale, allowing for the definition of spatially explicit ECC thresholds (i.e. maximum scallop biomasses), which may an even more meaningful output for local managers.

The evaluation of resilience, the third step (*Chapter 4*), was based on a method recently developed by Arreguín-Sanchez (2014) that uses the consumption matrix in Ecopath to calculate resilience. The author suggested to do so by plotting all functional groups onto a supply-demand-plot, where the sum of all consumption flows on other functional groups represents the "demand of energy", and the sum of all predation on the functional group itself describes the "supply of energy" to the ecosystem (Arreguín-Sánchez 2014). The regression slope of the log-log plots then reflects the resilience of the system. Following this method, I proposed to obtain the respective resilience value from a weighted least square regression. Considering the functional group's biomasses as weights allowed to account for the shift in community composition that was predicted to be increasingly dominated by scallops and its predators (in terms of biomass).

The method may, nevertheless, not be the most straightforward to understand, as the definition of resilience based on the system's energy flows may be a little abstract. The definition of "acceptable" ranges for this resilience indicator may be subjective. It was therefore recommended to use the point of optimum resilience as management target. In the end, resilience quantification is based on a number of assumptions, e.g. for the construction of the diet matrix. Resilience is defined by the energy available within the system, but it may be recommendable to combine this indicator with other measures of resilience, e.g. incorporating the social dimension, for its ultimate determination.

The analysis of historical, environmental, economic and societal factors provided insights into the question on why Sechura has become the center for scallop production in Latin America (*Chapter 5*). Since for this analysis the outcomes of the different preceding Ecopath-based studies of *Chapter 2, 3* and *4* were combined with data as obtained during the SASCA project and from literature, there is no need for further discussion here.

The only aspect to be mentioned is that the overall approach could have benefited from further socio-economic explorations, i.e. predictive modelling of the behavior of the social-ecological system in the face of future environmental disturbances and changes on the international market. This could be done, for example, using the Value Chain Approach of EwE (Christensen et al. 2011) that links the ecosystem model to socio-economic variables (volumes, revenue, costs) of the fisheries/aquaculture production chain, thus allowing for the evaluation of socio-economic consequences of aquaculture management scenarios.

In the end, the ecosystem-based estimation of ecological carrying capacity and the modelling and prediction of system's behavior in the face of future culture expansion are important steps towards a sustainable scallop aquaculture management. The combination of different Ecopath-approaches with non-Ecopath-methods allowed for a holistic evaluation of bivalve impacts by tackling the questions from different angles. The approach could be improved through the inclusion of environmental variability, as well as temporal and spatial considerations as discussed above. The method is nevertheless expected to be applicable to other aquaculture settings including finfish farming, a factor that will be discussed in the following section.

6.2.2 Transferring the Sechura case to the world: applicability & limitations

Generally, the approach to sustainable bivalve culture as presented in this thesis proved useful to evaluate scallop culture practices in Sechura Bay. As discussed in the preceding section, it represents one of the first approaches to ECC that considers the food web beyond the phytoplankton-bivalve interaction, and thus considerably contributes to the wider scientific discussion on evaluating aquaculture impacts. Its applicability is expected to hold true for other case studies apart from Sechura Bay. Provided that respective data is available, a food web model may be established for any other aquaculture system, including finfish farming. If cultures were about to be initiated, the approach may be used to accompany the introduction processes, while

monitoring and evaluating the induced ecological consequences. Whenever cultures are already in place, the different methods are still useful to constantly study and evaluate aquaculture performance.
The approach should, however, be adapted to case-specific situations. As an example, the trophic web of the here presented case included a single-species functional group for scallops, and one for *other filter feeders* (e.g. including other bivalves). Thus, the cultured organisms were not separated from its wild population. This makes sense for the case of Sechura Bay, in which cultured scallops are inseparably linked to natural scallop populations via larval flows and transport of adults via currents. For other systems, it may be more reasonable to include one particular functional group for cultured organisms, and one for its natural population. This makes in particular sense if predation and fishing pressure or distribution patterns differed for cultured and non-cultured populations.

The approach and the respectively presented thresholds are completely based on trophic interactions of the entire food web surrounding bivalve culture, but not accounting for other potential sources of ecosistemic impacts such as nutrient loading, waste dispersal or oxygen limitations. Though these aspects may be included into Ecosim simulations through mediation functions (as discussed in *section 6.2.1*) it may be necessary to account for small-scale spatial differences. Thus, the approach could be complemented with other types of environmental impact assessments and respective predictive modelling approaches, especially for those cases where cultures are expected to be environmentally more damaging (than bivalve aquaculture). Moreover, for situations in which farming is not conducted in the ecosystem context (e.g. in pond aquaculture systems, where little trophic linkages to other parts of the ecosystem occur) the applicability of the here presented approach is questionable. This is expected to hold true, for example, in the case of shrimp aquaculture where issues of nutrient loading (i.e. assimilative capacity) should be more important than purely ecological considerations.

6.3 TOWARDS SUSTAINABILITY OF BIVALVE AQUACULTURE: - MANAGEMENT & FUTURE DIRECTIONS -

6.3.1 Looking into the future of the Sechura Bay case study

Defining a long-term sustainable "safe operating space" for management
The approach as presented in this thesis (Figure 6.1) uses several different indicators for the evaluation of limits to aquaculture expansion, e.g. based on biodiversity (i.e. the depletion of other functional groups, Kluger et al. 2016a, i.e. *Chapter 3*), resilience, and functional diversity of trophic flows (*Chapter 4*). Based on each of these state indicators, system-specific limits to what would represent an acceptable change may be defined, i.e. the point at which environmental risks of the aquaculture activity compromises ecosystem health. These indicators therefore frame the ecological risks that aquaculture would impose on the system level, and may be used to identify specific management targets (e.g. for optimizing resilience). All indicators provide complementary information and from their combination a "safe operating space" (Tett et al. 2011) for management may be derived representing the range of bivalve biomass within which the system could be managed without setting ecosystem well-being at risk.

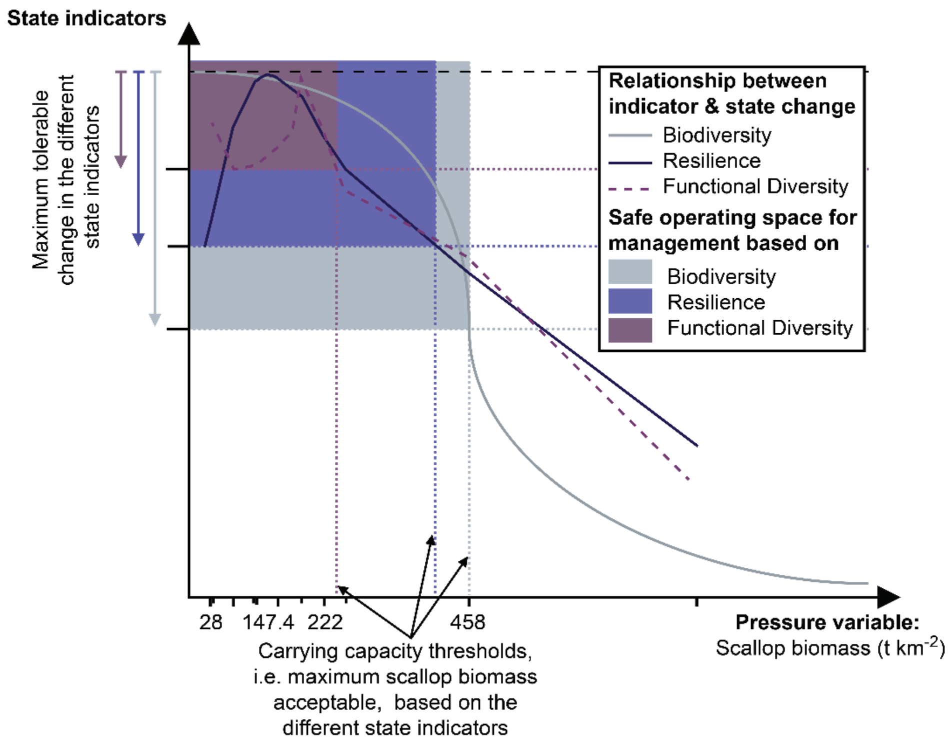

Figure 6.2. *Conceptual framework of carrying capacity (CC, after Figure 1.4, McKindsey et al. 2006a; Tett et al. 2011), describing the behavior of any state indicator in relation to the pressure variable (i.e. bivalve biomass). The CC is defined as the maximum level of the pressure variable not yet causing the state variable to exceed the maximum tolerable change. This range has to be defined for any state variable on a site-specific, but objective basis. As part of this thesis, measurable state indicators, based on biodiversity (Chapter 3), resilience and functional diversity of trophic flows (Chapter 4), were developed and a safe operating space for management of scallop aquaculture levels may be established considering optimum ranges of all state indicators. This graph represents Figure 4.10 of chapter 4.*

For the Sechura Bay system, simulations suggest to not exceed the ECC threshold of a culture intensity of 458 t km^{-2} scallop biomass (see Kluger et al. 2016a, *Chapter 3*, Figure 6.2) in order to not cause the loss of system's compartments. The functional diversity (FD) and resilience indicators peaked at lower scallop biomasses (185 and 133.6 t km^{-2}, respectively, see *Chapter 4*). The ECC threshold, and the FD and resilience optima describe different aspects of risk as imposed by the aquaculture operation on the system. Based on the presented simulations, management targets for the long-term sustainable use of the system will have to be defined. Following a precautionary perspective, it is recommendable to optimize the system and minimize the risks by managing the system at scallop levels biomass around resilience and FD optima. However, managing the system beyond these optima does not yet cause the system's structure to change significantly (*Chapter 4*). Consequently, higher biomass could be cultured representing an increasing pressure on the system (see Figure 6.2). This pressure would increase with cultured biomass until the ECC threshold is reached. This threshold represents a dramatic change in ecosystem's structure, after which the extinction of some functional groups and the change in ecosystem functioning is expected. Consequently, to surpass it should be avoided in order to guarantee the sustainability of the system.

Considering environmental variability

Several small-scale and long-term factors act on the Sechura Bay system, making the single-species dependent activity highly vulnerable towards external disturbances that may threaten scallop populations. Oxygen depletion in bottom waters due to low water exchange rates during summer months (due to temporarily decreased upwelling), harmful algae blooms (HAB), and/or sulfidic events may occur, as evident in 2012 (Gonzales et al. 2012).

On a different level, extreme climate events, such as the El Niño Southern Oscillation (EN) phenomena, may act on the system. During such an event, higher temperatures (of up to 29 °C) and strong rains (up to 30 times higher than during normal years) are usually expected for this region of Peru (Takahashi 2004). Respective biotic responses include changes in primary productivity, species composition, as well as species' survival rates and distribution. In particular, scallop populations are expected to be strongly negatively affected by decreasing salinities (caused by the heavy rains) and reduced food abundance. Nowadays, this would likely induce severe consequences for those local villagers relying strongly on the maricultures. At the moment, the last effects of a recent very strong EN event (2015/2016) can still be observed, having resulted in high scallop mortalities and reduced scallop larvae availability. In fact, scallop production in Sechura came to a halt, with scallop farmers searching for alternative incomes in other types of fisheries, and migrating towards other regions of the country (J. Alcanzar, pers. comm.). Surprisingly, the EN event seem to not have had a positive effect on scallop populations in the bays of the Pisco region (E. Torres Silva, pers. comm., J. Alcanzar, pers. comm.) as it had during the last strong EN 1983/84 and 1997/98 (Wolff 1984, 87, Wolff et al. 2007). Since the migration to other bays represents a traditional adaptation strategy during times of low production in Sechura – increasing individual's resilience –, the question arises how fishermen and scallop farmers will be

able to cope this time. Those farmers that were able to switch their target resource will potentially create conflicts by competing with traditional fishermen.
Individual resilience to such a disturbance is likely to differ on the different levels of the socio-ecological system (SES). Scallop processing companies, for example, may be able to cope with the effects of EN by processing and selling those fish species that migrate into the area, thus keeping economic losses to a minimum. For the processing of the "new" species, they need, however, the legal permission from local authorities, a precaution that only few companies have undertaken (J. Alcanzar, pers. comm.). People working in (scallop) processing plants (the majority being women), may have more difficulties to cope, since their work usually depends on scallop production volumes. It remains questionable, whether and how the SES may return to the pre-ENSO state, and feasibility will also depend on individual's income during the ENSO event. Scallop farmer associations require the financial resources (either from savings or from work during ENSO) for initial costs of scallop seed to be able to start a first post-ENSO grow-out cycle. Companies, in contrast, are likely to easier start off, especially if production during ENSO was maintained. Though these thoughts remain speculative, it becomes apparent how strong the effect of an external disturbance such as ENSO could be, resulting in a disruption of processes within the SES, negatively affecting components, and potentially causing a regime shift. Future investigation should accordingly address the vulnerability and resilience of the entire SES. The monitoring and prediction of such events and the integration of respectively expectable consequences into mitigation strategies on the management level are crucial.

In the context of these environmental risks for cultures in Sechura the risk of single-site collapse may be reduced by spreading cultures to other bay systems along the Peruvian coast. Hereby, a dynamic system could be created that should be (more) capable of responding to environmental perturbations while minimizing the risk of total production failure (Mendo et al. 2016). This would, in the end not only benefit scallop farmers in Sechura but the entire Peruvian economy by ensuring the progress of culture activities.

Future profitability

The future of Sechura Bay inseparately depends on its ability to compete with international scallop producers, in particular Chile, who produces the same species. As discussed in *Chapter 5*, Chilean scallop producers may only be able to re-enter the market if Peru dropped out, or if Peruvian production costs increased. The competition with other scallop producing countries, such as China, should also be important for the long-term projection of Sechura. Until recently, China was no competitor for Peru due to its limited access to European markets (J. Alcazar, pers. comm.). This has changed, however, in March 2016, when the European ban was lifted after a 19 years (Parker 2016) in the favour of one scallop (*Patinopecten yessoensis*) producing enterprise that had received the Marine Stewardship Council (MSC) certification in 2015 (MSC 2016). Though in China, different scallop species are cultured – obtaining smaller final sizes thus lower international prices – total scallop production is much higher than that of Peru. If China was to establish itself on a larger scale on European markets, it may out-compete Peru, mainly to its large production volumes (as Peru has done with Chile). This this would require, however, a shift in international demands (which at this point are directed towards large scallop adductors thus benefiting Peru).

Thus, these thoughts remain accordingly speculative, and require further investigation.

The import requirements of international (particularly the European) markets usually include the compliance with certain sanitary procedures as well as the traceability of products. Though in most cases no international agreements have been issued, these rules represent a certain regulatory mechanism on the local producer level since compliance ultimately ensures access to international markets. Since 2009, a first initiative of Peruvian legislation (Decreto Supremo N°016-2009-PRODUCE, Mendo 2015) has helped to launch a first organizational process in Sechura that aimed at spatially re-organizing thus terminating illegal culture activities and enhancing compliance with sanitary requirements for the export (Mendo 2015). As a result, chemical toilets – installed on guardian boats within culture areas – and the collection of respective waste is mandatory for scallop farmer cooperatives to obtain authorization. Harvested scallops are traced to their exact origin (i.e. exact culture area within bay) and the final product is monitored for bacteria contamination before export, whilst product not fulfilling requirements is directed towards the national market. This is just one example how international standards have changed local production conditions and potentially positively helped to guide the operations into more sustainable paths. One step further in guaranteeing long-term access to international markets may be to obtain a consumer-orientated aquaculture label, a thought that will be discussed in detail in the subsequent section.

6.3.2 Aquaculture certification – a desirable achievement?

A global, market-based movement for the development of an ecosystem approach to aquaculture was linked to the creation of different performance-based standards for certification schemes (Cranford et al. 2012). These private certification schemes aim at transforming aquaculture related processes towards sustainability by awarding best practices with a consumer-oriented label. Certification may reduce environmental impacts of aquaculture operations (Jonell et al. 2013), and enhance prices on the producer level (FAO 2007). *Aquaculture Stewardship Council* (ASC, www.asc-aqua.org), is one of many certification schemes that developed standards for responsible aquaculture production for seven different species groups (abalone, bivalves, pangasius, salmon, shrimps, tilapia, trout), against which aquaculture operations can be assessed by an independent third-party certification body (ASC 2012). Since the initiation of ASC in 2012, 252 aquaculture farms were certified, out of which 3.97 % (N=10) represent bivalve culture operations (ASC 2016, Figure 6.3).

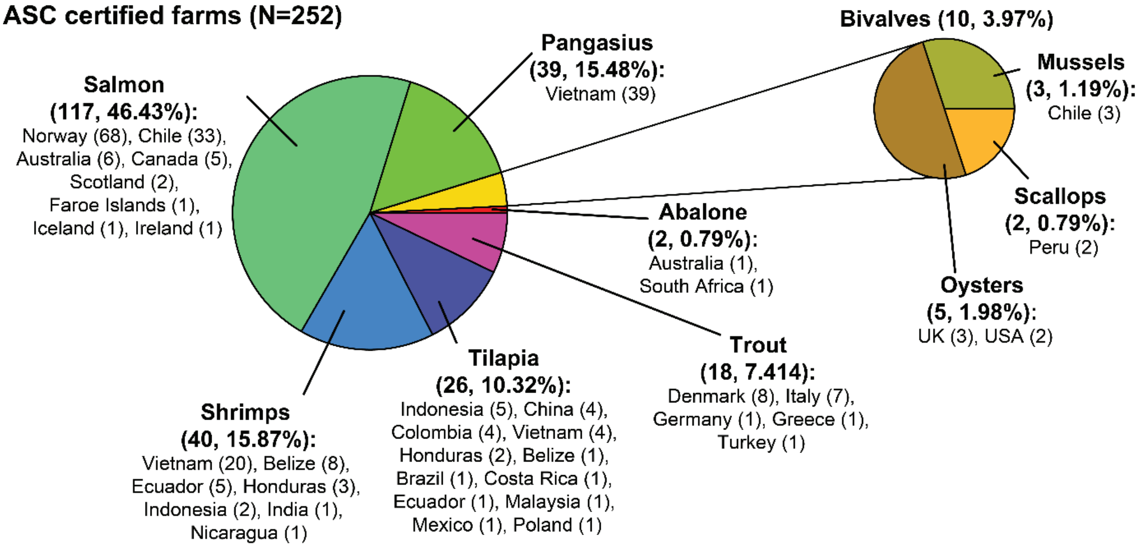

Figure 6.3. *Review of all aquaculture farms currently certified based on ASC criteria (N=252). For all seven species groups (abalone, bivalves, pangasius, salmon, shrimps, tilapia, trout), the number of certified farms and the respective percentage contribution to the total number are given (N, %). Moreover, all countries hosting the different certified farms are indicated for each species group, including the number of farms per country. The bivalve group is further split to show the number all certified farms for oysters, mussels, and scallops, with the percentage contribution to the total number of ASC certified farms indicated. Source of data: www.aqua-asc.org, accessed at 2016-06-05.*

The ASC bivalve standard comprises of seven key principles for assessment of potential negative social and environmental issues related to their aquaculture (ASC 2012, Table 6.1). For the low impact, on-bottom aquacultures in Sechura most of the ecological ASC criteria (e.g. principles 2 to 5, ASC 2012, Table 6.1) may be easily met, especially since ASC bivalve standards for maximum allowable sulfide concentrations and general organic enrichment (principle 2, criterion 2.1 Benthic effects) do not apply for on-bottom cultures (ASC 2012). The source of scallop seed for cultures, however, may represent an obstacle to certification, because farms using wild seed from open-access, unregulated sources are generally not eligible for certification (ASC 2012). This is additionally hampered by the fact that collection from natural banks is – with some exceptions – not permitted by Peruvian laws (Mendo 2015), which offends the ASC principle 1 (i.e. obeying the national laws and regulations, ASC 2012). With respect to social aspects (i.e. ASC principle 7), several points would have to be improved, including diver's health conditions, to comply with the certification standard (see Table 6.1).

At present, the world's only two scallop farms certified by ASC are located in Peru, with one being a cluster certification (i.e. more than one farm) just to the south of Sechura Bay. Those farms represent some of the few suspended culture examples found in Peru, and have successfully completed the process in 2015. One other Sechuran company is currently in the preparation process for application to certification (J. Alcanzar, pers. comm.). Though these companies hold at the moment a relatively small share of scallop production originating in Sechura, they have the advantage to obtain scallop seed mainly from laboratories (hatcheries) and artificial seed collectors. It needs careful monitoring of the process for the estimation of long-term effects for small-scale producers.

Price premiums and the better market access for certified products create financial incentives for producers to meet certification standards (Blackman & Rivera

2010), but small-scale producers may also be out-run if certification schemes increased local production requirements or decreased the demand for uncertified product. It is therefore recommendable to aim at obtaining certification for small-scale producers as well, for them to maintain their local competitiveness. Obtaining certification is time and resource costly, with the process primarily being producer-funded (Parkes et al. 2010), a potential problem for small-scale producers. Applying collectively for ASC certification would allow to reduce involved costs by distributing the costs of certification among a large number of small-scale producers. Though this would require a high degree of internal organization and cooperation among the scallop farmer associations, e.g. for the creation of a single representative entity as a client for certification, this community-based approach may help to maintain the small-scale nature of scallop production in Sechura, a factor that was identified as important for the long-term sustainability (*Chapter 5*). The source of scallop seed would nevertheless needed to be changed in order to be applicable for certification, e.g. by using artificial seed collectors. Local management authorities and governmental agencies should provide guidance and financial support to help small-scale producers in this transformation process. Then, certification through ASC may represent a chance for Sechura to position itself on international markets with a long-term perspective.

Table 6.1. *Overview of the seven principles as evaluated by the bivalve standard of the Aquaculture Stewardship Council (ASC) and the specific criteria that should be considered to address these issues ASC 2012). For a complete list of the indicators proposed for the assessment of the different criterions please consider the supplemental Table X). Based on own knowledge, the potential for Sechura Bay (SB) to get ASC certified is assessed (Compliance) and discussed for each criterion (Comments). Considerations are made on the farm level (excluding processing plants for which results are likely to differ).*

Principle	Criterion	Compliance	Comments
1. Obey the law and comply with all applicable legal requirements and regulations where farming operation is located	1.1. All applicable legal requirements and regulations where farming operation is located	Partly	On-bottom cultures in Sechura Bay are conducted accordingly to national regulations (1.1.1), except for the source of seed. Though the extraction of seed from natural banks is prohibited by law (Mendo et al. 2016), this represent the main source of seed for SB.
2. Avoid, remedy or mitigate significant adverse effects on habitats, biodiversity, and ecological processes	2.1. Benthic effects for off-bottom and suspended-culture methods	Yes	Does not apply for bottom cultures, though an evaluation may be recommendable (2.1.1-5).
	2.2. Pelagic effects	Yes	Does not apply for bottom cultures, though an evaluation may be recommendable (2.2.1-3).
	2.3. Critical habitat and species interactions	Yes	No harm to threatened/endangered species or habitats is imposed (2.3.1).
	2.4. Environmental awareness	Yes	Some effort or environmental training and best practices for management could be observed (2.4.1).
3. Avoid adverse effects on the health and genetic diversity of wild populations	3.1. Introduced pests and pathogens	Yes	Cultures do not involve illegal introduction of a non-native species (3.1.1), pest or pathogen (3.1.2) attributable.
	3.2. Sustainable wild seed procurement	No	Main source of scallop seed represents collected wild seed harvested from open-access (though access is officially prohibited, see 1.1), unregulated source (3.2.1).
	3.3. Introduced non-native cultivated species	Yes	No non-native species is cultivated (3.3.1).
	3.4. Native species cultivation	Yes	A native species is cultivated (3.4.1).
	3.5. Transgenic animals	Yes	No transgenic animals are cultivated (3.5.1).
4. Manage disease and pests in an environmentally responsible manner	4.1. Disease and pest management practices	Yes	No additives – pesticides (4.1.1), chemicals (4.1.2) - are used. Predators do not include critical species (4.1.3), no predator netting is used (4.1.4), and no explosives deployed (4.1.5).
5. Use resources efficiently	5.1. Waste management /pollution control	No	Solid wastes (produced onboard of boats used for harvest etc. and for the guardian) is collected, but no strategy for the reduction of waste (5.1.1), the appropriate storage and disposal of biological/chemical wastes (5.1.2/3), or for the prevention of spills (5.1.4) is in place.
	5.2. Energy efficiency	Partly	Evidence of energy use monitoring relative to production is present (5.2.1). Monitoring of the maintenance of farm equipment (e.g. boats and generators) is not conducted (5.2.2).

Table 6.1 (continued)

Principle	Criterion	Compliance	Comments
6. Be a good neighbor and conscientious coastal citizen	6.1. Community relations and interactions	Partly	Farm structures (guardian boats) are recognizable and of uniform color (6.1.1), and farm positioning clear (6.1.2). Floaters are not made from open-cell styrofoam (6.1.3), impact on others through noise or light emissions minimal (6.1.4). Navigational rules and regulations are followed (6.1.5). No strategy (6.1.6) nor the gear (6.1.8) for the recovery of lost gear from farms, and no mechanism for the decommissioning of abandoned farms (6.1.9) exists. Not all substantial gear identifiable to farm (6.1.7). No conflict resolution protocol for the registry of public complaints (6.1.10) or the outreach (communication with other stakeholders, 6.1.11) is evident.
7. Develop and operate farms in a socially and culturally responsible manner	7.1. Child labor	Yes	Members of scallop farmer cooperatives are usually >15 years (7.1.1).
	7.2. Forced, bonded or compulsory labor	Yes	Scallop farmer cooperatives consist of voluntarily associated members (7.2.1).
	7.3. Discrimination	Yes [1]	No records of discrimination could be made (7.3.1).
	7.4. Health and safety	No [1]	No records of health and safety related accidents are present, though safety conditions during diving are critical and long-term health of divers impacted (7.4.1). No occupational health and safety training is provided (7.4.2) and the situation of insurance is unclear (7.4.3).
	7.5. Fair and decent wages	Yes [1]	Individual revenue depends on the production volume of the farmer cooperative, but are usually higher when compared to other labour (7.5.1).
	7.6. Freedom of association and collective bargaining	Yes [1]	Scallop farmer cooperatives consist of voluntarily associated members, and are led by a temporarily elected president (7.6.1).
	7.7. Non-abusive disciplinary practices	Yes	No records of abusive disciplinary practices could be made (7.7.1).
	7.8. Working hours	Partly	During the work on the farm site, working time does not exceed a maximum of 8 hours. But, divers spend several hours under water, with little health precautions made (7.8.1). No overtime regulation in place.

[1] Please consider that this may be different for other parts of the scallop production chain, e.g. for contracted workers in scallop processing plants

6.4 Conclusions and future prospects

The results of this thesis provided a synthesis of the possible ecological and social consequences of scallop aquaculture on a coastal bay system. Findings suggested that the introduction of the bottom cultures has induced changes in the benthic community structure by providing settling substrate to hard-bottom fauna and food for higher trophic level species. The expansion of aquaculture activities would increase the risks for the loss of functional species groups and by that alter ecosystem functioning and decrease the system's resilience. Still, the comparatively low intensity and small-scale nature of aquaculture operations is likely to provide basis to its ecological long-term sustainability. The few technological requirements and low production costs make the conduction of cultures economically feasible for small-scale producers. Future emphasis should be given to guiding the social-ecological system towards increasing its resilience to external disturbances.

A promising and important field of research is the integration of the social carrying capacity (SCC, as discussed in *section 6.1.3*) that would complement the presented approach as to become a truly EAA (after Soto et al. 2008a). The concept is not only important for the social-ecological system (SES) of Sechura Bay – but for any other coastal aquaculture setting exposed to bivalve aquaculture. By integrating all important activities as to harmonize their conduction, this category is at the heart of integrated coastal zone management (ICZM) (McKindsey 2013). In addition, future research should address the assessment, simulation, and prediction of the risk of human activities related to aquaculture on the level of the SES. Due to the frequent occurrence of environmental disturbances such as ENSO, the Sechura Bay SES may in this context be used to study individual actor's and SES resilience. Management should focus on the maintenance of the small-scale nature of aquaculture operations, considering to help local producers to obtain international certification. The processes within the SES resulting from the recent ENSO 2015/16 should be carefully monitored, and the return of the system state to pre-ENSO conditions should be promoted.

The thesis successfully developed an ecosystem approach to aquaculture that integrates the entire ecosystem (i.e. food web dynamics). Although the Sechura case study represents a very unique coastal setting for bivalve aquaculture, the presented approach is still expected to be applicable to other systems (as discussed in *section 6.2.2*). By presenting methods for the estimation of ecological carrying capacity (i.e. the maximum "acceptable change", Ross et al. 2013) and resilience capacity this thesis provided a further step towards an ecosystem approach to aquaculture (see Figure 6.1). The approach should, nevertheless, be considered explorative. It goes beyond most single species methods for the estimation of ECC but may be adapted according to site-specific management targets that have to be carefully defined (see *section 6.2.1*).

On a global level, aquaculture receives increasing attention as a source of for protein produced for human consumption. The ever expanding industry faces several challenges related to setting the environmental and social limits to growth. Future aquaculture management will have, as an example, to acknowledge current environmental variability but also to address possible adaptation and mitigation strategies in the face of future developmental challenges and climate change. Increasing temperatures and enhanced ocean acidification may impact growth, reproduction, and survival of natural bivalve populations as well as cultured individuals. Regional environmental changes may shift distributional ranges of individual species, and may alter the range of areas suitable for aquaculture. The development of aquaculture projects, especially in tropical countries, needs to consider the ecological and social consequences – both short and long-term – resulting from these activities. The present thesis contributes to analyze in a quantitative form these potential consequences in a complex SES and provides a new set of tools that can be applied to other similar SES's where aquaculture is developed.

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ANNEX

ANNEX I

Supplements for Chapter 1

Supplemental Table S1.1. *World bivalve production originating from aquaculture during the period 1984-2013 (in metric tons) and the respective economic value (in US$). In addition, total production and economic value is shown for the different bivalve groups (oysters, clams, scallops, mussels), as well as the percentage contribution of these group's production and economic value to world bivalve production and value (% TP and % TV, respectively). Source of data: FAO 2016.*

Year	Total bivalve production		Oyster production					Clam production				
	tons	US$	tons	% TP	US$	% TV	US$ kg^{-1}	tons	% TP	US$	% TV	US$ kg^{-1}
1984	1916586	1864270	1030092	53.75	1247020	66.89	1.21	101694	5.31	164305.2	08.81	1.62
1985	2144329	2093206	1141354	53.23	1363400	65.14	1.20	121767	5.68	193235.4	9.23	1.59
1986	2309602	2527503	1179507	51.07	1634494	64.67	1.39	169993	7.36	259492.3	10.27	1.53
1987	2590454	2935754	1264703	48.82	1869828	63.69	1.48	211040	8.15	313373.9	10.67	1.49
1988	2925598	3348978	1331557	45.51	1976110	59.01	1.48	240898	08.23	426668.2	12.74	1.77
1989	2958368	3450252	1255774	42.45	1907519	55.29	1.52	312939	10.58	569294.8	16.50	1.82
1990	3049259	3811236	1250760	41.02	2192152	57.52	1.75	370344	12.15	613053.9	16.09	1.66
1991	3194975	4095498	1289008	40.35	2292909	55.99	1.78	452871	14.18	745640.2	18.21	1.65
1992	3875546	4796974	1554020	40.10	2443077	50.93	1.57	710748	18.34	1101812.6	22.97	1.55
1993	4899741	6324808	1876503	38.30	3070366	48.55	1.64	999677	20.40	1436350.2	22.71	1.44
1994	5890011	7619303	2649172	44.98	3955064	51.91	1.49	1218048	20.68	1713234.9	22.49	1.41
1995	6512072	8082274	3049489	46.83	4216234	52.17	1.38	1200501	18.44	1769987.9	21.90	1.47
1996	6609819	7927196	3036440	45.94	4018134	50.69	1.32	1201297	18.17	1740374.5	21.96	1.45
1997	6535431	7755848	2934841	44.91	3771809	48.63	1.29	1303958	19.95	1820259.9	23.47	1.40
1998	6790230	7131304	3275773	48.24	3534366	49.56	1.08	1411701	20.79	1935990.1	27.15	1.37
1999	7396790	7504361	3395621	45.91	3566496	47.53	1.05	1747666	23.63	2194689.9	29.25	1.26
2000	7541317	7756553	3611668	47.89	3604610	46.47	1.00	1574522	20.88	2032240.6	26.20	1.29
2001	8184043	7855833	3787803	46.28	3438752	43.77	0.91	1918815	23.45	2351318.2	29.93	1.23
2002	8696213	8275666	3885000	44.68	3538285	42.76	0.91	2145881	24.68	2606794.3	31.50	1.22
2003	9205336	8118780	4018401	43.65	2763018	34.03	0.69	2426699	26.36	2944353.3	36.27	1.21
2004	9600590	7700567	4157636	43.31	3043821	39.53	0.73	2652122	27.63	2137630.8	27.76	0.81
2005	9817634	8804706	4175147	42.53	3378224	38.37	0.81	2710728	27.61	2534867.3	28.79	0.94
2006	10321763	9532876	4331027	41.96	3461371	36.31	0.80	2955086	28.63	2845756.7	29.85	0.96
2007	10729042	10172976	4421183	41.21	3272406	32.17	0.74	3168140	29.53	3012622.2	29.61	0.95
2008	10485530	10712718	4169465	39.76	3552679	33.16	0.85	3237041	30.87	3136879.9	29.28	0.97
2009	11097244	10895844	4329467	39.01	3546063	32.55	0.82	3381677	30.47	3298164.5	30.27	0.98
2010	11913255	12097428	4549264	38.19	3827352	31.64	0.84	3762854	31.59	3637973.4	30.07	0.97
2011	11836772	12990016	4554428	38.48	4058452	31.24	0.89	3838418	32.43	3792856.7	29.20	0.99
2012	12219006	12820082	4745588	38.84	4096864	31.96	0.86	3935183	32.21	3849181.3	30.03	0.98
2013	12737849	14881826	4985985	39.14	4276462	28.74	0.86	4038589	31.71	3961349.3	26.62	0.98

Supplemental Table S1.1 (continued)

Year	Scallops					Mussels				
	t	**% TP**	**US$**	**% TV**	**US$ kg^{-1}**	**t**	**% TP**	**US$**	**% TV**	**US$ kg^{-1}**
1984	78588	4.10	100240.5	5.38	1.28	706212	36.85	352703.9	18.92	0.50
1985	122471	5.71	168141.7	8.03	1.37	758737	35.38	368429	17.60	0.49
1986	164274	7.11	242953.7	9.61	1.48	795828	34.46	390563.6	15.45	0.49
1987	196799	7.60	343489.1	11.70	1.75	917912	35.43	409062.3	13.93	0.45
1988	305554	10.44	533196.9	15.92	1.75	1047589	35.81	413003.5	12.33	0.39
1989	310991	10.51	492773	14.28	1.59	1078664	36.46	480665.3	13.93	0.45
1990	340807	11.18	548048.1	14.38	1.61	1087348	35.66	457982.2	12.02	0.42
1991	379215	11.87	617298.1	15.07	1.63	1073881	33.61	439650.8	10.74	0.41
1992	548862	14.16	863614.3	18.00	1.57	1061916	27.40	388470.7	8.10	0.37
1993	975337	19.91	1460658.5	23.09	1.50	1048224	21.39	357433.5	5.65	0.34
1994	1037543	17.62	1590059.2	20.87	1.53	985248	16.73	360944.7	4.74	0.37
1995	1153465	17.71	1646474.9	20.37	1.43	1108617	17.02	449577	5.56	0.41
1996	1276722	19.32	1690829.9	21.33	1.32	1095360	16.57	477857.3	6.03	0.44
1997	1206436	18.46	1682594.8	21.70	1.40	1090196	16.68	481184.4	6.20	0.44
1998	815910	12.02	1186665.9	16.64	1.45	1286846	18.95	474281.4	6.65	0.37
1999	874268	11.82	1255779.5	16.73	1.44	1379235	18.65	487395.9	6.50	0.35
2000	1047884	13.90	1527065.2	19.69	1.46	1307243	17.33	592637.3	7.64	0.45
2001	1102345	13.47	1456248.8	18.54	1.32	1375080	16.80	609514.2	7.76	0.44
2002	1113078	12.80	1437868.4	17.38	1.29	1552254	17.85	692718.9	8.37	0.45
2003	1066885	11.59	1426279.8	17.57	1.34	1693351	18.40	985129.6	12.13	0.58
2004	1047694	10.91	1597367.3	20.74	1.53	1743138	18.16	921748.4	11.97	0.53
2005	1138828	11.60	1831638.6	20.80	1.61	1792931	18.26	1059976.1	12.04	0.59
2006	1288410	12.48	1994917.7	20.93	1.55	1747240	16.93	1230829.8	12.91	0.70
2007	1452077	13.53	2214737.5	21.77	1.53	1687642	15.73	1673210.4	16.45	0.99
2008	1399744	13.35	2337554.4	21.82	1.67	1679281	16.02	1685605.3	15.74	1.00
2009	1568245	14.13	2489692.1	22.85	1.59	1817856	16.38	1561924.1	14.34	0.86
2010	1696145	14.24	2998071.9	24.78	1.77	1904993	15.99	1634029.9	13.51	0.86
2011	1489486	12.58	2811684.4	21.65	1.89	1954440	16.51	2327023.3	17.91	1.19
2012	1636292	13.39	2658039.6	20.73	1.62	1901942	15.57	2215997	17.29	1.17
2013	1850923	14.53	3267919.4	21.96	1.77	1862352	14.62	3376095	22.69	1.81

Supplemental Table S1.2. *Overview of all scallop producing countries for the year 2013, ranked according to their importance in term of production. For each country, the produced species and the respective percentage contribution to the country's total production are given (nei = not elsewhere included). Source of data: FAO 2016 (sum of culture and capture production).*

Rank	Country	Produced scallop species	Production (tons)
1	China	scallops nei (100%)	1608201
2	Japan	*Patinopecten yessoensis* (100%)	517744
3	USA	*Placopecten magellanicus* (98.62%), *Patinopecten caurinus* (0.59%), *Argopecten irradians* (0.53%), *Pecten maximus* (0.26%)	156897.8
4	Peru	*Argopecten purpuratus* (100%)	89872.4
5	Canada	*Placopecten magellanicus* (99.16%), *Chlamys islandica* (0.67%), scallops nei (0.17%)	64791
6	UK	*Pecten maximus* (62.3%), *Aequipecten opercularis* (37.7%)	50071
7	Argentina	*Zygochlamys patagonica* (100%)	42202
8	France	*Pecten maximus* (91.87%), *Aequipecten opercularis* (7.42%), scallops nei (0.71%)	30977
9	Australia	scallops nei (100%)	6750
10	Russia	*Patinopecten yessoensis* (79.27%), scallops nei (20.73%)	6199
11	Chile	*Argopecten purpuratus* (85.52%), scallops nei (14.48%)	5848
12	Faroe Islands	*Aequipecten opercularis* (100%)	5300
13	Isle of Man	*Aequipecten opercularis* (72.78), *Pecten maximus* (27.22%)	4769
14	Ireland	*Pecten maximus* (95.25%), *Aequipecten opercularis* (4.75%)	3077
15	Mexico	*Argopecten ventricosus* (100%)	2126
16	New Zealand	*Pecten novaezelandica* (93.29%), *Chlamys delicatula* (6.71%)	805
17	Indonesia	scallops nei (100%)	744
18	Norway	*Pecten maximus* (99.57%), scallops nei (0.43%)	704.01
19	Belgium	*Pecten maximus* (100%)	618
20	Greenland	*Chlamys islandica* (100%)	587
21	Republic of Korea	*Patinopecten yessoensis* (100%)	528
22	Italy	scallops nei (81.5%), *Pecten jacobaeus* (18.5%)	346
23	Spain	*Aequipecten opercularis* (52.03%), *Pecten maximus* (27.44%), scallops nei (20.36%), *Mimachlamy varia* (0.17%)	338.96
24	Thailand	scallops nei (100%)	324
25	Democratic People's Republic of Korea	*Patinopecten yessoensis* (100%)	200
26	Croatia	scallops nei (53.78%), *Pecten jacobaeus* (46.2%)	106
27	Philippines	scallops nei (100%)	45
28	Turkey	*Pecten jacobaeus* (100%)	3

Supplemental Table S1.3. *Overview of active contribution to conferences presenting parts of the PhD work as presented in this thesis.*

#	Conference name; location	Date	Authors	Title of presentation	Present. type
a	International Conference for Young Marine Researchers (YouMaRes) 4"; Oldenburg, Germany	Sep. 2013	**Kluger LC**, Wolff M, Taylor MH	Ecological and socio-economic feasibility of a long term scallop bottom culture in Sechura Bay, Northern Peru	Oral present.
b	"International Conference for Young Earth System Scientists (ICYESS)"; Hamburg, Germany	Sep. 2013	**Kluger LC**, Wolff M, Taylor MH	Ecological and socio-economic feasibility of scallop aquaculture in Sechura, North-Peru	Poster presenta -tion
c	"Rethinking Fisheries Sustainability – The Future of Fisheries Science"; Mazathlan, Mexico	Apr. 2014	**Kluger LC**, Wolff M, Taylor MH	Modelling trophic flows in a bay's system under the impact of intense scallop bottom culture	Poster presenta -tion
d	"IV Congreso de Ciencias del Mar del Perú" (CONCIMAR); Lima, Peru	Jun. 2014	**Kluger LC**, Wolff M, Taylor M	Modelando flujos tróficos en una bahía del Perú bajo el impacto del cultivo intensivo de concha de abanico (*A. purpuratus*)	Poster presenta -tion [in Spanish]
e	"IV Congreso de Ciencias del Mar del Perú" (CONCIMAR); Lima, Peru	Jun. 2014	Meyer S, Taylor MH, Aramayo Navarro VH, **Kluger LC**	Evaluación del impacto del cultivo de concha de abanico (*Argopecten purpuratus*) en la estructura de comunidad bentónica infaunal en la Bahía de Sechura, Peru	Poster presenta -tion [in Spanish] **
f	"Ecopath 30 years"; Barcelona, Spain	Nov. 2014	**Kluger LC**, Wolff M, Taylor MH	Carrying capacity simulations as a tool for ecosystem-based management of a scallop aquaculture system	Poster presenta -tion
g	"Congreso Latin-americano de ciencias del Mar" (COLACMAR); Santa Marta, Colombia	Oct. 2015	**Kluger LC**, Taylor MH, Mendo J, Wolff M, Taylor MH	Towards an ecosystem-based approach for the estimation of the ecological carrying capacity of a bay system exposed to scallop aquaculture	Digital oral /poster presenta -tion
h	"Congreso Latin-americano de Ciencias del Mar" (COLACMAR); Santa Marta, Colombia	Oct. 2015	Wolff M, Mendo J, Taylor MH, **Kluger LC**, Gil-Kodak P, Ysla L	SASCA – An interdisciplinary Peruvian-German research project towards a sustainability analysis of scallop culture in Sechura Bay, Peru.	Digital oral presenta -tion *

* The respective presentation was mainly prepared, and presented at the conference by LC Kluger
** The respective presentation was prepared mainly by S Meyer, and presented at the conference by LC Kluger

(a)

Kluger LC, Wolff M, Taylor M (09/2013):
Ecological and socio-economic feasibility of
a long term scallop bottom culture in Sechura Bay, Northern Peru.
- Oral presentation -
"International Conference for Young Marine Researchers" (YouMaRes) 4;
Oldenburg, Germany

ECOLOGICAL AND SOCIO-ECONOMIC FEASIBILITY OF A LONG-TERM SCALLOP BOTTOM CULTURE IN SECHURA BAY; NORTHERN PERU

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Aquaculture has become an important factor to support global fisheries in achieving sustainable levels for overexploited natural stocks. The Peruvian scallop *Argopecten purpuratus* represents one of the economically most important cultivated molluscs along the South American Pacific coast, with a major cultivation spot in Sechura Bay, North Peru (5.6 °S, 80.9 °W). Here, culture activities exponentially increased during the last years and today represent an important socioeconomic sector, directly involving about 2500 artisanal fishers and with an annual export value of >US$70million. A large part of the cultivation, however, is still conducted without legal authorization thus formal control. Multi-use of the bay, overlapping stakeholder groups, and complex political structures make interdisciplinary management efforts for the bay's system a challenging priority. A recently initiated study will determine the bay's ecological and economic carrying capacity in order to achieve sustainability of scallop culture in the region. Carrying capacity was defined as the maximum amount of cultivated organisms that a system can support without causing unacceptable impacts on the ecological or social level. Using different modeling approaches (e.g. ECOPATH), respective limits will be determined. Ecological experiments will provide information to establish a trophic model by investigating how the increase of scallops' biomass due to culture efforts has changed trophic fluxes within the system. Data from ecological and socio-economic surveys will be integrated to explore the response of the system under different environmental conditions and culture scenarios. However, for a holistic and realistic approach to analyze sustainable production levels, perceptions of different stakeholder groups towards sustainability and what represents unacceptable changes in the system need to be integrated. The resulting carrying capacity thresholds are urgently needed to establish a decision-framework supporting both local fishers and managers in their difficult task of finding an ecological and socio-economic sustainable level of scallop cultivation in this region of Peru.

Key words: Sustainable fisheries, ecological modelling, carrying capacity, scallop aquaculture

(b)

Kluger LC, Wolff M, Taylor MH (09/2013):
Ecological and socio-economic feasibility of scallop aquaculture in Sechura, North-Peru.
- Poster presentation -
"International Conference for Young Earth System Scientists (ICYESS)"; Hamburg, Germany.

ECOLOGICAL AND SOCIO-ECONOMIC FEASIBILITY OF SCALLOP AQUACULTURE IN SECHURA; NORTH-PERU

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Aquaculture has become an important factor to support global fisheries in achieving sustainable levels for overexploited natural stocks. The Peruvian scallop Argopecten purpuratus represents one of the economically most important bivalve along the Pacific coast of South America. Sechura Bay (5.6 °S, 80.9 °W), located close to the northern border of Peru, has become a major spot for its cultivation. Here, culture activities exponentially increased during the last years and today represent an important socio-economic factor, with approximately 2500 artisanal fishers involved and an export value of more than 70 million US$ per year. A large part of cultivation, however, is still conducted without legal authorization thus formal control, which makes management efforts for the bay's system a challenging priority. A recently initiated interdisciplinary study will therefore determine the bay's carrying capacity in ecological and socio-economic terms. Carrying capacity was defined as the maximum amount of cultivated organisms that a system can support without causing an unacceptable impact on the ecological or social level. Using different modelling approaches (e.g. ECOPATH), respective limits will be determined. Ecological experiments will provide information to establish a trophic model by investigating how the increase of scallops' biomass due to culture efforts has changed trophic fluxes. Data from ecological and socio-economic surveys will be integrated to explore the response of the system under different culture scenarios and environmental conditions, such as the occurrence of El Niño. Resulting carrying capacity thresholds are urgently needed to establish a decision-framework supporting both local fishers and managers in their difficult position of finding a sustainable long-term level of scallop culture in Sechura Bay, Peru. Understanding possible future statutes of this local bay and developing an according adaptive management plan will help to adapt other culture system worldwide to a changing earth environment.

Although the theory of carrying capacity appears straight forward, the modelling process is complicated by the lack of data, multi-use of the bay, overlapping stakeholder groups and complex political structures surrounding the bay's system. Careful observation and mapping of the social structure, consulting and integrating different stakeholder's interests are crucial for the identification of what represents unacceptable levels of disturbance. Effectiveness of resulting management suggestions will strongly depend on acceptance and active participation of the involved population. The challenge of ecological and socio-economic modelling is therefore not only to define certain limits to production, but also to establish a useful and applicable decision-framework for local stakeholders and managers. One key for a successful application of new management strategies will be a continuous communication flow between different participatory levels. Anticipating future scenarios of coastal systems became a key goal of ecosystem-based management, for which ecological modelling and the concept of carrying capacity represent important tools. Techniques to address the social level, however, still have to be further developed. The presented study therefore aims on contributing to on-going research on the estimation of carrying capacity for aquaculture by providing a holistic approach. Presented results can be taken as an example for the governance of other coastal system exposed to aquaculture.

(c)

Kluger LC, Wolff M, Taylor MH (04/2014):
Modelling trophic flows in a bay's system under the impact of intense scallop bottom culture.
- Poster presentation -
International Conference "Rethinking Fisheries Sustainability – The Future of Fisheries Science";
Mazathlán, Mexico.

MODELLING TROPHIC FLOWS IN A BAY'S SYSTEM
UNDER THE IMPACT OF INTENSE SCALLOP BOTTOM CULTURE

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The Peruvian scallop *Argopecten purpuratus* is the economically most important bivalve species along the Pacific coast of South America. Sechura Bay (North Peru) has developed into a hotspot for its cultivation. Here, culture activities exponentially increased during the last five years, with approximately 2500 artisanal fishers presently involved and export values of more than 70 million US$ per year. The present study aims at the determination of the bay's ecological carrying capacity in order to find ecologically sustainable limits to growth of this aquaculture activity. The system impact of scallop culture was analysed by comparing mass-balanced trophic models of the current with pre-culture conditions. Results suggest that the increased scallop biomass has changed system characteristics, e.g. a greater part of the phytoplankton is consumed, and biomass of its predators has largely increased, while competitors' biomass has decreased. Culture scallop biomass is currently at 162 t km^{-2} and ecological carrying capacity may soon be reached if management actions are not undertaken. Resulting thresholds are urgently needed to establish a decision-framework supporting both local fishers and managers in their challenging task of finding sustainable long-term levels for scallop culture in Sechura Bay.

(d)

Kluger LC, Wolff M, Taylor M (06/2014):
Modelando Flujos Tróficos en una Bahía del Perú Bajo el Impacto del Cultivo Intensivo de Concha de Abanico (A. Purpuratus)
Poster presentation [in Spanish];
Conference "IV Congreso de Ciencias del Mar del Perú (CONCIMAR)", Lima, Peru

MODELANDO FLUGOS TRÓFICOS EN UNA BAHÍA DEL PERÚ
BAJO EL IMPACTO DEL CULTIVO INTENSIVO DE CONCHA DE ABANICO
(*ARGOPECTEN PURPURATUS*)

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La bahía de Sechura en el norte de Perú se ha convertido en el centro del cultivo de la concha de abanico (*Argopecten purpuratus*) en América del Sur. Aquí las actividades de cultivo crecieron exponencialmente durante los últimos cinco años y actualmente existen 2500 pescadores artesanales vinculados a esta actividad que genera anualmente más de US$70 millones en exportaciones. El objetivo del presente estudio es la determinación de la capacidad de carga ecológica de la bahía de Sechura que permita identificar límites sostenibles para el desarrollo del cultivo. El impacto sistémico del cultivo se analizó mediante la comparación de modelos tróficos (usando Ecopath) de la bahía en la situación pre-cultivo (1996) y la situación actual. Los resultados preliminares sugieren que las características del sistema han cambiado debido a la introducción del cultivo y al subsecuente incremento de la biomasa de conchas: una mayor parte del fitoplancton es ahora consumida, y la biomasa de los depredadores de las conchas ha incrementado, mientras que la de los competidores ha disminuido. La biomasa de *A. purpuratus* actualmente es estimada en 162 t km^{-2} y la capacidad de carga ecológica del sistema puede ser alcanzada muy pronto si el volumen de las conchas cultivadas sigue aumentándose. Se espera que los resultados del presente estudio permitan beneficiar, tanto a los pescadores como a los administradores locales, en la difícil tarea de encontrar niveles sostenibles de cultivo de concha de abanico en la bahía de Sechura en el largo plazo.

Palabras claves: Concha de abanico, *Argopecten purpuratus*, modelamiento trófico, Ecopath, Bahía de Sechura /Perú

(e)

Kluger LC, Taylor MH, Mendo J, Wolff M (10/2015):
Towards an ecosystem-based approach for the estimation of the ecological carrying capacity of a bay system exposed to scallop aquaculture.
- Digital oral /poster presentation -
"Congreso Latinoamericano de Ciencias del Mar (COLACMAR)";
Santa Marta, Colombia.

TOWARDS AN ECOSYSTEM-BASED APPROACH FOR THE ESTIMATION OF THE ECOLOGICAL CARRYING CAPACITY OF A BAY SYSTEM EXPOSED TO SCALLOP AQUACULTURE

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Bivalve aquaculture production takes place in many coastal ecosystems, providing livelihood to thousands of people. Knowledge on the ecological carrying capacity (ECC) of an ecosystem under the impact of such cultures is crucial for long-term sustainability, since overstocking of culture combined with critical environmental changes may result in bivalve mass mortalities and may ultimately cause severe consequences for the entire ecosystem. As yet, most approaches have focussed on bivalve-food (phytoplankton) interactions, neither considering the interaction with other species, nor the overall impact on the ecosystem. The present study follows a holistic approach to estimate the ECC for a bay system in Northern Peru which has recently developed into a hotspot for scallop (*Argopecten purpuratus*) bottom culture. Using a trophic food web model, the further expansion of culture activities is explored by forcing scallop biomass to increase to 4 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 results of this work are expected to aid management of coastal ecosystems exposed to bivalve bottom culture by providing ecosystem-based estimates of ECC, defined as the maximum degree of tolerable change, in order to ensure the long-term sustainable use of these valuable marine resources.

Keywords: ecological carrying capacity, bivalve bottom culture, ecosystem-based coastal zone management, trophic modelling

(f)

Wolff M, Mendo J, Taylor MH, **Kluger LC**, Gil-Kodak P, Ysla L (10/2015):
SASCA – An interdisciplinary Peruvian-German research project towards a sustainability analysis of scallop culture in Sechura Bay, Peru.
- Digital oral /poster presentation -
"Congreso Latinoamericano de Ciencias del Mar (COLACMAR)";
Santa Marta, Colombia.

SASCA – AN INTERDISCIPLINARY PERUVIAN-GERMAN RESEARCH PROJECT TOWARDS A SUSTAINABILITY ANALYSIS OF SCALLOP CULTURE IN SECHURA BAY, PERU

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Aquaculture has become an important factor to support global fisheries in achieving sustainable levels for overexploited natural stocks. The Peruvian scallop *Argopecten purpuratus* represents one of the economically most important cultivated molluscs along the South American Pacific coast, with a major cultivation spot in Sechura Bay, Peru. Here, the species is grown in bottom cultures, and the intensity and area extent of the cultivation activities have continuously increased over the last years. About 2500 artisanal fishers and 20000 additional personnel are currently involved in the scallop production chain, and with an annual export value of 158mill.US$ (in 2013) the activity represents an important socioeconomic sector for the region. As overstocking, especially combined with critical environmental changes may lead to scallop mass mortalities and may ultimately cause severe impacts on the entire ecosystem, the understanding of already imposed changes is crucial for the identification of long-term sustainable levels. The introduction of large scallop biomass quantities may change the benthic community structure by providing settling substrate for hard-bottom fauna in an initially soft-bottom habitat. An interdisciplinary study (SASCA) initiated in 2013 aims at the determination of the bay's carrying capacity – the maximum amount of cultivated organisms that a system can support without causing unacceptable impacts on the system itself – with regard to the physical, production, ecological and social dimension. Several ecological and ecophysiological experiments were conducted to investigate the impact of scallop bottom culture on the benthic and infaunal community, as well as the respiratory demands and optimum growth of scallops. The systemic impact of scallop culture was evaluated using trophic modelling, and different modelling approaches were combined for the estimation of carrying capacity. Data from a socio-economic survey were integrated to explore the response of the system under different environmental conditions and culture scenarios. The here presented project aims at contributing to the on-going research on the estimation of carrying capacity for coastal systems exposed to bivalve aquaculture enterprises through a holistic research approach. The results are expected to help guiding the governance of Sechura bay and may also be relevant for other coastal systems exposed to aquaculture.

(g)

Cite as:
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Scientific advice for management

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 the center for mariculture in Peru. Here, the Peruvian bay scallop (*Argopecten purpuratus*) is grown in bottom cultures and the intensity and area extent of the cultivation activities have continuously increased over the years. Currently, the business involves 2500 artisanal fishermen and an export value of more than 100 million US$ per year, but activities are still expanding. For previous cultivation efforts it was shown that too high stocking densities of scallops combined with critical environmental changes may cause mass mortalities and eventually the total depletion of scallop populations (e.g. Wolff 1985; Wolff & Mendo 2000; Zhang et al. 2006; Koch et al. 2005). Accordingly, the ecosystem-based assessment of the current situation and the determination of long-term sustainable limits to scallop culture for the bay of Sechura became crucial. In order to evaluate ecosystem changes following the introduction of great amounts of scallop biomass to the bay and to estimate the long term carrying capacity of the bay for scallop culture, a bilateral German-Peruvian research project was initiated in 2012 (SASCA: **S**ustainability **A**nalysis of **Sca**llop Culture in Sechura Bay; www.sascaperu.wordpress.com). The results of this project may be applied to other coastal systems exposed to similar development by representing an ecosystem-based approach for integrated management. Monitoring data of the bay's benthic community, harvest volumes (scallops and other fishery target species) as well as data of density and biomass of cultivated scallops and of primary production were assembled. In addition, *in-situ* experiments on scallop filtration and respiration rates were conducted. The ecological and physiological data were used to construct a trophic steady state energy flow model and the ecological carrying capacity was estimated by a step-wise increase of scallop's biomass (Figure 1 and 2).

Ecological carrying capacity was reached when more food was needed than produced by the system, indicated by ecotrophic efficiencies for the phytoplankton group greater than one (after Wolff 1994; Jiang & Gibbs 2005; Byron et al. 2011a,b). The model was further subjected to the following scenarios of varying conditions and the system response was explored using the EwE software: 1) Seasonal changes in primary productivity as derived from satellite data and *in-situ* measurements; 2) Reduction in primary productivity as measured during the strong El Niño event in

1997/98; 3) Continuous increase in cultivated scallop biomass following the trajectory of the past five years, and 4) considering the “bottleneck month” (February) of lowest primary productivity in the bay.

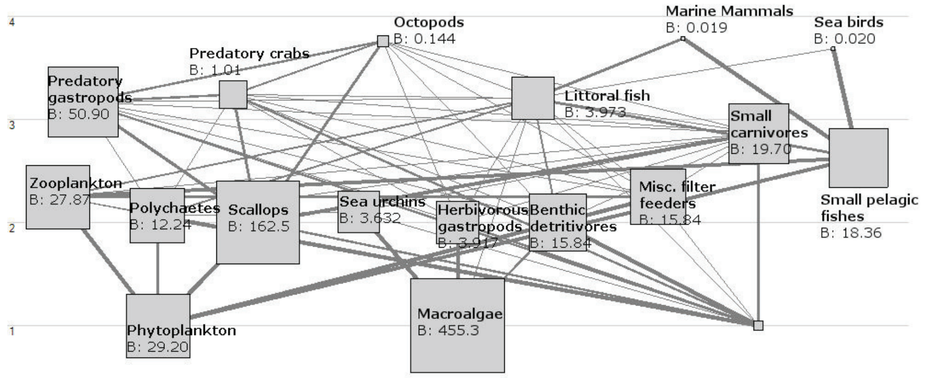

Figure 1. *Flow diagram of the trophic structure of the Sechura bay system. All biomass flows in t km^{-2}.*

Results from these model explorations suggest: that a) the current magnitude of scallop bottom culture appears sustainable under environmental conditions of normal years, b) the carrying capacity of the bay for scallop culture greatly varies seasonally and inter-annually, and c) that under conditions of an El Niño induced (several months) reduction in primary productivity the bay`s carrying capacity is expected to fall below the level of current magnitude of scallop bottom culture. Carrying capacity simulations can be used to limit aquaculture growth in a responsible way (Byron et al. 2011a). In the case of Sechura bay, resulting thresholds and management scenarios are urgently needed providing a valuable tool for both local fishers and managers in their challenging task of finding sustainable long-term levels for this important socio-economic activity in Sechura Bay.

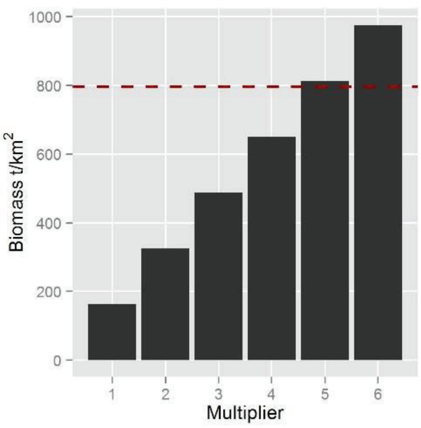

Figure 2. *Calculation of ecological carrying capacity by a step-wise increase of scallop’s biomass. Multiplier 1 represents current ecosytem state (with scallop biomass at 162 t km^{-2}). Dashed line represents the carrying capacity threshold of 796.25 t km^{-2} defined as the last system state at which ecotrophic efficiency (EE) of phytoplankton is still below 1.*

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ANNEX II

Supplements for Chapter 2

Supplemental Table S2.1. *Comparison of species comprising the different model compartments for the steady-state models for Sechura bay in 1996 (after Taylor et al. 2008d) and 2010.*

Functional group	1996	2010
2. Macroalgae	*Caulerpa sp.* (99.4%), *Rhodymenia sp.* (0.6%)	*Caulerpa sp.* (96.1%), *Chondracanthus chamissoi* (1.6%), *Rhodymenia sp.* (1.3%), *Rhodophyta* (0.4%), *Ulva fasciata* (0.2%), *Codium fragile* (0.2%), *Grateulopia doriphora* (0.1%), *Ulva sp.* (0.1%)
5. Scallops	*Argopecten purpuratus*	*Argopecten purpuratus*
6. Sea urchins	*Arbacia sp.* (98.3%), *Tetrapigus niger* (1.7%)	*Encope sp.* (54.9%), *Arbacea spatuligera* (45.1%)
7. Herbivorous gastropods	*Aplysia sp.* (51.2%), *Littorina sp.* (21.3%), *Scurria sp.* (10.7%), *Astrea buschii* (8.4%), *Tegula atra* (5.0%), *Tegula verrucosa* (1.1%), *Chiton sp.* (0.6%), *Tegula sp.* (0.5%), *Anachis sp.* (0.5%), *Mitrella sp.* (0.3%), *Columbella sp.* (0.2%)	*Aplysia juliana* (32.1%), *Tegula picta* (55.9%), *Mitrella sp.* (6.9%), *Chiton sp.* (2.6%), *Mitra swainsonii* (1.6%), *Anachis sp.* (0.9%)
8. Benthic detrivores	*Clypeasteroida* (35.8%), *Pagurus sp.* (21.5%), *Brandtothuria sp.* (7.7%), *Turritella broderipiana* (4.7%), *Ophiuroidea* (3.5%), *Majidae* (3.3%), *Eurypanopeus sp.* (1.7%), *Dissodactylus sp.* (1.2%), *Litopenaeus sp., Farfantepenaeus californiensis, Penaeus sp.*	*Cycloxanthops sexdecimdentatus* (18.0%), *Hepatus chiliensis* (15.8%), *Holothuria sp.* (15.2%), *Crepidula sp.* (10.6%), *Inachoides microhynchus* (8.5%), *Dromia sp.* (8.1%), *Turritella broderipiana* (6.7%), *Acanthonix petiverii* (5.0%), *Gammarus sp.* (3.0%), *Pleuroncodes monodon* (2.5%), *Petrochirus californiensis* (1.7%), *Panopeus sp.* (1.5%), *Pilumnoides sp.* (1.2%), *Ophiuroidea* (0.6%), *Microphrys platysoma* (0.6%), *Dardanus sp.* (0.4%), *Euripanopeus sp.* (0.3%), *Mursia gaudichaudii* (0.2%), *Pachycheles sp.* (0.1%), *Crucibulum monticulus* (0.1%), *Alpheus sp.* (0.1%), *Crepipatella sp.* (0.0%), *Petrolisthes sp.* (0.0%)
9. Miscellaneous filter feeders	*Actinia sp.* (61.6%), *Tagelus sp.* (26.7%), *Chione sp.* (5.8%), *Halodakra subtrigona* (3.4%), *Glycimeris sp.* (2.2%), *Terebra purdyae* (0.3%)	*Tagelus dombeii* (77.9%), *Transennella pannosa* (15.0%), *Porifera* (6.6%), *Pennatulacea* (0.3%), *Cnidaria* (0.1%), *Megabalanus sp.* (0.1%)
10. Predatory gastropods	*Sinum cymba* (45.5%), *Thais chocolata* (26.2%), *Bursa sp.* (9.6%), *Priene sp.* (7.8%), *Thais kiosquiformis* (3.7%), *Hexaplex brassica* (3.5%), *Thais haemastoma* (1.6%), *Bursa ventricosa* (1.3%), *Bursa nana* (0.5%)	*Bursa ventricosa* (42.7%), *Stramonita chocolata* (32.9%), *Sinum cymba* (11.3%), *Conus regularis* (5.5%), *Ocenebra buxea* (2.8%), *Hexaplex brassica* (2.5%), *Conus patricius* (2.1%)
11. Small carnivores	*Crassilabrum sp.* (54.4%), *Polinices uber* (26.4%), *Solenosteira fusiformes* (8.9%), *Triumphis distorta* (5.5%), *Natica unifasciata* (1.4%), *Nassencoarius sp.* (1.2%), *Prunum sp.* (1.1%), *Oliva sp.* (1.0%)	*Solenosteira gatesi* (46.0%), *Solenosteira fusiformes* (37.8%), *Prunum curtum* (10.1%), *Polinices uber* (4.0%), *Nassarius sp.* (1.0%), *Nassarius gayi* (1.0%), *Pseudosquillopsis sp.* (0.1%), *Ephitonium sp.* (0.0%)
12. Predatory crabs	*Cancer porteri* (94.2%), *Callinectes arcuatus* (4.2%), *Callinectes toxotes* (1.6%)	*Portunus asper* (77.7%), *Arenaeus mexicanus* (22.3%)
13. Octopods	*Octopus mimus*	*Octopus mimus*

Supplemental Table S2.2. *List of taxonomic groups (family-level) used for rank-log abundance and ABC plots. Groups are listed alphabetically, with biomass and abundance values (standardized per m^{-2} by dividing by the number of sampling stations) for both years (1996 vs. 2010) and respective ranks. A minus indicates absence of this group in the respective year*

Species	**Biomass**				**Abundance**			
	1996		2010		1996		2010	
	Weight	Rank	Weight	Rank	N°	Rank	N°	Rank
Actiniidae	7.1572	7	-	-	0.0423	28	-	-
Aethridae	-	-	2.2369	7	-	-	0.0484	23
Alpheidae	0.0410	35	0.0073	34	0.0423	29	0.0081	32
Aplysiidae	8.9754	5	1.0055	18	0.1409	18	0.0081	33
Arbaciidae	24.4640	1	1.6382	12	1.0704	7	0.0242	28
Balanidae	-	-	0.0050	35	-	-	0.0081	36
Buccinidae	0.9920	20	13.3848	2	0.0986	21	1.1371	6
Bursidae	5.1568	10	33.6194	1	0.2254	16	1.7581	4
Calappidae	-	-	0.0243	30	-	-	0.0081	37
Calyptraeidae	-	-	1.5126	14	-	-	1.5403	5
Cancellariidae	0.0458	34	-	-	0.0563	26	-	-
Cancridae	7.1452	8	-	-	0.1409	19	-	-
Chitonidae	0.1065	31	0.0812	28	0.3380	14	0.7419	9
Columbellidae	0.1779	27	0.2452	25	3.7183	2	0.5565	11
Conidae	-	-	5.9812	4	-	-	0.0161	30
Diogenidae	-	-	0.2925	24	-	-	0.7581	8
Dromiidae	-	-	1.1412	16	-	-	0.0565	21
Epialtidae	0.0135	39	0.7077	21	0.0423	27	0.6048	10
Epitoniidae	-	-	0.0017	36	-	-	0.0081	35
Gammaridae	0.0251	37	0.4267	22	0.3240	14	19.0726	1
Hiatellidae	0.2580	26	-	-	0.5916	9	-	-
Holothuriidae	2.6192	15	2.1564	9	0.0563	25	0.0403	24
Inachoididae	0.0207	38	-	-	0.3380	13	-	-
Littorinidae	3.7285	11	-	-	0.0141	37	-	-
Lottiidae	1.8852	16	-	-	1.5070	5	-	-
Majidae	1.1351	19	1.2897	15	42.2817	1	3.3307	3
Marginellidae	0.1252	29	1.5895	13	0.0704	24	0.9194	7
Mellitidae	12.18	4	1.9939	10	0.0141	35	0.0242	29
Mitridae	-	-	0.0515	29	-	-	0.0323	25
Munididae	-	-	0.3578	23	-	-	0.1855	16
Muricidae	21.7728	3	2.2034	8	0.5070	11	0.0565	22
Nassariidae	0.1338	28	0.3075	23	0.2817	15	0.4677	13
Naticidae	23.6870	2	9.5321	3	0.5493	10	0.1613	17
Neoleptonidae	0.3916	25	-	-	0.0141	36	-	-
Olvidae	0.1107	30	-	-	0.0141	38	-	-
Ophiactidae	0.0028	40	-	-	0.0704	23	-	-
Ophiuroidea	1.2009	18	0.0826	27	0.0282	32	0.0968	20
Paguridae	7.3066	6	-	-	0.1690	17	-	-
Parasquillidae	-	-	0.0182	32	-	-	0.0323	27
Pilumnoididae	0.0493	33	0.1702	26	0.1127	20	0.4677	14
Pinnotheridae	0.5487	23	-	-	0.6620	8	-	-
Porcellanidae	0.0593	32	0.0173	33	3.0704	3	0.0323	26
Portunidae	0.4423	24	1.01	17	0.0423	30	0.0968	19
Pseudolividae	0.6134	22	-	-	0.0423	31	-	-
Ranellidae	3.7125	12	0.0188	31	0.0704	22	0.0081	34
Solecurtidae	3.0989	13	4.0498	5	1.1972	6	0.4758	12
Terebridae	0.0293	36	-	-	0.0141	39	-	-
Turbinidae	2.6252	14	1.7505	11	1.6620	4	0.1936	15
Turritellidae	1.7242	17	0.9434	19	0.0282	33	0.0161	31
Veneridae	0.6787	21	0.7780	20	0.0141	34	0.1129	18
Xanthidae	7.0147	9	2.8049	6	0.3803	12	4.0323	2

Supplemental Table S2.3. *Results of the SIMPER analysis testing for the effect of year, listing the average contribution of each group to overall dissimilarity (contr), the respective standard deviation of contribution (sd), the ratio of average to standard deviation of contribution (ratio), the average biomasses of any group in each compared treatment (av.B (1996), av.B (2010), standardized per* m^{-2} *by dividing by the number of sampling stations), and the cumulative contribution of each group to overall dissimilarity, scaled to percentages(cumsum). Please note that all calculations (except for biomass) were done on fourth-root transformed data. Overall dissimilarity: 74.96%*

	contr	sd	ratio	av.B (1996)	av.B (2010)	cumsum
Caulerpaceae	0.10788	0.090426	1.1931	311.7267	437.6201	0.1439
Pectinidae	0.07967	0.079836	0.9979	20.8725	147.3884	0.2502
Bursidae	0.05499	0.060431	0.9099	5.1568	33.6194	0.3236
Xanthidae	0.03863	0.033988	1.1365	7.0147	2.8049	0.3751
Buccinidae	0.03826	0.045189	0.8466	0.9920	13.3848	0.4261
Arbaciidae	0.03209	0.058973	0.5442	24.4639	1.6382	0.4690
Naticidae	0.02909	0.049465	0.5881	23.6870	9.5321	0.5078
Majidae	0.02645	0.023194	1.1402	1.1351	1.2897	0.5430
Paguridae	0.02613	0.032546	0.8030	7.3066	0.0000	0.5779
Muricidae	0.02251	0.051187	0.4398	21.7728	2.2034	0.6079
Rhodymeniaceae	0.01731	0.040221	0.4304	1.9179	5.8635	0.6310
Epialtidae	0.01615	0.022000	0.7339	0.0135	0.7077	0.6526
Mellitidae	0.01557	0.047221	0.3296	12.1800	1.9939	0.6733
Marginellidae	0.01505	0.028621	0.5258	0.1252	1.5895	0.6934
Turbinidae	0.01480	0.032340	0.4575	2.6252	1.7505	0.7132
Littorinidae	0.01366	0.024030	0.5682	3.7285	0.0000	0.7314
Gammaridae	0.01349	0.021185	0.6367	0.0251	0.4267	0.7494
Solecurtidae	0.01279	0.040096	0.3189	3.0989	4.0498	0.7664
Portunidae	0.01080	0.029905	0.3611	0.4423	1.0100	0.7808
Cancridae	0.01068	0.032063	0.3331	7.1452	0.0000	0.7951
Aplysiidae	0.01027	0.033559	0.3059	8.9754	1.0055	0.8088
Diogenidae	0.00963	0.018356	0.5247	0.0000	0.2925	0.8216
Chitonidae	0.00924	0.014532	0.6357	0.1065	0.0812	0.8340
Gigartinaceae	0.00911	0.028229	0.3228	0.0000	7.1987	0.8461
Pilumnoididae	0.00799	0.014480	0.5514	0.0493	0.1702	0.8568
Columbellidae	0.00784	0.016896	0.4637	0.1779	0.2452	0.8672
Nassariidae	0.00761	0.018821	0.4042	0.1338	0.3075	0.8774
Calyptraeidae	0.00684	0.019631	0.3485	0.0000	1.5126	0.8865
Ophiuroidea	0.00672	0.020342	0.3304	1.2009	0.0826	0.8955
Holothuriidae	0.00638	0.035491	0.1798	2.6192	2.1564	0.9040
Turritellidae	0.00561	0.023486	0.2388	1.7242	0.9434	0.9114
Actiniidae	0.00552	0.032048	0.1722	7.1572	0.0000	0.9188
Aethridae	0.00513	0.025113	0.2041	0.0000	2.2369	0.9256
Munididae	0.00465	0.022729	0.2044	0.0000	0.3578	0.9318
Dromiidae	0.00428	0.017657	0.2423	0.0000	1.1412	0.9375
Pinnotheridae	0.00423	0.016125	0.2622	0.5487	0.0000	0.9432
Veneridae	0.00406	0.020320	0.1999	0.6787	0.7780	0.9486
Lottiidae	0.00402	0.017578	0.2288	1.8852	0.0000	0.9540
Neoleptonidae	0.00357	0.019315	0.1849	0.3916	0.0000	0.9587
Halymenciaceae	0.00331	0.015743	0.2101	0.0000	0.5290	0.9632
Pseudolividae	0.00326	0.019920	0.1636	0.6134	0.0000	0.9675
Codiaceae	0.00314	0.014314	0.2194	0.0000	0.9200	0.9717
Olvidae	0.00287	0.010837	0.2651	0.1107	0.0000	0.9755
Conidae	0.00284	0.021732	0.1306	0.0000	5.9812	0.9793
Ranellidae	0.00274	0.015282	0.1795	3.7125	0.0188	0.9830
Porcellanidae	0.00259	0.010210	0.2541	0.0593	0.0173	0.9864
Alpheidae	0.00191	0.008993	0.2122	0.0410	0.0073	0.9890
Mitridae	0.00158	0.010155	0.1557	0.0000	0.0515	0.9911
Cancellariidae	0.00153	0.009508	0.1613	0.0458	0.0000	0.9931
Hiatellidae	0.00127	0.010722	0.1188	0.2580	0.0000	0.9948
Parasquillidae	0.00112	0.005945	0.1877	0.0000	0.0182	0.9963
Terebridae	0.00094	0.008082	0.1168	0.0293	0.0000	0.9976
Inachoididae	0.00054	0.004492	0.1200	0.0207	0.0000	0.9983
Ophiactidae	0.00041	0.003480	0.1188	0.0028	0.0000	0.9989
Calappidae	0.00037	0.003924	0.0945	0.0000	0.0243	0.9993
Balanidae	0.00029	0.003068	0.0941	0.0000	0.0050	0.9997
Epitoniidae	0.00020	0.002150	0.0943	0.0000	0.0017	1.0000

ANNEX III

Supplements for Chapter 4

Supplemental Table S4.1. *Supply-demand information for all functional groups as extracted from the Ecopath models at simulation year 100 for all culture scenarios. The scenario number (N°) and respectively introduced scallop biomass (Scallop B, in t km^{-2}), the functional group numbers (Group) and respective functional group's biomass (Group B) as well as the percentage contribution of a functional group to total system biomass (% of TSB) is given. D_i = supply (predation), S_i = demand (consumption), with Sum D_i describing the sum of predation flows on group i, and Sum S_i depicting the sum of all predation flows to group i.*

N°	Scallop B	Group	Group B	% of TSB	Sum D_i	Log (D_i)	Sum S_i	Log (D_i)
1	28	3	29.303	8.32	4635.99	3.67	1272.58	-3.11
		4	133.762	37.96	194.59	2.29	105.77	-2.02
		5	27.491	7.80	310.35	2.49	9.55	-0.98
		6	3.720	1.06	10.86	1.04	1.79	-0.25
		7	3.955	1.12	13.63	1.13	4.21	-0.63
		8	18.224	5.17	25.59	1.41	25.01	-1.40
		9	19.713	5.59	89.16	1.95	19.09	-1.28
		10	65.267	18.52	212.26	2.33	103.94	-2.02
		11	20.544	5.83	41.31	1.62	10.24	-1.01
		12	0.954	0.27	6.83	0.84	1.75	-0.24
		13	0.088	0.03	1.23	0.09	0.29	0.54
		14	2.402	0.68	29.36	1.47	1.88	-0.27
		15	24.554	6.97	519.88	2.72	16.56	-1.22
		16	2.399	0.68	18.78	1.27	0.91	0.04
2	37	3	28.998	8.10	4555.66	3.66	1251.13	-3.10
		4	131.347	36.68	190.49	2.28	103.94	-2.02
		5	36.847	10.29	409.19	2.61	13.08	-1.12
		6	3.718	1.04	10.85	1.04	1.79	-0.25
		7	3.961	1.11	13.66	1.14	4.22	-0.63
		8	18.089	5.05	25.52	1.41	24.81	-1.40
		9	19.253	5.38	87.06	1.94	18.65	-1.27
		10	65.660	18.33	214.42	2.33	104.64	-2.02
		11	20.385	5.69	41.00	1.61	10.15	-1.01
		12	0.956	0.27	6.85	0.84	1.75	-0.24
		13	0.089	0.03	1.24	0.09	0.29	0.54
		14	2.386	0.67	29.11	1.46	1.86	-0.27
		15	24.078	6.72	509.36	2.71	16.17	-1.21
		16	2.359	0.66	18.45	1.27	0.89	0.05
3	74	3	27.864	7.30	4258.49	3.63	1171.74	-3.07
		4	121.704	31.90	174.48	2.24	96.73	-1.99
		5	73.694	19.32	768.91	2.89	28.76	-1.46
		6	3.709	0.97	10.80	1.03	1.78	-0.25
		7	3.983	1.04	13.77	1.14	4.23	-0.63
		8	17.553	4.60	25.21	1.40	24.01	-1.38
		9	17.432	4.57	78.81	1.90	16.93	-1.23
		10	67.902	17.80	225.78	2.35	108.64	-2.04
		11	19.793	5.19	39.84	1.60	9.84	-0.99
		12	0.966	0.25	6.98	0.84	1.77	-0.25
		13	0.091	0.02	1.27	0.10	0.30	0.53
		14	2.330	0.61	28.21	1.45	1.79	-0.25
		15	22.292	5.84	469.99	2.67	14.70	-1.17
		16	2.216	0.58	17.22	1.24	0.82	0.09

Supplemental Table S4.1 (continued)

N°	Scallop B	Group	Group B	% of TSB	Sum D_i	Log (D_i)	Sum S_i	Log (D_i)
4	111	3	26.829	6.61	3988.72	3.60	1099.61	-3.04
		4	111.649	27.49	158.39	2.20	89.35	-1.951
		5	110.541	27.22	1087.43	3.04	48.24	-1.683
		6	3.695	0.91	10.74	1.03	1.76	-0.25
		7	4.001	0.99	13.87	1.14	4.23	-0.63
		8	16.994	4.18	24.84	1.40	23.21	-1.37
		9	15.563	3.83	70.43	1.85	15.17	-1.18
		10	71.528	17.61	242.92	2.39	115.08	-2.06
		11	19.263	4.74	38.84	1.59	9.56	-0.98
		12	0.987	0.24	7.19	0.86	1.81	-0.26
		13	0.094	0.02	1.32	0.12	0.31	0.51
		14	2.282	0.56	27.43	1.44	1.73	-0.24
		15	20.626	5.08	433.48	2.64	13.36	-1.13
		16	2.089	0.51	16.14	1.21	0.76	0.12
5	133.6	3	26.229	6.21	3832.30	3.58	1057.76	-3.02
		4	105.001	24.87	148.08	2.17	84.53	-1.93
		5	133.6	31.64	1268.73	3.10	63.18	-1.80
		6	3.684	0.87	10.68	1.03	1.75	-0.24
		7	4.008	0.95	13.92	1.14	4.24	-0.63
		8	16.623	3.94	24.57	1.39	22.69	-1.36
		9	14.345	3.40	65.01	1.82	14.04	-1.15
		10	74.742	17.70	257.67	2.41	120.79	-2.08
		11	18.968	4.49	38.30	1.58	9.41	-0.97
		12	1.006	0.24	7.38	0.87	1.84	-0.27
		13	0.098	0.02	1.37	0.14	0.32	0.50
		14	2.256	0.53	26.99	1.43	1.70	-0.23
		15	19.635	4.65	411.88	2.62	12.59	-1.10
		16	2.018	0.48	15.54	1.19	0.76	0.14
6	147.4	3	25.886	5.99	3743.01	3.57	1033.88	-3.02
		4	100.846	23.34	141.76	2.15	81.53	-1.91
		5	147.388	34.11	1371.18	3.14	73.46	-1.87
		6	3.675	0.85	10.65	1.03	1.74	-0.24
		7	4.011	0.93	13.95	1.15	4.23	-0.63
		8	16.391	3.79	24.38	1.39	22.38	-1.35
		9	13.591	3.15	61.67	1.79	13.33	-1.13
		10	77.115	17.85	268.42	2.43	125.02	-2.10
		11	18.806	4.35	38.01	1.58	9.33	-0.97
		12	1.021	0.24	7.52	0.88	1.87	-0.27
		13	0.100	0.02	1.41	0.15	0.33	0.48
		14	2.242	0.52	26.74	1.43	1.67	-0.22
		15	19.059	4.41	399.36	2.60	12.14	-1.08
		16	1.979	0.46	15.21	1.18	0.71	0.15
7	185	3	25.017	5.43	3514.75	3.55	972.80	-2.99
		4	88.541	19.23	123.54	2.09	72.65	-1.86
		5	185.0	40.17	1630.28	3.21	108.71	-2.04
		6	3.645	0.79	10.53	1.02	1.72	-0.24
		7	4.011	0.87	13.99	1.15	4.23	-0.63
		8	15.699	3.41	23.77	1.38	21.46	-1.33
		9	11.391	2.47	51.94	1.72	11.28	-1.05
		10	85.941	18.66	307.99	2.49	140.80	-2.15
		11	18.435	4.00	37.41	1.57	9.15	-0.96
		12	1.077	0.23	8.04	0.91	1.98	-0.30
		13	0.110	0.02	1.55	0.19	0.36	0.44
		14	2.208	0.48	26.14	1.42	1.63	-0.21
		15	17.543	3.81	366.58	2.56	11.00	-1.04
		16	1.885	0.41	14.41	1.16	0.66	0.18

Supplemental Table S4.1 (continued)

N°	Scallop B	Group	Group B	% of TSB	Sum D_i	Log (D_i)	Sum S_i	Log (D_i)
8	222	3	24.262	4.94	3311.63	3.52	918.49	-2.96
		4	74.390	15.13	103.32	2.01	62.31	-1.80
		5	222.0	45.16	1859.42	3.27	159.65	-2.20
		6	3.602	0.73	10.37	1.02	1.69	-0.23
		7	3.994	0.81	13.98	1.15	4.22	-0.63
		8	14.894	3.03	22.96	1.36	20.43	-1.31
		9	8.919	1.81	41.01	1.61	8.96	-0.95
		10	99.906	20.32	370.12	2.57	166.00	-2.22
		11	18.203	3.70	37.15	1.57	9.06	-0.96
		12	1.168	0.24	8.87	0.95	2.16	-0.34
		13	0.126	0.03	1.79	0.25	0.42	0.38
		14	2.183	0.44	25.68	1.41	1.59	-0.20
		15	16.114	3.28	335.92	2.53	9.97	-0.10
		16	1.81338	0.37	13.81	1.14	0.63	0.20
9	258	3	23.862	4.52	3195.78	3.51	887.58	-2.95
		4	62.732	11.89	87.17	1.94	53.61	-1.73
		5	257.929	48.87	1994.04	3.30	213.39	-2.33
		6	3.559	0.67	10.22	1.01	1.67	-0.22
		7	3.964	0.75	13.91	1.14	4.20	-0.62
		8	14.223	2.70	22.19	1.35	19.62	-1.29
		9	6.935	1.31	32.18	1.51	7.06	-0.85
		10	115.764	21.93	440.27	2.64	194.88	-2.29
		11	18.203	3.45	37.34	1.57	9.09	-0.96
		12	1.272	0.24	9.80	0.99	2.37	-0.39
		13	0.145	0.03	2.07	0.32	0.49	0.31
		14	2.176	0.41	25.50	1.41	1.57	-0.20
		15	15.219	2.88	316.90	2.50	9.36	-0.97
		16	1.790	0.34	13.60	1.13	0.62	0.21
10	458	3	23.724	3.12	3092.39	3.49	860.70	-2.94
		4	31.710	4.17	44.97	1.65	28.89	-1.46
		5	457.848	60.20	2162.90	3.34	440.74	-2.64
		6	3.354	0.44	9.58	0.98	1.59	-0.20
		7	3.739	0.49	13.24	1.12	4.04	-0.61
		8	12.218	1.61	19.48	1.29	17.30	-1.24
		9	1.846	0.24	8.88	0.95	1.97	-0.30
		10	186.646	24.54	760.17	2.88	328.11	-2.52
		11	19.455	2.56	40.74	1.61	9.88	-1.00
		12	1.748	0.23	14.04	1.15	3.35	-0.52
		13	0.235	0.03	3.38	0.53	0.82	0.09
		14	2.254	0.30	26.39	1.42	1.62	-0.21
		15	13.910	1.83	289.94	2.46	8.63	-0.94
		16	1.893	0.25	14.43	1.16	0.66	0.18
11	829	3	24.045	1.88	3062.50	3.49	854.58	-2.93
		4	0.087	6.76E-05	0.13	-0.89	0.09	1.06
		5	829.098	64.82	2276.63	3.36	1009.15	-3.00
		6	2.717	0.21	7.85	0.90	1.36	-0.13
		7	2.970	0.23	10.78	1.03	3.38	-0.53
		8	8.289	0.65	13.62	1.13	12.40	-1.09
		9	4.88E-08	3.81E-11	2.56E-07	-6.59	5.71E-08	7.24
		10	366.309	28.64	1619.66	3.21	686.31	-2.84
		11	25.084	1.96	55.26	1.74	13.24	-1.12
		12	2.993	0.23	25.59	1.41	6.00	-0.78
		13	0.454	0.04	6.67	0.82	1.66	-0.22
		14	2.781	0.22	33.04	1.52	2.06	-0.31
		15	11.922	0.93	250.53	2.40	7.78	-0.89
		16	2.271	0.18	17.55	1.24	0.83	0.08

Supplemental Table S4.1 (continued)

N°	Scallop B	Group	Group B	% of TSB	Sum D_i	Log (D_i)	Sum S_i	Log (D_i)
12	1200	3	24.421	1.30	3065.91	3.49	857.43	-2.93
		4	3.44E-07	1.83E-10	5.38E-07	-6.27	3.68E-07	6.43
		5	1200.348	63.96	2316.04	3.37	1705.89	-3.23
		6	1.881	0.10	5.59	0.75	1.00	-1.02E-03
		7	2.006	0.11	7.51	0.88	2.42	-0.38
		8	4.525	0.24	7.65	0.88	7.13	-0.85
		9	6.13E-16	3.27E-19	3.38E-15	-14.47	7.54E-16	15.12
		10	587.214	31.29	2721.84	3.44	1146.75	-3.06
		11	34.864	1.86	81.06	1.91	19.18	-1.28
		12	4.598	0.25	41.14	1.61	9.57	-0.98
		13	0.710	0.04	10.65	1.03	2.71	-0.43
		14	3.625	0.19	43.98	1.64	2.80	-0.45
		15	9.755	0.52	207.27	2.32	6.78	-0.83
		16	2.810	0.15	22.09	1.34	1.08	-0.03
13	1572	3	24.907	1.00	3093.20	3.49	866.91	-2.94
		4	5.92E-11	2.38E-14	9.45E-11	-10.03	6.57E-11	10.18
		5	1571.598	63.01	2334.62	3.37	2466.73	-3.39
		6	1.009	0.04	3.09	0.49	0.57	0.24
		7	1.137	0.05	4.38	0.64	1.44	-0.16
		8	1.555	0.06	2.68	0.43	2.56	-0.41
		9	1.00E-20	4.01E-24	6.97E-20	-19.16	1.62E-20	19.79
		10	823.312	33.01	3919.85	3.59	1649.82	-3.22
		11	47.679	1.91	115.97	2.06	27.20	-1.44
		12	6.373	0.26	58.85	1.77	13.65	-1.14
		13	0.989	0.04	15.05	1.18	3.88	-0.59
		14	4.543	0.18	56.25	1.75	3.63	-0.56
		15	7.810	0.31	167.83	2.23	5.74	-0.76
		16	3.482	0.14	27.88	1.45	1.40	-0.15
14	7369	3	28.008	0.22	3310.32	3.52	961.94	-2.98
		4	4.40E-16	3.46E-20	6.17E-16	-15.21	5.40E-16	15.27
		5	7369.0	57.98	2355.15	3.37	15860.40	-4.20
		6	1.62E-12	1.27E-16	6.71E-12	-11.17	1.37E-12	11.86
		7	2.61E-19	2.06E-23	1.13E-18	-17.95	4.04E-19	18.39
		8	1.22E-14	9.63E-19	1.91E-14	-13.72	2.34E-14	13.63
		9	1.00E-20	7.87E-25	8.85E-20	-19.05	2.19E-20	19.66
		10	4834.769	38.04	24597.31	4.39	10466.09	-4.02
		11	392.178	3.09	1171.67	3.07	267.52	-2.43
		12	38.540	0.30	405.79	2.61	94.24	-1.97
		13	5.816	0.05	95.34	1.98	26.06	-1.42
		14	21.230	0.17	313.08	2.50	22.32	-1.35
		15	1.03E-11	8.10E-16	2.39E-10	-9.62	1.07E-11	10.97
		16	20.641	0.16	191.88	2.28	11.61	-1.07

Supplemental Table S4.2. *Model output estimating the resilience from linear and weighted least sum of square (weighted) regression, indicating the scenario number (N°), the respectively introduced scallop biomass (B), the type of regression (linear vs. weighted), the respective slope (representing resilience), intercept, adjusted sums of squares (Adj. R^2), the F-value, and the p-value.*

N°	B	regression	slope	intercept	Adj. R^2	F	p
1	28	linear	-0.931	0.629	0.754	40.79	< 0.0001
		weighted	-0.825	0.130	0.474	12.73	0.0039
2	37	linear	-0.926	0.618	0.756	41.36	< 0.0001
		weighted	-0.775	0.035	0.424	10.58	0.0069
3	74	linear	-0.921	0.605	0.767	43.8	< 0.0001
		weighted	-0.607	-0.303	0.310	6.839	0.0226
4	111	linear	-0.924	0.608	0.777	46.22	< 0.0001
		weighted	-0.530	-0.468	0.306	6.722	0.0235
5	133.6	linear	-0.929	0.614	0.782	47.71	< 0.0001
		weighted	-0.519	-0.496	0.342	7.76	0.0165
6	147	linear	-0.932	0.618	0.785	48.58	< 0.0001
		weighted	-0.522	-0.493	0.373	8.745	0.0120
7	185	linear	-0.944	0.634	0.794	51.05	< 0.0001
		weighted	-0.558	-0.430	0.487	13.36	0.0033
8	222	linear	-0.959	0.653	0.802	53.53	< 0.0001
		weighted	-0.621	-0.310	0.611	21.39	0.0006
9	258	linear	-0.971	0.668	0.807	55.46	< 0.0001
		weighted	-0.680	-0.195	0.693	30.36	0.0001
10	458	linear	-1.000	0.696	0.824	61.95	< 0.0001
		weighted	-0.861	0.170	0.839	68.61	< 0.0001
11	829	linear	-0.989	0.654	0.969	412.9	< 0.0001
		weighted	-1.165	0.916	0.921	152.7	< 0.0001
12	1200	linear	-0.990	0.641	0.991	1476	< 0.0001
		weighted	-1.241	1.040	0.848	73.7	< 0.0001
13	1572	linear	-0.991	0.629	0.995	2410	< 0.0001
		weighted	-1.101	0.481	0.635	23.64	0.0004
14	7369	linear	-0.996	0.542	0.996	3276	< 0.0001
		weighted	-0.062	-3.824	-0.075	0.088	0.7714

Supplemental Table S4.3. *Overview of different ecological network analysis indicators, shown for all scallop scenarios (N°) with respectively introduced scallop biomasses (Scallop B): system's developmental capacity (Capacity (C), in t km^{-2}), ascendency (Ascend. (A)), and overhead (O), with the latter two as percentage of system's capacity (A/C and O/C, respectively). Described are also the different flow components of the system's overhead export (O_{export}), respiration (O_{resp}), and internal flow overhead (IFO), all as percentage of system's capacity (O_{export}/C, O_{resp}/C, and IFO/C, respectively), the latter also depicted as percentage of system's overhead (IFO/O).*

N°	**Scallop B**	**Capacity (C)**	**Ascend. (A)**	**Overh. (O)**	**O_{export}**	**O_{resp}**	**IFO**	
		flowbits	% (A/C)	% (O/C)	% (O_{export}/C)	% (O_{resp}/C)	% (IFO/C)	% (IFO/O)
1	28	133260	42.5009	57.4991	1.7756	8.1909	47.5326	0.8267
2	37	133807.7	42.2919	57.7081	1.8326	8.3321	47.5434	0.8239
3	74	135785.7	41.6990	58.3011	2.0425	8.7511	47.5075	0.8149
4	111	137843.3	41.3377	58.6623	2.2343	9.0401	47.3879	0.8078
5	133.6	139313.7	41.1951	58.8050	2.3459	9.1796	47.2795	0.8040
6	147	140299.6	41.1365	58.8635	2.4094	9.2517	47.2024	0.8019
7	185	143601.9	41.0759	58.9241	2.5683	9.4165	46.9393	0.7966
8	222	148304.8	41.1741	58.8259	2.6973	9.5495	46.5792	0.7918
9	258	153961.7	41.3416	58.6584	2.7975	9.6645	46.1965	0.7876
10	458	181588.8	42.1213	57.8786	3.2527	10.0214	44.6045	0.7707
11	829	238422.5	43.8371	56.1629	3.6835	10.4045	42.0749	0.7492
12	1200	300698.2	44.9339	55.0661	3.8484	10.8715	40.3462	0.7327
13	1572	363372.6	45.7669	54.2332	3.9307	11.2233	39.0792	0.7206
14	7369	1347115	48.3062	51.6938	3.8298	13.2489	34.6152	0.6696

Supplemental Figure S4.1. *Comparison of resilience calculation as the slope of linear (red line) and weighted (blue line) least square regression for all culture scenarios at year 100, representing the indicator as calculated after Arreguín-Sanchez 2014 and as proposed in this work, respectively. Dispersion of functional groups on the supply-demand plot are shown, with the area of circles being proportional to the group's biomass, and each number representing the corresponding functional group: (3)* Zooplankton, *(4)* Polychaetes, *(5)* Scallops, *(6)* Sea urchins, *(7)* Herbivorous gastropods, *(8)* Benthic detritivores, *(9)* Miscellaneous filter feeders, *(10)* Predatory gastropods, *(11)* Small carnivores, *(12)* Predatory crabs, *(13)* Octopods, *(14)* Littoral fish, *(15)* Small pelagic fish, *(16)* Pelagic predatory fish. *The food web's centroid (dark grey dashed line), and the -1 slope (the light grey dashed line) are shown, the latter representing the point at which a functional group is demanding as much from the system as it's supplying, i.e. is preyed upon.*

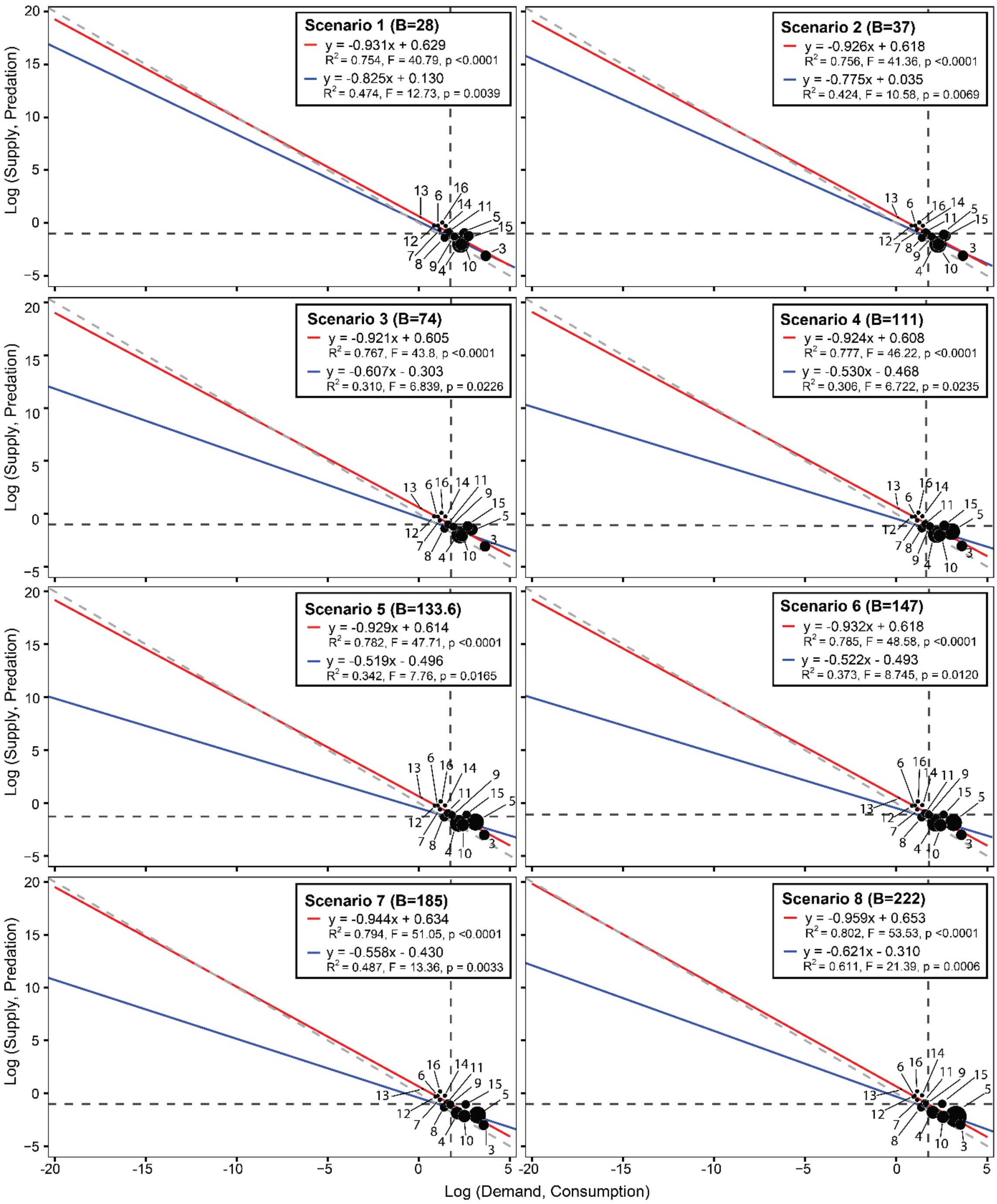
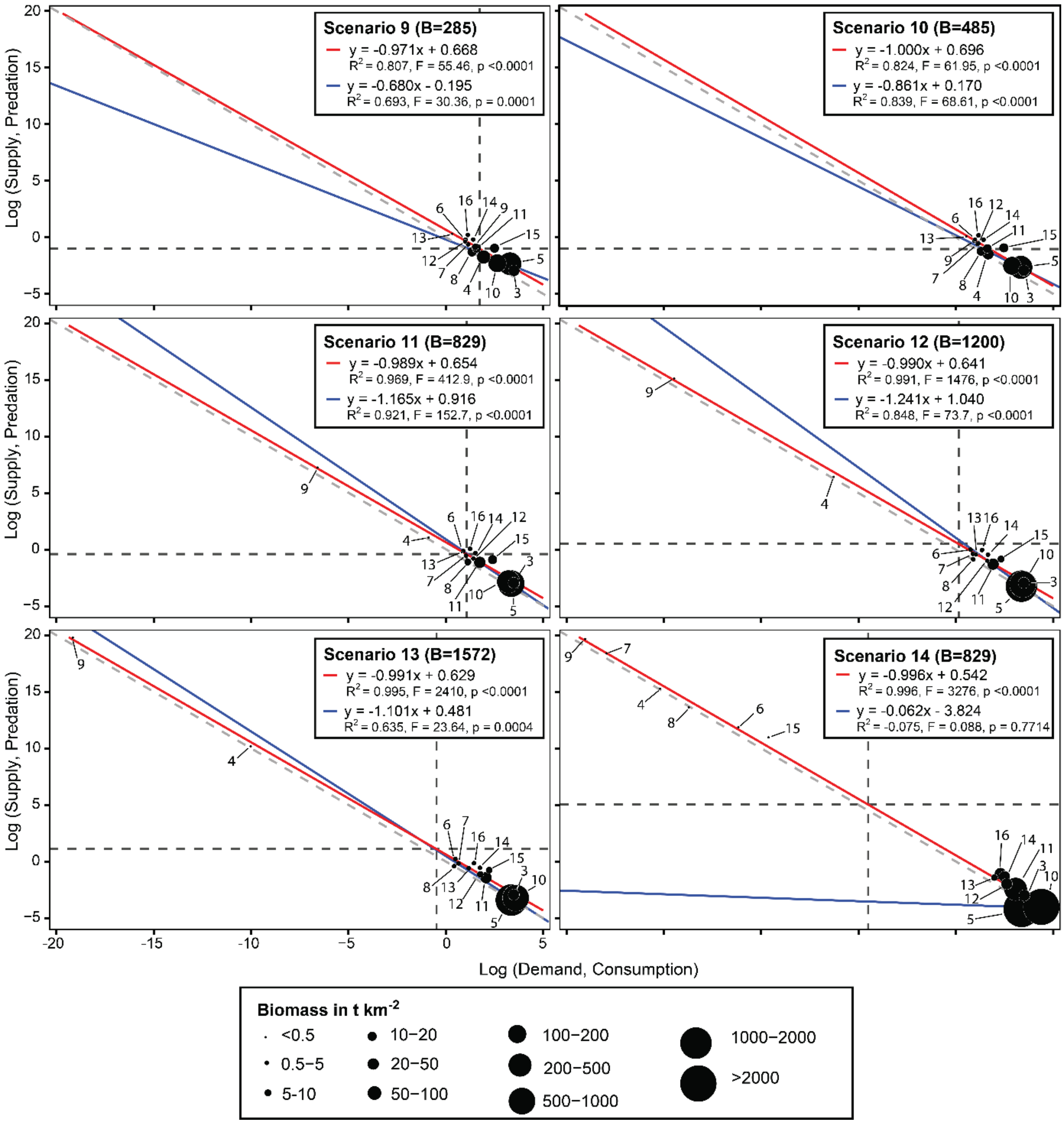


Figure S-1 (continued)



ANNEX IV

Supplements for Chapter 5

Supplemental Table S5.1. *List of all actors in the Sechura Bay network, including individual nodal degree (ND) and the betweenness centrality (BC) measure. Here, nodal degree was defined as the total number of adjacent (incoming (i.e. In-ND) and outgoing (i.e. Out-ND)) links (Wasserman & Faust 1994), with average nodal degree for the Sechura network resulting in 6.76±5.31. Plant = processing plants, with PP = primary processing (shucking and cleaning of scallops), SP secondary processing (preparation of final product for end consumer), E = Export.*

Id	Name	ND	In-ND	Out-ND	BW
1	Scallop farmer associations	26	8	18	171.04
2	Informally operating scallop producers	10	3	7	12.31
3	Boat owner	4	3	1	0
4	Contracted divers	2	1	1	0
5	Independent scallop seed divers	5	1	4	0
6	Owner hatchery	6	1	5	13
7	Personnel hatchery	2	1	1	0.33
8	Supplier other materials	12	12	0	0
9	Taxi drivers	20	19	1	16
10	Personnel scallop transport	8	7	1	2.4
11	Legal entities	8	8	0	0
12	Personnel sanitary monitoring	8	7	1	1.63
13	Personnel landing site	2	1	1	0
14	Owner Plant1 (PP)	17	5	12	61.03
15	Personnel processing Plant1 (PP)	2	1	1	0.2
16	Personnel administration Plant1 (PP)	2	1	1	0.2
17	Independent scallop processers	9	7	2	1.14
18	Intermediate buyers	17	8	9	66.5
19	Owner Plant2 (SP)	15	4	11	33.98
20	Personnel processing Plant2 (SP)	2	1	1	0.25
21	Personnel administration Plant2 (SP)	2	1	1	0.25
22	Owner Plant3 (PP + SP)	15	4	11	43.11
23	Personnel processing Plant3 (PP + SP)	2	1	1	0.2
24	Personnel administration Plant3 (PP + SP)	2	1	1	0.2
25	Exporter	10	4	6	17.07
26	National market	12	6	6	39.92
27	International market	6	3	3	14
28	Contracted guards	2	1	1	0
29	Owner Plant4 (SP + E)	12	3	9	35.94
30	Personnel processing Plant4 (SP + E)	2	1	1	0.35
31	Personnel administration Plant4 (SP + E)	2	1	1	0.35
32	Owner Plant5 (PP + SP + E)	10	2	8	40
33	Personnel processing Plant5 (PP + SP + E)	2	1	1	0.3
34	Personnel administration Plant5 (PP + SP + E)	2	1	1	0.3

Supplemental Table S5. 2. *List of all actors in the Tongoy Bay network, including individual nodal degree (ND) and the betweenness centrality (BC) measure. Here, nodal degree was defined as the total number of adjacent (incoming (i.e. In-ND) and outgoing (i.e. Out-ND)) links (Wasserman & Faust 1994), with average nodal degree for the Tongoy network resulting in 2.91±2.70.*

Id	Name	ND	In-ND	Out-ND	BC
1	Owner company	19	3	16	46
2	Personnel scallop culture	2	1	1	0.25
3	Personnel scallop processing	2	1	1	0.25
4	Personnel hatchery	2	1	1	0.25
5	Personnel scallop transport	2	1	1	0.25
6	Personnel sanitary monitoring	2	1	1	0.25
7	Personnel divers	2	1	1	0.25
8	Personnel boat drivers	2	1	1	0.25
9	Personnel guards	2	1	1	0.25
10	Personnel administration (supervision scallop processing)	2	1	1	0.25
11	Personnel maintenance	2	1	1	0.25
12	Personnel administration (supervision scallop production/culture)	2	1	1	0.25
13	Supplier other materials	3	3	0	0
14	Taxi drivers	13	12	1	11
15	Legal entities	1	1	0	0
16	National market	2	1	1	0
17	International market	2	1	1	0
18	Independent seed producer	4	1	3	0.25

ANNEX V

Supplements for Chapter 6

Supplemental Table S6. 1. Overview of the seven principles as evaluated by bivalve standard of the Aquaculture Stewardship Council (ASC) (ASC 2012).

Criterion	Indicators	Requirements
Principle 1: Obey the law and comply with all applicable legal requirements and regulations where farming operation is located		
1.1 All applicable legal requirements and regulations where farming operation is located	1.1.1 Evidence of compliance with all applicable legal requirements and regulations where the farming operation is located (e.g. permits, licencses, evidence of lease, concessions, and right to land and/or water use)	Yes
Principle 2: Avoid, remedy or mitigate significant adverse effects on habitats, biodiversity, and ecological processes		
2.1. Benthic effects for off-bottom and suspended-culture methods	2.1.1 Acceptable levels of total “free” slfide in surficial sediment (0-2 cm from the surface) measured beneath the farm in comparison to control sites	≤ 1500 µM, monitoring every five years is required ≥ 1500 µM and ≥ 3000 µM, monitoring every year is required
	2.1.2 Unacceptable levels of total “free” sulfide in surficial sediment measured beneath the farm in comparison to control sites	≥ 3000 µM
	2.1.3 In cases where natural background sulfide levels exceed 3000 µM, the annual S concentrations should not significantly exceed levels measured at reference sites located outside the farm	Yes
	2.1.4 Sulfide analysis may be replaced by direct analysis of benthic community structure (i.e. infaunal surveys in areas where this biotic approach is preferred by the applicant or is already mandated by a regulatory body	Yes
	2.1.5 Allowance for bivalve aquaculture over areas that provide a particularly sign. Or essential biological or ecological function within the broader ecosystem	None
2.2. Pelagic effects	2.2.1 The ratio of clearance time (CT) over retention time (RT) (If the area of all farms within a water body as defined Appendix I, inclusive of the certification unit, is less than 10 % of the total area of the water body, then requirements 2.2.1 & 2.2.2 need not apply)	>1
	2.2.2 Where CT is less than RT, the ratio of CT over primary production time	>3
	Equivalency with requirements of 2.2.1 or 2.2.2 may be demonstrated, if a farm or group of farms is able to prove, though more comprehensive carrying capacity modelling that, in aggregate, they do not exceed the ecological carrying capacity of the applicable water body in which they are located	Yes
2.3. Critical habitat and species interactions	2.3.1 Allowance for harm to threatened /endangered species or habitat on which they depend	None
2.4. Environmental awareness	2.4.1 Evidence of environmental training, compliance to regional codes of practices or implementation of environmental management plans	Required

Supplemental Table S6.1 (continued)

Criterion	Indicators	Requirements
Principle 3: Avoid adverse effects on the health and genetic diversity of wild populations		
3.1. Introduced pests and pathogens	3.1.1 Allowance for the illegal introduction of a non-native species, pest or pathogen attributable to the farm within 10 years prior to assessment	None
	3.1.2 Documentation of compliance with established protocol or evidence of following appropriate best management practices for preventing and managing disease and pest introductions with seed and/or farm equipment	Required
3.2. Sustainable wild seed procurement	3.2.1 Excluding larval collection, evidence that purchased or collected wild seed is not harvest from an open-access, unregulated source [1]	Required
3.3. Introduced non-native cultivated species	3.3.1 Evidence of responsible introduction of non-native cultivated species	Required
3.4. Native species cultivation	3.4.1 For hatchery produced seed, documentation of efforts made to address genetic concerns specific to species and geographic region where the seed will be out-planted (See Appendix II for guidance)	Required
3.5. Transgenic animals	3.5.1 Allowance for farming of transgenic animals	None
Principle 4: Manage disease and pests in an environmentally responsible manner		
4.1. Disease and pest management practices	4.1.1 Allowance for the application of mutagenic, carcinogenic or teratogenic pesticides on the farm or farmed animals	None
	4.1.2 Allowance for the application of chemicals that persist as toxins in the marine environment or on the farm or farmed animals	None
	4.1.3 Only non-lethal management (e.g. exclusion, deterrents and removal) of critical species that are pests or predators	Yes
	4.1.4 Allowance for the use of leadline or lead sinkers on predator netting	None
	4.1.5 Allowance for the use of explosives	None
Principle 5: Use resources efficiently		
5.1. Waste management /pollution control	5.1.1 Evidence of waste reduction (e.g. reuse and recycling) programs	Yes
	5.1.2 Evidence of appropriate storage and/or disposal of biological waste	Yes
	5.1.3 Evidence of appropriate storage and/or disposal of chemical and hydrocarbon wastes	Yes
	5.1.4 Spill prevention and response plan for chemicals /hydrocarbons originating from farming operations	Required
5.2. Energy efficiency	5.2.1 Evidence of energy use monitoring relative to production and ongoing effort to improve efficiency	Yes
	5.2.2 Maintenance records for farm equipment (e.g. boats and generators) are up to date and available	Yes

[1] The issue of translocation probably arises most often in shellfish aquaculture with respect to sourcing of wild seed to stock farms. An environmental requirement for shellfish aquaculture operations that rely upon translocations of wild seed necessitates an assessment of the potential risk for overfishing the reproductive sustainability of the wild source stock. Therefore, if growers are transporting seed or spat collected from other regions or harvesting excessive amounts of seed locally, an assessment is necessary to determine whether or not the manner in which the wild seed is collected for grow-out adversely affects recruitment or demography of local bivalve populations. For this reason, farms that use wild seed from open-access, unregulated sources will be ineligible for certification. For this reason, farms that use wild seed from open-access, unregulated sources will be ineligible for certification

Supplemental Table S6.1 (continued)

Criterion	Indicators	Requirements
Principle 6: Be a good neighbor and conscientious coastal citizen		
6.1. Community relations and interactions	6.1.1 Visible floats must be of a uniform color, except where otherwise specified by law (if applicable to growing area)	Required
	6.1.2 Uniform positioning and orientation of visible farm structures, except where specified by law (if applicable to growing area)	Required
	6.1.3 Allowance for floats made out of open-cell Styrofoam	None
	6.1.4 Noise, light and odor originating from the farm are minimized in areas where it may impact others (if applicable to growing area)	Required
	6.1.5 Evidence of compliance with all applicable navigational rules and regulations	Required
	6.1.6 Documented cleanup of receiving shoreline in response to gear loss based on local conditions	Required
	6.1.7 Substantial gear (e.g. floats, cages, bags, predator nets and racks) is identifiable to farm (if applicable to growing area)	Yes
	6.1.8 Provision of equipment for gear recovery (e.g. scoop nets and grapple hooks)	Required
	6.1.9 A mechanism (e.g. insurance or an industry agreement to collect derelict gear) is in place for the decommissioning of abandoned farms	Yes
	6.1.10 Conflict resolution protocol, including publicly available registry of complaints and evidence of due diligence to resolve them	Required
	6.1.11 Evidence of outreach (e.g. meeting records, newsletters, consultation with communities and indigenous groups, or membership in association with documented outreach program	Required
	6.1.12 Evidence of acknowledgment of indigenous group's rights (if applicable to growing area)	Required

Supplemental Table S6.1 (continued)

Criterion	Indicators	Requirements
Principle 7: Develop and operate farms in a socially and culturally responsible manner (see Appendix III for details)		
7.1. Child labor	7.1.1 Incidences of child [1] labor [2]	0
7.2. Forced, bonded or compulsory labor	7.2.1 Incidences of forced, bonded, or compulsory labor	0
7.3. Discrimination	7.3.1 Incidences of discrimination	0
7.4. Health and safety	7.4.1 All health and safety related accidents and violations are recorded and corrective actions is taken when necessary	Yes
	7.4.2 Occupational health and safety training is available for all employees	Yes
	7.4.3 Employer responsibility and proof of insurance (accident or injury) for employee medical costs in a job-related accident or injury, unless otherwise covered	Yes
7.5 Fair and decent wages	7.5.1 Payment of fair and decent wages	Yes
7.6 Freedom of association and collective bargaining	7.6.1 Employees have access to freedom of association and collective bargaining	Yes
7.7 Non-abusive disciplinary practices	7.7.1 Incidences of abusive disciplinary practices occurring on the farm	0
7.8 Working hours	7.8.1 Incidences, violations or abuse of working hours and overtime laws or expectations	None

[1] A child is defined as any person less than 15 years of age. A higher age would apply if the minimum age law stipulates a higher age for work or mandatory schooling. If, however, the local minimum age law is set at 14, in accordance with developing country exceptions under ILO Convention 138, the lower age will apply.
[2] Child labor is defined as any work by a child younger than the age specified in the definition of a child, except for light work as provided for by ILO Convention 138, Article 7.

Eidesstattliche Versicherung

ERKLÄRUNG

Hiermit erkläre ich, dass ich die Doktorarbeit mit dem Titel:

– Ecological and socio-economic feasibility of scallop bottom culturein Sechura Bay, Northern Peru –

selbstständig verfasst und geschrieben habe und außer den angegebenen Quellen keine weiteren Hilfsmittel verwendet habe.

Ebenfalls erkläre ich hiermit, dass es sich bei den von mir abgegebenen Arbeiten um drei identische Exemplare handelt.

(Unterschrift)