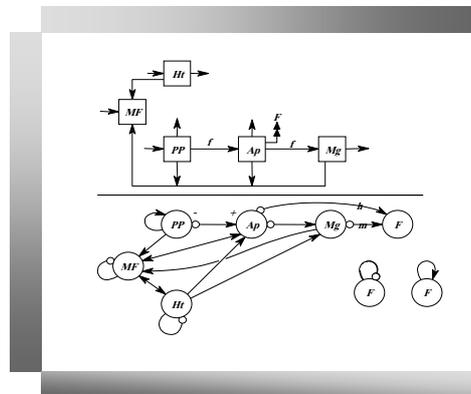


Holistic modelling of a subtidal benthic ecosystem of northern Chile (Tongoy Bay), to improve the knowledge and understanding of its structure and function: assessing the effects of intensive fisheries upon different invertebrates and algae species



Dissertation
Zur Erlangung des Grades
Doktor der Naturwissenschaften
- Dr. rer. nat. (PhD) -
dem Fachbereich 2 (Biologie / Chemie) der Universität Bremen
vorgelegt von Marco Ortiz
Bremen 2001

Gutachter der Dissertation:

Professor Dr. Matthias Wolff, Zentrum für Marine Tropenökologie (ZMT), Universität Bremen, Deutschland.

Professor Dr. Wolf Arntz, Alfred Wegener Institut (AWI), Universität Bremen, Deutschland.

Dedicado a Lidia, Domingo, Eduardo, Claudia y Sharon

“Das Wahre ist das Ganze”

(“The true is the whole”)

Friedrich Hegel

“There is a disjunction in science between the exquisite sophistication of the small and the irrationally of the enterprise as a whole”

Richard Levins (TREE 10 (7), 1995)

Acknowledgements

As a way to deal justly, I would like to thank to each person and friend according to a temporal succession of their appearance in my life. Therefore, my special thanks go to my mother Lidia, my father Domingo and my brothers Eduardo, Sharon and Claudia, who have given me not only love but also spiritual support.

I would like to thank Prof. Dr. Wolfgang Stotz for having given me the opportunity to work out my Diploma in Marine Biology in his working group (Universidad Católica del Norte), and afterwards to support the sampling programme for my PhD under a FONDECYT project (Fondo Nacional de Desarrollo Científico y Tecnológico). Many thanks, Wolfgang! Special thanks to my colleague and friend Sandra Jesse. Both tendered a very productive intellectual partnership not only in my country, but also in Bremen. Please, you must not forget that for me the door into Germany was *the door* into your world and your friends, especially Carsten and Heidi, infinite thanks!! Prof. Dr. Matthias Wolff, what can I say, with which specific words or sentences can I best express my gratitude. During four years we worked together with many interesting intellectual discussions about theoretical aspects in science, ecology, statistics, modelling, reductionism, holism and other interesting topics. Thus, many thanks for having given me the opportunity to read, write, think and to conduct my thesis. I Also want to thank Prof. Dr. Richard Levins from Harvard University, who analysed, studied and discussed with me other possibilities for the modelling of complex systems during my very fruitful stay in Boston. Your comments and your work, Richard, transformed my way to see the scientific objects of interest! ... many thanks!!

I would like to thank warmly every colleague and person from the ZMT who participated direct and indirectly in my stay and work here in Bremen.

Thanks to the DAAD who provided me with the scholarship which allowed a dream to become reality. To all people who conformed my internal and external surroundings, many thanks!!

Abstract	i
Zusammenfassung	iii
1. Introduction & Scope	1
2. Summary of Methods & Main Findings	6
2.1. Chapter I & II: preliminary analysis of the data set	6
2.2. Chapter III, IV, & V: steady-state, dynamical and spatial modelling	6
2.3. Chapter VI: qualitative modelling, <i>Loop Analysis</i>	11
2.3.1. Local stability properties as sustainability measure	12
2.3.2. Qualitative predictions	12
3. References	15
4. Chapter I	19
<i>“Seasonal variation in biomass and productivity of dominant species in four subtidal communities of north-central Chile”</i>	
4.1. Abstract	20
4.2. Problem	20
4.3. Material and Methods	21
4.4. Results	23
4.5. Discussion	25
4.6. Conclusions	27
4.7. Literature Cited	27
4.8. List of Tables and Figures	33
5. Chapter II	50
<i>“Observations in feeding behaviour of the asteroid <i>Meyenaster gelatinosus</i> as response to changes in abundance of the scallop <i>Argopecten purpuratus</i> in benthic system of northern Chile”</i>	
5.1. Abstract	51
5.2. Introduction	51
5.3. Material and Methods	53

5.4. Results	54
5.5. Discussion	55
5.6. References	56
5.7. List of Tables and Figures	60
6. Chapter III	71
<i>“Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and assessment of management strategies”</i>	
6.1. Abstract	72
6.2. Introduction	72
6.3. Material and Methods	74
6.4. Results and Discussion	76
6.5. References	79
6.6. List of Tables and Figures	84
7. Chapter IV	104
<i>“Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios”</i>	
7.1. Abstract	105
7.2. Introduction	105
7.3. Material and Methods	107
7.4. Results and Discussion	108
7.5. References	110
7.8. List of Tables and Figures	113
8. Chapter V	125
<i>“Spatially explicit modelling of a harvested benthic ecosystem in Tongoy Bay (central-northern Chile)”</i>	
8.1. Abstract	126
8.2. Introduction	126
8.3. Methods	127
8.4. Results	130
8.5. Discussion	131
8.6. References	132
8.7. List of Tables and Figures	134

9. Chapter VI	146
<i>“Application of Loop Analysis to benthic systems in northern Chile for the elaboration of sustainable strategies”</i>	
9.1. Abstract	147
9.2. Introduction	147
9.3. Material and Methods	148
9.4. Results	152
9.5. Discussion	153
9.6. Conclusions	155
9.7. Literature Cited	155
9.8. List of Tables and Figures	159
10. Chapter VII-Discussion & Conclusions	177
<i>“Quantitative and qualitative holistic modelling of complex benthic systems to improve sustainable interventions: a comparative analysis”</i>	
10.1. Abstract	178
10.2. Analysis	178
10.3. References	181
10.4. List of Tables and Figures	182
11. Appendix	188

Abstract

Along the Chilean coast an intensive harvest of intertidal and subtidal benthic resources has been developed historically. As a consequence, many invertebrate and macroalgae species are over-exploited with the additional negative impact on their biological fitness (possible reduction of niche width), ecological interactions, recruitment success, etc, as well as on the community function as whole. Management strategies are required to avoid these negative impacts and to arrive at a sustainable fishery. However, most of the policies in use follow a *Cartesian* or *Newtonian Philosophy*, which means a reduction of the complexity of the whole systems to particular small parts (the commercial species). Unfortunately, by this single species approaches the short-term dynamics and proximate responses are insufficient to understand and predict changes of the quality and trajectory of the system. In the present contribution, therefore, it followed a *Hegelian Philosophy*. The harvest activities and other man-made interventions were analysed considering the commercial species as part of the entire system. Based on the holistic modelling the following questions were explored and answered: (1) How is the biomass distribution and biomass flow structure in the system?; (2) What are the principal benthic predators, their consumption rates and prey item?; (3) What is the carrying capacity of the systems in terms of food availability for target species and predators?; (4) Is it possible to recognise and quantify *Redundancy* (several species of similar trophic roles) in the system?; (5) Which are the species most likely affected by different management scenarios?; (6) How sustainable are different management policies?

A seasonal survey was carried out (from June 1996 to May 1997) to determine abundance, productivity and trophic relationships for the most relevant benthic invertebrate and macroalgae species of the management area of Puerto Aldea, Tongoy Bay (30°16'S – 71°30'W). Two species, the scallop *Argopecten purpuratus* and the red algae *Chondrocanthus chamissoi* are intensively exploited in this area. Four different habitats were recognised and used as modelling unit: (1) the seagrass meadows, (2) the sand-gravel areas, (3) sandy habitats and (4) mud beds. As the seasonal variation of total biomass was insignificant, the use of average annual value for each habitat and the whole area seemed the best option for modelling.

Four different holistic modelling approaches were applied to each of the four habitat and the entire area: (1) the quantitative trophic modelling at steady-state, ECOPATH II. This approach combines abundance, production, food spectrum dynamic of ecosystem compartments with Ulanowicz's flow network analysis for the calculation of ecosystem indices. Within these indices the *Relative Ascendency* and *Redundancy* are relevant because both describe the system's ability to withstand perturbations; (2) the ECOSIM approach is a dynamical extension of ECOPATH II. Based on this modelling approach the *System Recovery Time* (as resilience measure) and the maximum sustainable fishing (F_{MSY}) can be estimated; (3) the ECOPACE is spatially explicit extension of ECOPATH II. This approach is a useful tool for displaying propagated changes in the compartments as response to if all fishery activities are applied; (4) the Levins's LOOP ANALYSIS allows to extend the boundaries of the trophic models integrating other ecological interactions such as competence, amensalism, commensalism and mutualism. The holistic sustainability (local stability) and the propagation of direct and indirect effect could be estimated. Using these different modelling approaches, harvesting effects at different food web levels, the removal of "undesirable" predators that feed upon the commercial species, and the effect of fishermen dynamics on the holistic sustainability of each of the model systems could be assessed.

According to the ECOPATH II models all habitat systems appear immature and highly resistant to external perturbations. The seagrass and sand-gravel habitats have a potential for a three fold increase of the present standing stock of the scallop *A. purpuratus* and the red algae *Ch. chamissoi*. Any management policy aimed at an increase in the standing stock (through seeding and increase of the available substrate for settlement) of *A. purpuratus* and *Ch. chamissoi* in seagrass and sand-gravel habitats, and a removal of the sea star *M. gelatinosus* in the seagrass habitat appear justified. The ECOSIM dynamical models also revealed that a removal of the sea star *M. gelatinosus* would greatly increase the availability of scallops in the seagrass, sand-gravel and in the model combining all habitats. In contrast, a harvest of the beach clam *Mulinia* sp. would drastically change the properties of the model for the sand habitat and the model for the entire area. This clam may thus be considered a keystone species. Predictions of the maximum sustainable yield (F_{MSY}) for the scallop *A. purpuratus* were relatively lower than those estimated by single species approaches previously applied in this system. Therefore, it recommends to design long-term and holistic explorations as alternative strategies for the determination of a maximum sustainable fishing effort. The dynamical and spatial simulation by ECOSPACE revealed that if all fishery activities are applied in the seagrass and sand habitats the population of the sea star *Luidia magallanica*, the seagrass *Heterozostera tasmanica* and the crab *Paraxanthus barbiger* would increase. An exclusive fishing in the sand-gravel habitat, on the other hand, would only cause small effects on the remainder species, which suggests that this habitat is the most resistant one to harvest. The simultaneous fishing on two or three habitats would have the largest negative effect on the entire system. Therefore, a habitat rotation fishery is recommended. The results obtained by the LOOP ANALYSIS ecological models also suggest that a partial removal of the three predatory sea star species *Heliaster helianthus*, *L. magallanica* and *M. gelatinosus* in the seagrass habitat and the removal of just *H. helianthus* in the sand-gravel should be implemented to increase the standing stock of the adult scallops. The increase of available artificial substrate would not produce the expected positive effect on the abundance of the commercial red algae *Ch. chamissoi*. The extended model system for the seagrass and sand-gravel, which integrates the fishermen as a predator, were found sustainable only if the fishermen were “self-damped”, which means when the fishing effort and fish quota are restricted.

As could be demonstrated, any management policy must not be determined thinking only in the target species as an isolated object. The ecological models explored within the present work demonstrate that more ecological information is required if an understanding of the functioning of the whole systems and a holistic reasoning of sustainability are of interest. It suggests to apply the here presented holistic theoretical frameworks as complementary ways to develop and predict man-made interventions in other benthic management areas along the Chilean coast and other comparable complex systems.

Zusammenfassung

Entlang der chilenischen Küste hat sich im Laufe der Zeit eine intensive Befischung von benthischen Ressourcen des Sublitorals und des Gezeitenbereiches etabliert. Der Bestand vieler Invertebraten und Makroalgen ist heute überfischt, es zeigen sich negative Auswirkungen auf deren biologische Fitness (mögliche Reduktion der Nischenweite), die ökologischen Interaktionen, den Rekrutierungserfolg u.a. und auf die Funktionsfähigkeit der Gemeinschaft. Managementstrategien werden benötigt, um diesen negativen Auswirkungen gegenzusteuern und eine nachhaltige Fischerei zu etablieren. Die meisten der applizierten Fischereistrategien beruhen jedoch auf der *kartesischen* oder *newtonschen Philosophie*, die eine Reduktion der Komplexität von Lebensgemeinschaften auf kleinere Untereinheiten (die kommerziell genutzten Arten) bedeutet.

Die Kenntnis von kurzfristigen Dynamiken und Reaktionen bei den auf einer Art beruhenden Modellierungsansätzen ermöglichen jedoch keine ausreichende Aussage über grundlegende Änderungen in Qualität und über die längerfristige Weiterentwicklung des Systems. Der hier vorliegenden Arbeit liegt daher der *hegelschen Philosophie* zu Grunde. Die Fischerei und andere anthropogene Eingriffe wurden analysiert, und wurden kommerziell genutzte Arten als ein Teil des ganzen Systems betrachtet. Mittels holistischer Modellierungen wurden folgende Fragen analysiert und beantwortet: (1) Welche Verteilungsmuster ergeben sich in Bezug auf Biomasse und Biomassenfluß des Systems, (2) Welches sind die wesentlichen benthischen Räuber, ihre Konsumptionsraten und Bäuteorganismen?, (3) Wie ist die Tragfähigkeit des Systems hinsichtlich der Nahrungsverfügbarkeit für die Zielarten und Räuber, (4) Ist es möglich, Redundanz (mehrere Arten mit ähnlicher trophischer Funktion) zu erkennen und zu quantifizieren?, (5) Welche Arten sind mit der höchsten Wahrscheinlichkeit von den verschiedenen Managementstrategien betroffen?, (6) Inwieweit erfüllen die unterschiedlichen Managementstrategien als Kriterium der Nachhaltigkeit?

Um Abundanz, Produktivität und trophische Beziehungen für die wichtigsten benthischen Invertebraten und Makroalgen des Managementgebietes bei Puerto Aldea in der Tongoy Bucht (Chile) (30°16'S – 71°30'W) zu bestimmen, wurde eine ganzjährige Untersuchung (Juni 1996 – Mai 1997) durchgeführt. In dem Untersuchungsgebiet werden zwei Arten, die Pilgermuschel *Argopecten purpuratus* und die Rotalge *Chondrocanthus chamissoi* intensiv befischt bzw. geerntet. Vier verschiedene Habitattypen werden unterschieden und als Modellierungseinheit verwendet: (1) Seegraswiesen, (2) das Sand-Kiesel-Habitat, (3) Sand- und (4) Schlammflächen. Da die jahreszeitliche Variation der Gesamtbiomasse unbedeutend war, wurden Jahresmittel für jeden Habitattyp und das Gesamtgebiet als Parameter für die Modellierung verwendet.

Vier verschiedene holistische Modellierungsansätze werden sowohl für jedes der vier Habitate als auch für das Gesamtgebiet angewandt: (1) die quantitative trophische Modellierung im Fließ-Gleichgewicht, ECOPATH II. In diesem Ansatz werden Entwicklungen von Abundanz, Produktion und Nahrungsspektrum der Ökosystemeinheiten mit der Fluß-Netzwerk Analyse von Ulanowicz genutzt, um Ökosystem-Indizes zu ermitteln. Besonders die „*Relative Ascendency*“ und die „*Redundancy*“ sind hier von Bedeutung, da beide die Fähigkeit des Systems beschreiben, Störungen abzufangen; (2) der ECOSIM Ansatz ist eine dynamische Erweiterung des ECOPATH II Modells. Basierend auf diesem Modellierungsansatz kann die „*System Recovery Time*“ (als Maß der Resilienz) und die

maximale Tragfähigkeit des Systems in Hinblick auf die Befischung der kommerziell genutzten Arten (F_{MSY}) ermittelt werden; (3) ECOPACE ist eine der, räumliche Erweiterung von ECOPATH II. Dieser Ansatz stellt ein nützliches Werkzeug um fortschreitende Änderungen in den Habitateinheiten als Antwort auf maximalen Fischereidruck aufzuzeigen; (4) mit der LOOP ANALYSIS von Levins können die Grenzen der trophischen Modellierung erweitert werden, in dem weitere ökologische Interaktionen integriert werden. Dies sind z.B. Kompetenz, Amensalismus, Komensalismus und Mutualismus. Die holistische Tragfähigkeit (lokale Stabilität) und die Fortpflanzung direkter und indirekter Einwirkungen kann abgeschätzt werden. Durch die Anwendung dieser unterschiedlichen Modellierungsansätze konnten die Auswirkungen der Befischung auf verschiedenen Ebenen des Nahrungsnetzes, die Auswirkungen der Eliminierung „unerwünschter“, sich von kommerziell attraktive Arten ernährenden Räuber und der Effekt von variablem Fischereidruck auf die Tragfähigkeit des Systems festgestellt werden.

Die ECOPATH II Modelle sagen aus, daß alle Habitateinheiten sich in einem Entwicklungszustand befinden und einen starken Widerstand gegen externe Störungen aufweisen. Die Seegraswiesen und das Sand-Kiesel-Habitat besitzen zudem das Potential, dem gegenwärtigen Ernteertrag von *A. purpuratus* und *Ch. chamissoi* zu verdreifachen. Dies scheint Managementstrategien zu rechtfertigen, die auf einen Zuwachs des Ernteertrages von *A. purpuratus* und *Ch. chamissoi* im Seegras und im Sand-Kiesel-Habitat (durch Aussäen und durch Erweiterung der Substratverfügbarkeit), und auf die Entfernung des Seesterns *M. gelatinosus* in den Seegraswiesen hinzielten. Die dynamische Modellierung mit ECOSIM zeigte ebenfalls, daß ein Entfernen des Seesterns *M. gelatinosus* die Verfügbarkeit der Pilgermuscheln in den Seegraswiesen, im Sand-Kiesel-Habitat und im Gesamtgebiet steigern würde. Eine Befischung der Strandmuschel *Mulina* sp. würde hingegen die Eigenschaften des Sand-Habitats und des Gesamtgebietes stark verändern. Diese Muschel kann daher als Schlüsselart angesehen werden. Aussagen über den maximal vertretbaren Ertrag (F_{MSY}) der Muschel *A. purpuratus* liegen unter den Prognosen für das Gebiet, die Modellierungen mit nur einer Art ergeben hatten. Daher wird empfohlen, langfristige und holistische Untersuchungen als Alternative zur Ermittlung des maximal tragfähigen Fischereidrucks zu entwickeln. Die dynamische und räumliche Simulation durch ECOPACE zeigte, daß die Populationen des Seesterns *Luidia magallanica*, des Seegrases *Heterozostera tasmanica* und der Krabbenart *Paraxanthus barbiger* zunehmen würden, falls alle Fischereiaktivitäten auf die Seegraswiesen und das Sand-Habitat beschränkt bleiben. Andererseits würde eine auf das Sand-Kiesel-Habitat beschränkte Fischerei nur geringe Effekte auf die verbleibenden Arten haben. Dies zeigt, daß dieses Habitat die höchste Resistenz in Hinblick auf Befischung aufweist. Die gleichzeitige Befischung von zwei oder drei Habitaten würde den größten negativen Effekt auf das System haben. Es wird daher eine rotierende Habitatbefischung empfohlen. Die Ergebnisse, die durch die ökologischen Modelle der LOOP ANALYSIS ermittelt wurden, zeigen ebenfalls, daß die partielle Eliminierung der drei räuberischen Seesternarten *Heliaster helianthus*, *Luidia magallanica* und *Meyenaster gelatinosus* in den Seegraswiesen und die Eliminierung von *H. helianthus* im Sand-Kiesel-Habitat genutzt werden kann, um dem Ernteertrag der Adultstadien von *A. purpuratus* zu steigern. Die Aufstockung an verfügbarem, künstlichen Substrat würde nicht zu dem erwarteten Anstieg in der Abundanz der Rotalgenart *Ch. chamissoi* führen. Das um Seegraswiesen und Sand-Kiesel-Habitat erweiterte Modell, welches die Fischer als Räuber integriert, zeigt, daß eine nachhaltige Nutzung nur dann möglich ist, wenn eine Selbstregulation auf Ebene der Fischer stattfindet, d.h., wenn Fischereidruck und Fangquoten beschränkt werden.

Es konnte gezeigt werden, dass keine Managementstrategie allein darauf beruhen sollte, die Zielart als isoliertes Objekt zu betrachten. Die ökologischen Modelle, die in der vorliegenden

Arbeit präsentiert wurden, zeigten, dass eine Vielzahl an ökologisch relevanter Information benötigt wird, wenn es gilt, die Funktionsweise ganzer Systeme zu verstehen und eine holistische Überprüfung der Nachhaltigkeit von Interesse ist. Es wird vorgeschlagen, den hier vorgestellten, holistisch-theoretischen Rahmen zu nutzen, um menschliche Interventionen in anderen benthischen Managementgebieten an der chilenischen Küste oder in anderen, vergleichbar komplexen, natürlichen Systemen zu evaluieren, zu steuern und ihren Effekt auf das System vorherzusagen.

1. Introduction & Scope

There are few coastal countries whose benthic systems support successful industries based on the natural production and aquaculture of macroalgae and invertebrate species (Siegfried et al. 1994). Along the Chilean coast harvesting activities go back about 10.000 years (Llagostera 1979), and during the last 40 years important fishery and recreational industries have been widely developed (Siegfried et al. 1994).

About 60 benthic shellfish and macroalgae species are exploited, which constitute the main economic source for many artisanal fishery organisations (Bustamante & Castilla 1987, Castilla 2000). Molluscs represent the most important species group with an average of 1.5 % of the world production until 1978. The “loco snail” or “false abalone” *Concholepas concholepas* was the most relevant during 1984 and the gastropod with the highest catch values world wide (Bustamante & Castilla 1987). Other important molluscs are the scallop *Argopecten purpuratus*, the clams *Mesodesma donacium*, *Venus antiqua* and *Protothaca thaca* with an average annual landing about 35.000 t (metric tonnes) (Siegfried 1994) (Fig. 1a). The remaining shellfish species include some decapods, galateids, pandalids and barnacles (Fig. 1b). Additionally, the landings of the “red sea urchin” *Loxechinus albus* and the “sea squirt” *Pyura chilensis* have increased until ca 40.000 t in 1994 (Fig. 1b) (Servicio Nacional de Pesca “SERNAP” 1997) (National Fisheries Service). The macroalgae become the predominant component in the last 10 years, yielding ca 180.000 t annually (Santelices & Griffiths 1994). The main exploited algae are the phaephytes *Gracilaria* sp., *Gelidium chilense*, *Iridaea laminarioides*, *Porphyra columbina*, *Lessonia nigrescens*, *L. trabeculata*, *Durvilaea antarctica* and the rodophytes *Chondrocanthus radula*, *Ch. skottsbergii* and *Ch. chamissoi* (Fig. 1c).

As a consequence of the intensive fisheries many species have been overexploited with deleterious effect on their abundance, productivity and fitness (Bustamante & Castilla

1987). There are even cases where the fishery has collapsed, producing a gradual deterioration of the ecosystems (Beddington 1984, Castilla & Camus 1992, Branch & Moreno 1994). The principal effects in the intertidal communities of central and southern coastal ecosystems are changes in their species structures, ecological interactions (e.g. inter-intraspecific competition), a decrease of biomass and productivity, and decrease in size range and recruitment success (Moreno & Jara 1984, Castilla & Durán 1985, Oliva & Castilla 1986, Castilla & Paine 1987, Bustamante & Castilla 1990, Parra et al. 1992, Branch & Moreno 1994, Santelices & Griffiths 1994, Vasquez 1995). Despite this intensive exploitation few studies have been carried out to obtain biological and ecological information of these systems in central and northern Chile (Siegfried 1994).

Even though regulatory policies such as minimum landing size, closed seasons, catch quotas and fishing arts have been historically implemented in order to mitigate the negative effects of fisheries on the target species (SERNAP 1993), they were not effective enough, in part due to the lack of controlling along a coastline of over 4.600 km. Under such circumstances, an innovative regulatory policy was established by the New Chilean Law Fishery and Aquaculture of 1992. It was defined as “Areas of management and exploitation for benthic resources”. These areas are assigned to local artisanal fishery organisations. Fishermen can implement different management strategies to maximise the standing stock and production of the commercial species and to apply a multispecies fishery within sustainable boundaries. However, other more risky management options focusing on the introduction of non-indigenous species of commercial interest, the artificial increasing of resident commercial

species (e.g. man-made seeding and substrate introduction to improve the settlement and recruitment rates) and the removal of “undesirable” predatory species, which feed on the target species may be also implemented (e.g. MacKenzie 1970, Kassner & Malouf 1982, Kennedy

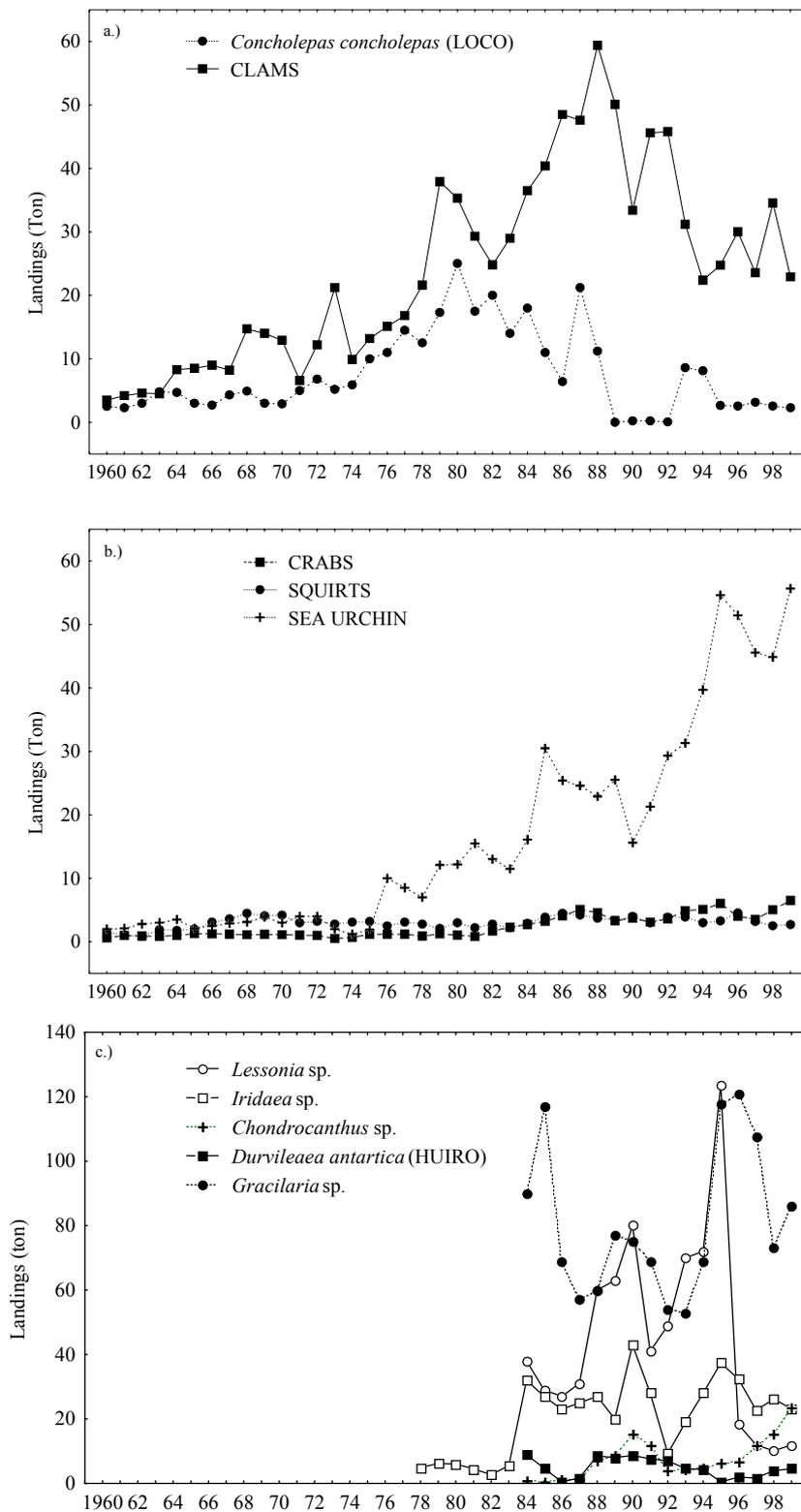


Fig. 1. Chilean landings registered between 1960 and 1999 for: a.) the snail *C.concholepas*, and clams, b.) other invertebrates species, and c.) macroalgae species (see text for more details).

1989, Whitlatch & Osman 1994, Stotz 1997).

Most of the fishery management strategies have followed historically a *Cartesian* or *Newtonian philosophy* assuming that the isolated study of the single species is sufficient for the understanding of underlying processes in the ecosystems and for the sustainable use of natural systems (Levins & Lewontin 1985). However, the reductionistic character of this assumption seems to be -in part- one of the reasons for the common failure of fisheries around the world with deleterious effects on the commercial species and severe alteration of their ecosystems (Larkin 1977, Patten 1997, Roberts 1997, Walters et al. 1999). An alternative and complementary way for the design and assessment of management policies is through the large-scale or holistic integration of the entire community and ecosystem processes. Following this *Hegelian philosophy*, the System Analysis allows for: (1) the understanding of underlying mechanisms in the complex ecological system studied, (2) the assessment of the systems' ability to withstand perturbations, and (3) the estimation of the sustainability and ecological consequences of man-made interventions. Likewise, one of the central questions in ecology which relates biodiversity to ecological function can also be addressed by this holistic approach.

Four competing hypothesis can be involved. The "species richness-diversity hypothesis" states that through the addition of species to an ecosystem the number of ecological functions present is increased and with it stability (MacArthur 1955). The "idiosyncratic hypothesis" proposes that the degree of stability in a community depends upon the particular nature of the interspecific interactions (Lawton 1994). The "rivet hypothesis" suggests that the ecological functions of different species overlap and that to a certain degree a species loss can be complemented through the activity of the remainder species (Ehrlich & Ehrlich 1981). And the "drivers and passengers hypothesis" accepts the notion of complementary species and extends it by proposing that the ecological function resides in driver species or in functional groups of such species (Walker 1992). It is similar to the concept of keystone species (Paine 1966) or ecological engineers (Jones et al. 1994).

The objective of the present work is to model and simulate the behavior of a harvested benthic system of northern Chile using a holistic theoretical framework. Based on the models developed, quantitative and qualitative predictions of the system responses to different alternative management scenarios (sensu Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999) will be assessed.

The following definitions will be given to approach the reader to the concepts described above. *Systems Analysis* is the study of an aggregation of entities or objects which interact together in space and time (Kitching 1983). *System ecology* aims at the understanding of the structure and function of levels of organization beyond the population level (Odum 1964). A *Complex System* is a structured set of contradictory processes that give meaning to its elements, maintains the temporary coherence of the whole and also eventually transforms it into something else, dissolves it into another system, or leads to its disintegration (Levins 1998a).

According to Levins (1966, 1988) and May (1974), the models are intellectual constructions, which are not chosen to represent any particular population, community and ecosystem, but rather to grasp an essential type of relationships. Three model building strategies can be distinguished (Levins 1966, 1993): (1) those that sacrifice generality for realism and precision which reduces the parameter and variables to those relevant in a short-term behavior of the organism, (2) those that sacrifice realism for generality and precision, an approach popular among physicist who enter in the field of, and often use general, but unrealistic equations, and (3) those that sacrifice precision for generality and realism. These models are concerned

with qualitative rather than quantitative data and they only assume functions that are increasing or decreasing.

The present scientific contribution is constituted by six chapters or scientific articles. In each of them the principal author analyses and describes intensively the available biological and ecological information in order to guide the reader from a reductionistic to a holistic understanding of the complex system under study.

The study area. The study area of Puerto Aldea (Fig. 2) corresponds to one of 168 management areas (territorial use rights for fisheries) established along the Chilean coast (Castilla 2000). These areas are assigned to local fishermen associations in order to maximize, within sustainable boundaries, the production and exploitation of commercial resources. In this area the following benthic habitats can be recognized: (1) seagrass meadows of *Heterozostera tasmanica* from 0 to 4m depth, (2) sand and gravel between 4 and 10m, (3) sand flats between 10 and 14m, and (4) mud flats > 14m depth. The Tongoy Bay and the benthic system of Puerto Aldea are protected from the prevailing south-west winds by Lengua de Vaca peninsula. The upwelling center near this peninsula is among the most important ones of northern Chile (Acuña et al. 1989, Daneri et al. 2000, Montecinos & Quiroz 2000), supplying nutrients to the ecosystem and simultaneously preventing the establishment of a stable thermocline during summer by the permanent intrusions of upwelled water into the bay. Temperature of bottom water reaches 13°C and 17°C in winter and autumn respectively (Jesse 2001). In this management area only four species are harvested: the rodophyte *Chondrocanthus chamissoi* (ca. 114 ton/year), the scallop *Argopecten purpuratus* (ca. 16 ton/year), the snail *Xantochorus cassidiformis* (ca. 0.6 ton/year) and the crab *Cancer polyodon* (ca. 0.4 ton/year).

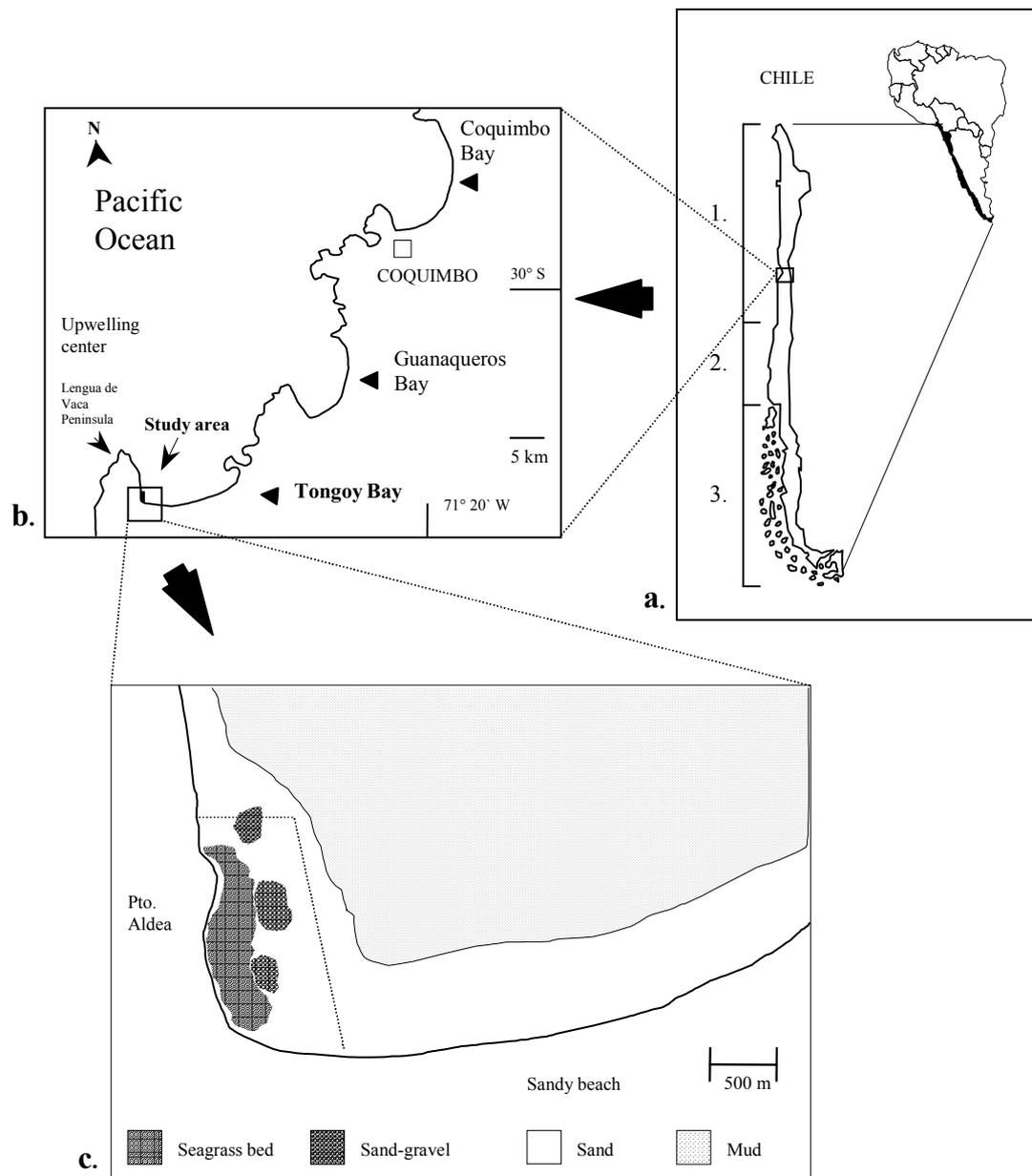


Fig. 2. a.) The main littoral types along the Chilean coast: 1 = dominated by exposed compact shores; 2 = dominated by exposed sandy shores; 3 = mostly insular systems; b.) the principal bay systems of the IV Region of Coquimbo, Chile; c.) study area of Puerto Aldea located at southern of Tongoy Bay.

2. Summary of Methods & Main Findings

2.1. Chapter I & II

Preliminary analysis of data set

In the two first chapters a reductionistic analysis of the ecological information was done. Chapter I shows in which temporal (year or seasonal) and spatial scale the models should be formulated. A seasonal sampling programme between winter 1996 and autumn 1997 was undertaken to assess the significance of the changes in the abundance of the commercial and other dominant species. The species productivity was also estimated. The *a priori* and *a posteriori* statistical power analysis was implemented to define the sample size and to estimate the robustness of the statistical tests in the assessment of the working hypothesis, respectively. One-way ANOVA was applied to evaluate the work hypothesis and non-Metric Multidimensional Scaling (n-MDS) and ANOSIM (analysis of similarities) were also used to separate spatial assemblages by species and samples (*R* and *Q* strategies). The principal results were the following: (1) the seasonal changes in biomass were insignificant for the entire study area, the habitats, and also for most of the single species; (2) the principal factors affecting seasonal biomass dynamic are harvest and migratory behaviour of the unexploited crabs; (3) the sand-gravel and the seagrass habitats account for 81.94% and 12.20% of the total secondary production, while sand and mud habitats contributed only 4.79% and 1.09%, respectively.

Chapter II describes the food spectrum and the changes in the feeding behaviour of the sea star *Meyenaster gelatinosus*, one of the most abundant benthic predators in this area, as response to significant changes in the abundance (by harvest) of its scallop prey *Argopecten purpuratus*. This asteroid has been frequently classified as being a generalist feeder. One of the generalised models for sympatric predator-prey combinations, which predicts that the predator consumes preferably small sizes of prey, was also assessed. The principal findings were: (1) before harvest started, *A. purpuratus* constituted the principal prey for *M. gelatinosus* in the seagrass habitat, whereas in the sand-gravel all prey types were equally distributed in its diet; (2) after harvesting, the frequency of occurrence of the scallop decreased in the stomachs of the sea star in the seagrass but was substituted by the group of small epifauna; (3) the breadth of the feeding-niche increased, however, indicating that *M. gelatinosus* became a more generalist feeder as the scallop decreased in abundance. In the sand-gravel, the diet composition remained unaltered, but *M. gelatinosus* showed an inverse tendency specialising on the scallop; (4) *M. gelatinosus* increased its feeding preferences on *A. purpuratus* in both habitats when the abundance of the scallop declined as shown by the Ivlev index; and (5) *M. gelatinosus* feeds on a wide size-range (4 to 14 cm) of the scallop *A. purpuratus* with a marked preference for larger sizes. This finding contradicts the feeding behaviour of sympatric predator-prey combinations proposed by Stephens & Krebs (1986).

2.2. Chapter III, IV & V

Steady-state, dynamical and spatial trophic modelling

The theoretical framework of this modelling approach is based on the input-output analysis developed originally in economic science by Leontief (1951), which quantifies the amount of raw materials and industrial services required to produce a quantity of consumer good. Hannon (1973) was the first to apply this analysis to ecological systems, where the concept of

flow analysis emerged. In this analysis, flows into each compartment are defined as linear or non-linear functions of the total outflow from that compartment (Kay et al. 1989). Different topics related to the flow analysis in ecological systems have been widely addressed by several authors (e.g. Finn 1976, Patten et al. 1976, Barber 1978a,b, Patten 1985). The network analysis allows to consider several ecological concepts such as food chain, food webs, species richness, and diversity, among others. In this approach ecosystems are represented as a number of compartment (nodes) interconnected by flows of energy or matter (edges). Model compartments are defined by the scientist and they may be species, functional groups, a nutrient pool, particulate organic matter, etc. The analysis depends upon the structure of flows among the system components and their magnitude as measured, estimated, or deduced by the researcher. Flows are expressed as rates per unit of time, which at ecosystem level are more usually measured on a daily, monthly, seasonal or annual scale.

Indices of ecosystem growth and development. Margalef (1968) and Odum (1969) have described the changes in biomass, production to biomass and production to respiration ratios, etc. which occur as a food web develops. While these successional changes happen, the network of flows evolves to become more complex with richer connections. The ecosystems are considered open complex structures which allow to select the direction of its development and to self-organise as response to the external changes. The self-organising capacity is a result of the multiple connections between its compartments and processes (Ulanowicz 1986, 1997, Odum 1988, Jørgensen 1992, Bendoricchio & Jørgensen 1997, Bianciardi & Ulgiati 1998, among others). An ecosystem is a very dynamic system, all components and particularly the biological ones are steadily moving and their properties are steadily modifying. This means that ecosystems are not homogeneous structures in relation to properties concerning matter, energy and information. (Ulanowicz 1986, 1997, Bendoricchio & Jørgensen 1997, Bianciardi & Ulgiati 1998, Jørgensen 1999). Additionally, the ecosystems dissipate energy by which they evolve towards the adaptation of its structure through varying the compartments (e.g species, functional groups, etc.) and processes to maintain its basic thermodynamic function far from an equilibrium (Nicolis & Prigogine, 1977, Ulanowicz 1986, 1997, Patten, 1985, Jørgensen 1992, 1998, Bendoricchio & Jørgensen 1997, Bianciardi & Ulgiati 1998).

Ulanowicz (1986, 1997) proposed two indices to determine the maturity of an ecosystem using three measures based on information theory.

- 1.- *Total System Throughput (T)* measures the size or growth of the system in terms of the flows through all its components, the more material flowing through the system, the bigger the *T*.
- 2.- *Ascendency (A)* represents both the size (growth) and organisation (development) of the flows in a single measure, that is, the product of *T* and the *Average Mutual Information (AMI)*. *AMI* is related to the diversity of flows in a system. According to Ulanowicz's Theory, as an ecosystem matures and goes through a series of successional stages, the *Ascendency* of the system should increase. Therefore, if a system is affected by disturbance or pollution, this should be reflected by change in the flows of energy or materials through the system, and *Ascendency* should decrease.

The thermodynamic term to calculate *Ascendency* is the following:

$$A = - T x \sum_{j=0}^n Q_j x \log Q_j - [- T \sum_{j=0}^{n+2} \sum_{j=0}^{n+2} f_{ij} x Q_j x \log (f_{ij} x Q_j / Q_i)] \quad (1)$$

where $A = \textit{Ascendency}$

$T = \textit{Total systems throughput}$

n = Number of compartment

f_{ij} = Probability of any quantum of flow leaving compartment i directly contributing to the sustenance of compartment j

$Q_i = T_i/T$, the sum of all inputs to compartment i divided by the total system throughput

$Q_j = T_j/T$, the sum of all outputs from compartment j divided by the total system throughput.

Here the Shannon entropy is applied as a uncertainty measure, which is given by

$$H(x) = - \sum_{j=1}^n p(j) \log p(j) \quad (2)$$

where, $H(x)$ = The function of probability distributions that satisfies a certain set of properties which any reasonable measure of uncertainty should possess

$p(j)$ = The likelihood of j outcome is given by a probability of distribution, being $p(j) \geq 0, j = 1, 2, 3, \dots, n$

- 3.- *Development Capacity (C)* measures the potential of a particular network to develop, given its particular set of connections and total throughflow. C gives the highest possible value of A . This term corresponds to the first term in (1). The relative *Ascendency (A/C)* ratio describes the degree of maximum specialisation that is actually realised in the system. A/C is considered as an index of the maturity and the system's ability to withstand perturbations (Ulanowicz 1986,1997).

The second term in (1), the conditional entropy, will be referred to hereafter as the *internal overhead (O)*. But the overhead includes four important components, that is;

$$\text{Overhead} = \text{Import (I)} + \text{Export (E)} + \text{Respiration (S)} + \text{Redundancy (R)} \quad (3)$$

where I = Degree of dependence of the system to external energetic sources, such as, nutrients, radiation, biomass, etc.

E = Loss of energy of the system as heat and biomass.

S = The maintenance cost of the system's structure.

R = It is a measure of ambiguity, that is, it mostly results from the multiplicity of pathways between two arbitrary compartments. This also is a measure of resistance to external perturbations (Ulanowicz 1986, 1997) or several species of similar trophic roles (sensu Lawton 1994).

In chapter III the above mentioned indices were calculated by the ECOPATH II software (Christensen & Pauly 1992) to characterise the benthic systems studied. This model approach represents a steady-state approach in which system compartments are balanced by consumption and exports. It combines the approach of Polovina (1984) to estimate the biomass and food consumption of the ecosystem components (species or groups) and Ulanowicz's (1986) network analysis. Based on this approach the following questions were explored: (1) How is the biomass distribution and biomass flow structure in each habitat type; (2) What are the principal benthic predators in each system, their consumption rates and prey items?; (3) What is the carrying capacity of the system in term of food availability for target species and predators?; (4) Is it possible to recognise and quantify redundancy in the system?; Which are the species most likely affected by different management policies?; How sustainable are different management strategies?

The basic equation for this steady-state modelling can be expressed as:

$$\frac{dB_i^*}{dt} = P_i - (B_i \cdot M 2_i) - P_i \cdot (1 - EE_i) - EX_i \quad (4)$$

where * = at steady-state (= 0)

P_i = the production of species or compartment i ($\text{g/m}^2 \text{ year}^{-1}$)

B_i = the biomass of i (g/m^2)

$M2_i$ = the depredation mortality of i (year^{-1})

$1-EE_i$ = the ecotrophic efficiency of i (%)

EX_i = the export of i ($\text{g/m}^2 \text{ year}^{-1}$)

For more detail see Chapter III.

The principal results of this section were the following: (1) the highest total biomass and system throughput ($33579.3 \text{ t/km}^2/\text{year}$) was calculated for the sand-gravel habitat; (2) the sand habitat had a negative net system production due to the amount of primary production imported from deeper waters to satisfy the food requirements of the large beach clam *Mulinia* sp.; (3) the mean trophic level of the fishery varied between 2.06 (sand-gravel) and 3.92 (sand) reflecting the fact that the fishery concentrates on primary producers (i.e. algae and filter feeding) and on top predators (i.e. snails and crabs) respectively; (4) fishery is strongest in the sand-gravel habitat, where annual catches amount to 122.05 g/m^2 ; (5) low values of the relative Ascendency (A/C) (from 27.4 to 32.7%) suggest that the systems analysed are immature and highly resistant to external perturbations; (6) manipulations of the input data for exploited species suggest that seagrass and sand-gravel habitats have a potential for a ca. 3 times higher than the present production of scallop *A. purpuratus* and the red algae *Ch. chamissoi*; (7) Mixed Trophic Impacts Analysis suggests that management policies aimed at a man-made increase in the standing stocks of *A. purpuratus* and *Ch. chamissoi* in seagrass and sand-gravel habitats, and also a removal of the sea star *M. gelatinosus* in the seagrass habitat appear justified.

In chapter IV a dynamical extension of the static models described in the previous section was applied. By using the ECOSIM software of Walters et al (1997) different management scenarios were simulated for seagrass, sand-gravel, sand habitats and for an overall integrated system (combining all habitats) in order to explore strategies of sustainable resource use. Furthermore, the fishing mortality for maximum sustainable fishing (F_{MSY}) for the scallop *A. purpuratus* in the seagrass, sand-gravel and the combined model was estimated. The basic function of ECOSIM is written as:

$$\frac{dB_i}{dt} = g_i \cdot \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + E_i) \cdot B_i \quad (5)$$

where g_i = growth efficient of i compartment

C_{ji} = consumption rates of j by i compartments

C_{ij} = consumption rates of i by j compartments

I_i = immigration rate of i

M_i = total mortality of i

F_i = fishing mortality of i

E_i = emigration rate of i

and additionally we have,

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v'_{ij} + (a_{ij} \cdot B_j)} \quad (6)$$

where, v_{ij} and v'_{ij} = rates of behavioral exchange between invulnerable and vulnerable states, v_{ij} can be defined as the transference rate which determines if the control is top-down, bottom-up or mixed.

a_{ij} = rate of effective search by predator j for prey i .

For more details see chapter IV.

The most important findings of this section were: (1) an increase in the harvest of the scallop *A. purpuratus* did not drastically effect the global properties of the systems; (2) a depletion of its principal predator, the sea star *M. gelatinosus*, greatly improved the availability of scallops in the subsystem seagrass, sand-gravel as well as in the integrated model; (3) a biomass reduction of the snail *Xantochorus cassidiformis* produced only a small negative impact on the *System Recovery Time* (a measure of internal stability of the systems), while a simulated harvest on the beach clam *Mulinia* sp. drastically changed the system properties suggesting that this clam may be considered as a keystone species; (4) predictions of the maximum sustainable yield (*MSY*) of the scallop were lower than those obtained by single species approaches. Based on the simulations it is possible to conclude that a strong fishery on the scallop predator, the sea star *M. gelatinosus*, would greatly increase the yield of the scallop and the other populations or of the systems.

In chapter V, spatially explicit simulations were done by using the ECOSPACE program routine (Walters et al. 1999). The objective of this section was to assess the impact of harvest of the red algae *Ch. chamissoi*, the scallop *A. purpuratus*, the snail *X. cassidiformis* and the crab *C. polyodon* in the seagrass, sand-gravel, and in the sand habitat. This modelling approach is based on the same functions as ECOSIM described above (equations 5 and 6), but allows for a spatial analysis of the study area. ECOSPACE defines rectangular grids of spatial cells which describe a homogeneous biomass. For each cell, the immigration rate I_i (equation 5) is assumed to consist of four emigration flows from the surroundings cells. This modelling might be comparable to cellular automata. The emigration flows are represented as instantaneous movement rates m_i times biomass B_i in each cell as follows:

$$B_{i(x,y)} = m_{i(x,y)} \cdot B_{i(x,y)} \quad (7)$$

where, x,y represent cell row and column.

Additionally, the fishing mortality (F_i) can be spatially represented by using a gravity model as follows:

$$G_{kc} = \frac{O_{kc} \cdot U_{kc} \left(\sum_i p_{ki} \cdot q_{ki} \cdot B_{ic} \right)}{C_{kc}} \quad (8)$$

where G_{kc} = the weighted attractiveness of cell c to fleet k

O_{kc} = is 1 if cell c is open to fleet k , and 0 is closed to harvest

U_{kc} = is 1 if it was specified that gear k can harvest, and 0 otherwise

p_{ki} = relative price assigned for compartment i by fleet k fishers

q_{ki} = catchability of compartment i by fleet k

B_{ic} = biomass of the compartment i in cell c , and

C_{kc} = relative cost of fishing in cell c by gear k .

Finally, the spatial simulation searches for a moving equilibrium for each biomass compartment or group based on the following function:

$$B_{i(t+\Delta t)} = W_{i(t)} \cdot B_{i(t)} + (1 - W_{i(t)}) \cdot B_{i(e)} \quad (9)$$

where $B_{i(t+\Delta t)}$ = biomass of compartment i moving toward the equilibrium along the time trajectory.

$B_{i(t)}$ = biomass of compartment i at initial time of simulation

$B_{i(e)}$ = biomass of compartment i at equilibrium

$W_{i(t)}$ = is the exponential weight for compartment i .

Assuming it as:

$$W_{i(t)} = e^{-(Z_i + E_i) \cdot \Delta t} \quad (10)$$

where Z_i = total instantaneous mortality rate

E_i = total instantaneous emigration rate

For more details see chapter V.

The principal results of the current chapter were: (1) an exclusive fishing in the seagrass and sand habitats produces a population increase in the sea star *Luidia magallanica*, the seagrass *Heterozostera tasmanica*, and in the crab *Paraxanthus barbiger*; (2) an exclusive fishing in the sand-gravel habitat causes only small effects on the remainder compartments, which suggests that this habitat is the most resistant one to harvest; and (3) the simultaneous fishing on two or three habitats would produce the largest negative effect on the entire system. Therefore, a habitat rotation fishery is recommended.

2.3. Chapter VI

Qualitative modelling, Loop Analysis

An useful way to analyse interconnected entities (variables) and to estimate the propagation of direct and indirect effects is the *Loop Analysis* (Levins 1974, 1975, 1998b). Loop models provide a theoretical framework for formulating qualitative relationships between variables within a particular system and the estimation of local stability properties (sustainability) based on the dominance of negative and positive feedbacks. The relationships are shown as signs, indicating the type of influence each variable has upon another, namely whether it is positive, negative or neutral (zero). For instance, in ecological relationships, (+,-) denotes a predator-prey or parasite-host interaction, (-,-) represents competition between two species, while (+,+), (+,0) and (-,0) represent mutualism, commensalism and amensalism respectively. A complex system is shown graphically as a network of vertices and edges. Each variable is represented by a large circle and edges represent direction and type of interactions. Thus, if at one extreme there is an arrow, it means positive effect, while a circle means negative and zero means no effect.

A dynamical system, in particular one that can be represented by a set of differential equations as;

$$\frac{dX_i}{dt} = f_i(X_1, X_2, \dots, X_n; C_1, C_2, \dots, C_n) \quad (11)$$

where X_n represent the variables and C_n the parameters, can be drawn as a signed digraph in which the variables are the nodes or large circles, while the directed links or edges are the elements of the interaction coefficient matrix (community matrix coefficients). The link from X_j to X_i is similar to the α_{ij} in Levins (1968), where

$$\alpha_{ij} = \frac{\partial f_i(X)x^*}{\partial X_j} \quad (12)$$

* evaluated at equilibrium.

The element of the graph representing the link from j to i is signum (α_{ij}) where the function signum (X) is 1 when $X > 0$, 0 when $X = 0$, and -1 when $X < 0$.

A path is a series of links from one variable through one or more remaining variables, without crossing any variable twice. A loop is any closed path which returns to its starting point, not crossing any intermediate variable twice. The length of a loop is defined by the number of variables the path enters. A self-loop that starts and ends on the same variable (without passing through another variable), hence is of length 1. A negative self-loop is called self-damping and a positive is termed self-enhancing. The value of the path or loop is the product of the signs of the interaction coefficients, the α_{ij} 's. If the value of the coefficient is known, a number can be obtained. There is usually more than one and often are many loops in a signed digraph. A comparison among loops will show that some have variables in common and these are disjunct loops.

2.3.1. Local stability properties

Feedback at level k , where k is the number of variables, is calculated by,

$$F_k = \sum (-1)^{m+1} L(m, k) \quad (13)$$

and $L(m, k)$ is the product of m disjunct loops whose combined total length is k . Feedback has the same value as the determinant of order k in the interaction coefficient matrix. In other words, F_k is the coefficient of the $(n-k)^{th}$ term in the characteristic polynomial equation. Local stability, as determined by the Routh-Hurwitz criteria, translates into loop terms as:

Condition 1. $F_k < 0$, for all k . That is, the negative feedback at every level must exceed the positive feedback.

Condition 2. Negative feedback at the higher levels can not be too large compared with negative feedback at the lower levels in order to conserve the qualitative stability properties of the systems. This condition is a sequence of inequalities which are related to oscillation trajectory of the system after external perturbation. Where the general expression is the following: $F_{n-2} F_{n-1} + F_{n-3} F_n > 0$.

F_n is the feedback of the entire system (n = total number of variables in the system). It is assumed that the system is locally stable when F_n is negative. The stronger the negative feedback F_n is, the greater the resistance to external changes will be (Levins 1998b). Based on this local stability criteria it is possible to estimate the sustainability of man-made interventions in the systems and simultaneously explore strategies for its increase.

2.3.2. Qualitative predictions

If the parameters (C_n in equation 11) of the system are changing, slow enough for the variables to track the movement of the equilibrium, then the equilibrium values of the variables, which are changing in magnitude, and the direction of that change can be evaluated by:

$$\frac{\partial X_i}{\partial C_h} = \frac{\sum \frac{\partial f_j}{\partial C_h} \cdot \sum p_{ij}^{(k)} \cdot F_{n-k}^{(comp)}}{F_n} \quad (14)$$

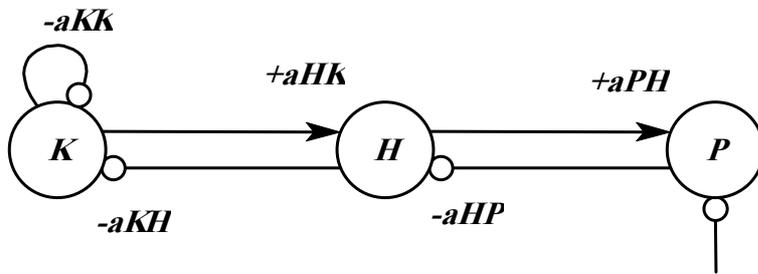
where, C_h is the h^{th} parameter that is changing because of an environmental impact (“impact entering at h ”),

is the effect of C_h parameter change on the state of the j^{th} variable,

$p_{ij}(k)$ is the path from j^{th} to the i^{th} variable and includes k variables,

$F_{n-k}^{(comp)}$ is the feedback of the complementary subsystem. This subsystem is formed by those variables which are not on the path of $p_{ij}(k)$; and F_n is the feedback of the whole system, which integrates all variables. When the complementary subsystem feedback and the feedback of the whole system have the same sign, the effect of a parameter change is the same as the sign of the product of the path. Feedback of opposite sign reverses the effects of the path. The disjunct and complementary feedback loops allow to estimate simultaneously the propagation of direct and indirect effects in the systems and the qualitative local stability.

The analysis of the following simple conceptual model, which has been deeply studied by Estes & Palmisano (1974), Estes & Duggings (1995), will serve to better understand the theoretical framework of the *Loop Analysis*. Suppose that system is constituted by the three principal variables:



where K is kelps of brown algae, H represents the sea urchin herbivores, and P the sea otters predators. The nominal character of the interactions are represented by $-aKH$ and $+aHK$ which grasp a plant-grazer pair, $-aHP$ and $+aPH$ that capture prey-predator combination, and $-aKK$ describes a self-damped dynamic for kelps due to its sessile behaviour and limitation of substrate.

In this model we can recognise the following loops:

Loops of length 1:

(i) $(-aKK)$

Loops of length 2:

(i) $(-aKH * +aHK)$

(ii) $(-aHP * +aPH)$

Conjunct loops:

(i) $(-aKK)$ and $(-aKH * +aHK)$

Disjunct loops:

(i) $(-aKK)$ and $(-aHP * +aPH)$

Complement loops:

(i) Path : K to $H = (+aHK)$ and its complement ($= 0$)

(ii) Path : P to $H = (-aHP)$ and its complement $(-aKK)$

(iii) Path : P to H to $K = (-aHP * -aKH)$ its complement ($F_0 = -1$).

By using the equation 13 we can calculate the feedback at each as follows:

$$F_0 = -1 \quad (-)$$

$$F_1 = (-aKK) + 0 \quad (-)$$

$$F_2 = (-aKH * +aHK) + (-aHP * +aPH) + 0 \quad (-)$$

$$F_3 = 0 + (-1) * (-aHP * +aPH) * (-aKK) + 0 \quad (-)$$

In this model, F_3 corresponds to the holistic feedback F_n . Finally, the qualitative changes in the standing stock of the variables K and H as response to an external negative impact on sea otter (P) can be calculated by equation 14 as:

$$\frac{\partial K}{\partial C_p} = \frac{(-) \cdot (+) \cdot (-1)}{(-)} = \frac{(+)}{(-)} = (-)$$

$$\frac{\partial H}{\partial C_p} = \frac{(-) \cdot (-) \cdot (-)}{(-)} = \frac{(-)}{(-)} = (+)$$

Both qualitative responses agree with the tendencies observed in experimental studies (see Estes & Palmisano 1974, Estes & Duggings 1995).

In the present chapter qualitative extensions of the trophic models (of previous sections) integrating other ecological interactions, such as competence, comensalism, amensalism and mutualism were developed. Ecological and extended eco-social qualitative models were developed for seagrass, sand-gravel and sand habitats to propose sustainable management strategies for the harvest of the red algae *Ch. chamissoi*, the scallop *A. purpuratus*, the snail *X. cassidiformis*, and the crab *C. polyodon*. The ecological models integrate the available ecological information previously described, while the second extended models consider the fishermen as another predator in the systems. Based on Levins's Theory it was possible to estimate both the local stability (sustainability) for each of these model systems and to simulate the changes in the standing stocks of the main groups as response to external factors. Our results suggest that to increase the standing stock of adult scallops the following man-made interventions should be implemented: (1) Seagrass habitat: partial removal of the three predatory sea star species *L. magallanica*, *H. helianthus* and *M. gelatinosus*; (2) Sand-gravel habitat: seeding of the scallop recruits and juveniles, and removal of just the sea star *H. helianthus*. According to our results, the sand habitat would not support any harvest. The extended model for the seagrass and sand-gravel habitats were found sustainable only if the fishermen were "self-damped", that is, when the fishing effort and fish quota are restricted.

3. References

- Acuña E, Moraga J & E Uribe. 1989. La zona de Coquimbo: un sistema nerítico de alta productividad. *CPPS Rev Pacífico Sur*, Número Especial 145-157.
- Barber M. 1978a. A retrospective Markovian model of ecosystem resource flow. *Ecological Modelling* 5: 125-135.
- Barber M. 1978b. A Markovian model for ecosystem flow analysis. *Ecological Modelling* 5: 193-206.
- Beddington JR. 1984. The response of multispecies systems to perturbations. In: May R (Ed.), *Exploitation of marine communities*. Dahlem Konferenzen, Springer-Verlag, Berlin, pp. 209-225.
- Bendoricchio G & SE Jørgensen. 1997. Exergy as goal function of ecosystems dynamic. *Ecological Modelling* 102: 5-15.
- Bianciardi C & S Ulgiati. 1998. Modelling entropy and exergy changes during a fluid self-organisation process. *Ecological Modelling* 110: 255-267.
- Branch GM & CA Moreno. 1994. Intertidal and subtidal grazers. In: W. Roy Siegfried (Editor). *Rocky shores: exploitation in Chile and South Africa*. Ecological Studies, 103:75-100.
- Bustamante RH & JC Castilla. 1987. The shellfishery in Chile: an analysis of 26 years of landings (1960-1985). *Biología Pesquera* (Chile) 16:79-97.
- Bustamante RH & JC Castilla. 1990. Impact of human exploitation on the population of the intertidal southern bull-kelp *Durvillaea antarctica* (Phaeophyta, Durvilliales) in central Chile. *Biological Conservation* 52:205-220.
- Castilla JC. 2000. Roles of experimental marine ecology in coastal management and conservation. *Journal of Experimental Marine Biology and Ecology* 250: 3-21.
- Castilla JC & PC Camus. 1992. The Humboldt-El Niño Scenario: coastal benthic resources and anthropogenic influences, with particular reference to the 1982/83 ENSO. In: Payne, A. Y. L., Brink, K. H., Mann, K. H. and R Hilborn (Eds), *Benguela Trophic Functioning*. South African Journal of Marine Science 12:703-712.
- Castilla JC & LR Durán. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects of on *Concholepas concholepas* (Gastropoda). *Oikos* 45:391-399.
- Castilla JC & RT Paine. 1987. Predation and community organization on Eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural* 60:131-151.
- Christensen V & D Pauly. 1992. ECOPATH II- a software for balancing steady-state ecosystem models and calculating network characteristic. *Ecological Modelling* 61: 169-185.
- Daneri G, Dellarossa V, Quiñones R, Jacob B, Montero P & O Ulloa. 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Marine Ecology Progress Series* 197: 41-49.
- Ehrlich PR & AH Ehrlich. 1981. *Extinction: the causes and consequences of the disappearance of species*. Random House, New York.
- Estes J & J Palmisano. 1974. Sea Otters: their role in structuring nearshore communities. *Science* 185: 1058-1060.
- Estes J & D Duggins. 1995. Sea otters and kelp forests in Alaska: generality and observation in a community ecological paradigm. *Ecological Monographs* 65(1): 75-100.

- Finn JT. 1976. Measures of the ecosystem structure and function derived from analysis of flows. *Journal Theoretical Biology* 56: 363-380.
- Hannon B. 1973. The structure of ecosystems. *Journal Theoretical Biology* 41: 535-546.
- Hilborn R, Walters C & C Ludwig. 1995. Sustainable exploitation of renewable resources. *Annual Review of Ecological Systematics* 26: 45-67.
- Jesse S. 2001. Comparative ecology of sympatric brachyuran crab species in the shallow sub-tidal of the Pacific Coast on North Chile and their importance for the artisanal fishery in Puerto Aldea. PhD. Dissertation, University of Bremen, Germany.
- Jones C, Lawton JH & M Shachak. 1994. Organism as ecosystem engineers. *Oikos* 69: 373-386.
- Jørgensen SE. 1992. Integration of Ecosystem Theories: A Pattern. Kluwer, Dordrecht, 383 pp.
- Jørgensen SE. 1998. Exergy and Ecological Systems Analysis. In: Patten B & SE Jørgensen (eds.), *Complex Ecology: The Part-Whole Relation in Ecosystems*, Prentice Hall, Englewood, pp. 568-584.
- Jørgensen SE. 1999. State-of-the-art of ecological modelling with emphasis on development of structural dynamic models. *Ecological Modelling* 120: 75-96.
- Kassner J & R Malouf. 1982. An evaluation of "spawner transplants" as a management tool in Long Island's hard clam fishery. *Journal Shellfish Research* 2: 165-172.
- Kay J, Graham L & R Ulaniwicz. 1989. A detailed guide to network analysis. In: Wulff F, Field JG & KH Mann (eds), *Network Analysis in Marine Ecology: Methods and Applications*. Lecture Notes on Coastal and Estuarine Studies, Springer-Verlag, NY, 284 pp.
- Kennedy V. 1989. The Chesapeake Bay oyster fishery: traditional management practices. In: Caddy JF (Ed.), *Marine Invertebrate Fisheries: Their Assessment and Management*. Wiley, NY, pp. 455-477.
- Kitching RL. 1983. *System Ecology: An introduction to Ecological Modelling*. University of Queensland Press, St. Lucia, 280 pp.
- Larkin P. 1977. An epitaph for the concept of maximum sustainable yield. *Transactions of American Fisheries Society* 106(1): 1-11.
- Lawton JH. 1994. What do species do in ecosystems? *Oikos* 71: 367-374.
- Leontief WW. 1951. *The structure of the US economy*. 2nd Edition Oxford University Press, NY.
- Levins R. 1966. The strategy of model building in population biology. *American Scientific* 54(4): 421-431.
- Levins R. 1968. *Evolution in changing environments*. Princeton Monographs Series, Princeton University Press, NJ, 120 pp.
- Levins R. 1974. The qualitative analysis of partially specified systems. *Annals of New York Academic Sciences* 231: 123-128.
- Levins R. 1975. Evolution in Communities near Equilibrium. In: Cody M, Diamond J (eds), *Ecology and evolution of communities*. Harvard University Press, MA, pp. 16-50.
- Levins R. 1988. The controlling factor in biological communities. *Ceonoses* 3(3): 149-154.

- Levins R. 1993. A response to Orzack and Sober: formal analysis and the fluidity of science. *The Quarterly Review of Biology* 68(4): 547-555.
- Levins R. 1998a. Dialectics and systems theory. *Science & Society* 62(3): 375-399.
- Levins R. 1998b. Qualitative Mathematics for Understanding, Prediction, and Intervention in Complex Ecosystems. In: Rapport D, Costanza R, Epstein P, Gaudet C, Levins R (eds), *Ecosystem Health*. Blackwell, MA, pp. 178-204.
- Levins R & R Lewontin. 1985. *The dialectical biologist*. Harvard University Press, MA, 303 pp.
- Llagostera A. 1979. 9,700 Years of maritime subsistence on the Pacific: an analysis by means of bioindicators in the north of Chile. *American Antiquity* 44: 309-324.
- MacArthur RH. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533-536.
- MacKenzie CL Jr. 1970. Oyster culture in Long Island Sound, 1966-69. *Comm Fish Rev* 859: 27-40.
- Margalef R. 1968. *Perspectives in Ecological Theory*. University of Chicago Press, Chicago, 111 pp.
- May R. 1974. *Stability and complexity in model ecosystem* 2nd Edition. Monographs in Population Biology N°6, Princeton University Press, NJ, 265 pp.
- Montecinos V & D Quiroz. 2000. Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30°). *Aquatic Science* 62: 364-380.
- Moreno CA & HF Jara. 1984. Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fueguian Islands, Chile. *Marine Ecology Progress Series* 15: 99-107.
- Nicolis G & I Prigogine. 1977. *Self-organisation in Non-equilibrium Systems: from dissipative structure to order through Fluctuations*. Wiley, NY, 492 pp.
- Odum EP. 1964. The new Ecology. *BioScience* 14: 14-16.
- Odum EP. 1969. The strategy of ecosystem development. *Science* 104: 262-270.
- Odum HT. 1988. Self-organisation, transformity and information. *Science* 242: 1132-1139.
- Oliva D & JC Castilla. 1986. The effects of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *PSZN: Marine Ecology* 7:201-217.
- Paine R. 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65-75.
- Parra B, Westermeier R & CA Moreno. 1992. Effect of human exploitation on the intertidal community structure at the Valdivian coast, Chile. In: Seeliger U (Ed.), *Coastal Plant Communities of Latin America*. Academic press, San Diego, pp. 65-76.
- Patten B. 1985. Energy cycling in the ecosystem *Ecological Modelling* 28: 1-71.
- Patten B. 1997. Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. *Ecological Modelling* 100: 11-42.

- Patten B, Bosserman R, Finn JT & W Gale. 1976. Propagation of cause in ecosystems. In: Patten B (Ed.), *System Analysis and Simulation in Ecology*, Vol.4, pp.457-579.
- Polovina JJ. 1984. An overview of the ECOPATH model. *Fishbyte* 2(2): 5-7.
- Roberts C. 1997. Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution* 12: 35-38.
- Santelices B & C Griffiths. 1994. Seaweeds as resources. In: Siegfried WR (Ed.), *Rocky shores: exploitation in Chile and South Africa*. *Ecological Studies*, 103: 33-53.
- SERNAP. 1993. Servicio Nacional de Pesca: Instructivo de Fiscalización Pesquera, Chile.
- SERNAP. 2000. Servicio Nacional de Pesca: Anuario Estadístico de Desembarques, Chile.
- Siegfried WR. 1994 (Ed.). *Rocky shores: exploitation in Chile and South Africa*. *Ecological Studies*, 103: 1-167.
- Stephens D & J Krebs. 1986. *Foraging theory*. Princeton University Press, NJ.
- Stotz W. 1997. Las áreas de manejo en la Ley de Pesca y Acuicultura: primeras experiencias y evaluación de la utilidad de esta herramienta para el recurso loco. *Estudios Oceanológicos (Chile)* 16: 67-86.
- Ulanowicz R. 1986. *Growth and Development: Ecosystems Phenomenology*. Springer-Verlag, NY, 203 pp.
- Ulanowicz R. 1997. *Ecology, The Ascendent Perspective*. Columbia University Press, NY, 201 pp.
- Vasquez J. 1995. Ecological Effects of Brown Seaweed Harvesting. *Botanica Marina* 38: 251-257.
- Walker B. 1992. Biological diversity and ecological redundancy. *Conservation Biology* 6: 18-23.
- Walters C & R Hilborn. 1978. Ecological optimisation and adaptive management. *Annual Review of Ecology and Systematics* 9: 157-188.
- Walters C & J Korman. 1999. Cross-scale modelling of Ripirian ecosystem responses to hydrologic management. *Ecosystems* 2: 411-421.
- Walters C, Christensen V & D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Review in Fish Biology and Fisheries* 7: 139-172.
- Walters C, Pauly D & V Christensen. 1999. Ecospace: prediction mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2: 539-554.
- Whitlatch R & R Osman. 1994. A qualitative approach to managing shellfish populations: Assessing the relative importance of trophic relationships between species. *Journal Shellfish Research* 13(1): 229-242.

4. Chapter I

“Seasonal variation in biomass and productivity of dominant species in four subtidal communities of north-central Chile”

Marco Ortiz¹, Sandra Jesse¹, Matthias Wolff¹ & Wolfgang Stotz²

¹ Center for Tropical Marine Ecology, Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@zmt.uni-bremen.de, jesse@zmt.uni-bremen.de, mwolff@zmt.uni-bremen.de). Fax : +49 (0) 421 238 00 30

² Universidad Catolica del Norte, Grupo de Ecología y Manejo de Recursos, Larrondo 1281, Casilla 117, Coquimbo, Chile (eMail: wstotz@socompa.cecun.ucn.cl)

Key words: Upwelling, management, statistical power analysis, ANOSIM, predation, secondary productivity.

2001

The first author developed the conceptual frame of this paper. The first and second author carried out the sampling programme. Data processing, analysis and interpretation were conducted by the first author. The first version of this work was written by the first author and it was improved with the cooperation of the other co-authors.

Abstract: The annual biomass dynamics and productivity of harvested macrofauna and macroalgae along with those of their trophically linked species were assessed in four shallow subtidal communities (habitats) in northern Chile. The study objective was to assess the effect of fishery activities, population processes (reproductive, recruitment and migratory cycles) and abiotic conditions (upwelling dynamics) on the observed seasonal dynamics. Factors affecting seasonal biomass dynamic are the fishery and the migratory behaviour of the unexploited decapods. Our results suggest that seasonal biomass changes were unexpectedly of small scale for the entire study area, the habitats and also for the most of single species. The overall biomasses of the dominant crab species and the mussel *Mulinia* sp. were higher than reported for comparable habitats. Sand-gravel and seagrass habitats account for 81.94% and 12.20% of total system secondary production, while sand and mud habitats contributed only 4.79% and 1.09%, respectively. This study is the ground work for ongoing studies aimed at the impact assessment of population management strategies on the global properties of these systems. Based on the results of this study, it seems more adequate to construct “average” annual models, than seasonal ones, for each community and the entire area.

Problem

Even though at least three principal shore types can be distinguished along the 4.600 km Chilean coastline, such as exposed rocky shores, exposed sandy shores and insular littoral, fiords and channels (Fig. 1a) (Bustamante & Castilla, 1987), the vast majority of ecological studies have been done in intertidal rocky shores (e.g. Castilla, 1981; Santelices, 1981, 1989, 1990; Moreno & Jaramillo, 1983; Jara & Moreno, 1984; Ojeda & Santelices, 1984a; Vasquez & Santelices, 1984, 1990; Gonzalez et al., 1991; Stotz et al., 1991; Buschmann, 1992; Moreno et al., 1993, 1998; Castilla et al., 2000), and in sandy beaches (e.g. Jaramillo, 1978, 1982, 1987; Jaramillo et al., 1993; Ortiz & Stotz, 1996; Jaramillo et al., 2000; among others). Subtidal communities have received less attention although they extend over much larger areas than the adjacent intertidal habitats. The reason seems to be the difficulty to develop rigorous experiments for testing ecological hypothesis and theories (Castilla, 2000). The few studies in subtidal communities have been done on exposed rocky bottoms, especially in areas dominated by large brown algae associations (e.g. Castilla & Moreno, 1982; Moreno & Sutherland, 1982; Moreno & Jara, 1984; Ojeda & Santelices, 1984b; Santelices & Ojeda, 1984 a,b; Vasquez & Castilla, 1984; Vasquez et al., 1984; Villouta & Santelices, 1984, 1986; Santelices, 1991; Vasquez, 1991, 1992, 1993, 1995).

The lack of studies in subtidal habitats seems difficult to understand as many of these benthic systems are inhabited by commercially exploited invertebrate and macroalgae species. Thus, it is necessary to obtain biological and ecological information of these populations and habitats to know and understand the community structure (multispecies dynamics), productivity, and the resource potential. The present study concentrates on a small subtidal benthic ecosystem situated at the southern end of Tongoy Bay (Fig. 1b), which lies near to an important upwelling center of northern Chile (Acuña et al., 1989; Daneri et al., 2000; Montecinos & Quiroz, 2000). It includes large patches of the seagrass *Heterozostera tasmanica* (Martens ex Ashers) and several invertebrates and algae species of commercial importance. Species of highest values are the scallop *Argopecten purpuratus* and the macroalgae rodophyta *Chondrocanthus chamissoi*. Both species support an intensive fishery, which has reached about 130 ton annually in recent years.

Besides seagrass beds it is possible to distinguish three further deeper subtidal habitats: sand-gravel, sand and mud (Fig. 1c). Each habitat can be characterised by a specific pattern of ecological relationships like prey-predator and/or plant-herbivorous as shown in Fig. 2.

Some knowledge about the related species (Fig. 2) is available from baseline studies on distribution pattern, size composition, reproductive strategy (cycles) and population dynamics of the commercially exploited and not exploited species such as the red algae *Ch. chamissoi*, the scallop *A. purpuratus* (Stotz & Gonzalez, 1997), the clam *Mulinia* sp. (Fuentes, 1988) and the decapods *Cancer polyodon*, *C. coronatus*, *C. porteri*, *Paraxanthus barbiger* (Jesse, 2001). According to these studies, most of these species have similar reproductive cycles which peak annually between spring and summer. For the remaining species, similar dynamics may be inferred based on species of the same genus at other places in northern Chile and Perú (Illanes, 1985; Wolff, 1988; Wolff & Soto, 1992). Likewise, some crabs are expected to undergo seasonal migrations principally due to food depletion after intensive feeding during winter and spring (Jesse, 2001) and annual temperature variations (Arntz & Fahrbach, 1986; Wolff pers. Comm.). Primary production (phytoplankton) peaks during spring months as a response to the coastal upwelling processes (Santelices, 1991; Alheit & Bernal, 1993). An intensive fishery on *Ch. chamissoi* and *A. purpuratus* is carried out between spring and summer.

In the past decades, much theoretical and experimental attention has been addressed to the dominance of direct and indirect interactions and causality effects in determining the structure and functioning of natural communities and ecosystems (Levins, 1974; Lawlor, 1979; Paine, 1980; Patten, 1981, 1982, 1985; Abrams, 1991; Wissinger & McGrady, 1993; Billick & Case, 1994; Miller, 1994; Wootton, 1994; Menge, 1995; Fath & Patten, 1999; Underwood, 1999). The present work was designed to test the hypothesis that the interaction of the biological and physical factors described above, would produce significant natural variations in the seasonal biomass of exploited and related species as well as of the total biomass by habitat and the entire ecosystem. Consequently, these changes may heavily influence the energy flows within the food webs propagating their direct and indirect effects through these communities. To test this hypothesis, seasonal biomass of the target and linked species and their productivity in each community were monitored by habitat and the entire system.

This study represents the ground work for large scale models for each habitat and the whole ecosystem. These models should be used for an integration of the trophic interactions among populations of this management area and for the development a sustainable multispecies fishery.

Material and Methods

Description of study area

The study was carried out in Tongoy Bay (30°15'S – 71°31'W) IV Region of Coquimbo (Chile) (Fig.1). Tongoy Bay and particularly the benthic area of Puerto Aldea are protected from the prevailing south-west winds by Lengua de Vaca peninsula (Berrios et al., 1985). Ortiz & Stotz (1996) classified the beaches of the bay as belonging to the intermediate morphodynamic state (sensu Brown & McLachlan, 1990). Water circulation is dominated by tidal cycles and current velocities of 2.5 m/s, causing a high degree of water exchange with adjacent open water bodies (Olivares, 1988). The upwelling center near Punta Lengua de Vaca (Acuña et al., 1989; Daneri et al., 2000; Montecinos & Quiroz, 2000) supplies nutrients to the system and at the same time prevents the establishment of a stable thermocline during summer. Oxygen saturation reaches 100% (more than 8 ml/l) in shallow waters (< 20m), but in deeper water drops to about 3 ml/l (Moraga & Olivares, 1989). Bottom water temperature (3-4 m depth) ranges between 13°C and 17°C (Jesse, 2001). Salinity remains around 34.3 ‰ throughout the year and does not differ from open ocean waters (Pacheco et al., 1987).

The area of Puerto Aldea (Fig. 1c) can be divided into four different habitat types: seagrass beds, sand-gravel, sand and mud habitat of ~ 60, 40, 150 and 75 ha of surface area respectively. The seagrass beds extend between 0 and 4 m depth. The sand-gravel (between 4 and 10 m depth) constitutes a transition zone between seagrass meadows and open sandy sediments. It is characterised by its high heterogeneity, with sectors dominated by gravel, stones or rocks. The substrate between 10 and 14 m depth is dominated by coarse sand and silt with low organic content. Towards deeper waters (> 14 m), substrates become muddy and the organic content increases (Ortiz & Stotz, 1996).

Sampling design.

A preliminary sampling was done in the study area to estimate the optimum sample size and the size of the sample unit by species, considering time, operational capacity, distribution and abundance of populations, and previous estimations of effect sizes, when feasible (see Table 1). Seasonal invertebrate and macroalgae abundance was determined (from June 1996 to May 1997) for each habitat at five random stations, taking three random samples by station.

Productivity estimations.

Estimates of annual productivity for the crabs species and the scallop *A. purpuratus* were taken from Jesse (2001) and Stotz & González (1997) respectively. For the remaining invertebrate species, productivity (P) was estimated empirically using the following allometric equation (sensu Warwick & Clarke, 1993), that is,

$$P = \left(\frac{B}{A} \right)^{0.73} \cdot A$$

Where B/A is the mean body-size (biomass/density), and 0.73 is the exponent of a regression of annual production on body-size for macrobenthic invertebrates derived from Brey (1990).

Statistical analysis.

Hierarchical cluster (dissimilarity %) analysis with group-average linking and non-metrical multidimensional scaling (MDS) (Kruskal, 1964) with $R-Q$ (species-samples) mode resemblance were performed with biomass (g/m^2) values of each species per sample using the PRIMER software package (Clark & Warwick, 1994). An a priori test of the differences between samples from different habitats was performed using the ANOSIM (analysis of similarity). Data were double root-transformed ($\text{data}^{1/4}$) prior to calculation of the similarity matrix. The Bray-Curtis similarity coefficient was used for the calculation of similarities between samples and species. The resulting triangular similarity matrices were then input to both ordination routines. Hierarchical clustering with group-average linking and non-metrical MDS based on sample similarity (dissimilarity) matrices of Bray-Curtis have proved to be useful tools in many descriptive ecological studies over the last years (e.g. Clarke et al., 1993; Warwick & Clarke, 1993; Clarke & Warwick, 1994).

The Bartlett and Hartley's test were used to evaluate the normality of data and Cochran's test to evaluate the heterogeneity of variances (Underwood, 1981, 1997). When non-normality and heterogeneity were significant ($p < 0.005$) the logarithmic transformation of data (\log_{10} data) was applied (Sokal & Rohlf, 1995; Underwood, 1981, 1997), satisfying the assumptions of the statistical test. The lower p-level (< 0.005) was considered because parametric tests are robust with non-normality of data and non-severe heterogeneity of variance (Box, 1953; Tiku et al., 1986; Underwood, 1981, 1997; Weerahandi, 1995). However, if there were zeros in the data, the transformation was not used and the statistical

test were done with crude data (Underwood, 1997). When the assumptions for parametric tests were satisfied, one-way ANOVAs were applied with $p < 0.05$ (or $p < 0.005$ if transformation was not used). In cases of statistical significance the post hoc analysis Student-Newman-Keuls was used (Steel & Torrie, 1988; Underwood, 1981, 1997) with $p < 0.07$ (Type I error) according to the adjustment recommended by Day & Quinn (1989). *A priori* statistical power was applied for the planing of the optimum sample size with a power = 0.80 and previous estimations of effect size (minimal detectable difference) according to the strategy described by Underwood (1997) and Ortiz (in press). *A posteriori* statistical power was calculated in those cases where the null hypothesis (H_0) (e.g. biomass dynamic is independent of the seasonal cycle) was not rejected. In situations where non statistical differences with low power (power < 0.80) were matched, rigorous conclusions are unjustified. Therefore, a qualitative analysis was preferred in this case, as another way to analyse the information, in order to recognise putative similar tendencies of biomass patterns (minimum and maximum magnitudes) between species by seasonal periods.

Results

Multivariate patterns

Fig. 3a,b and 4a,b show the dendrograms and MDS-plots with R - Q resemblance derived from the annual average of the biomass data. Only the MDS-plot based on Q -resemblance (species) matched the cluster dendrogram. The cluster dendrogram and MDS-plot with R -resemblance (stations) separated only two principal groups of species. The algae *Ch. chamissoi*, Rodophyta and the *Tegula* sp. (grazer snail) formed an evident cluster. A large cluster is formed by the remainder species and the scallop *A. purpuratus*, the seastar and decapods constituted a distinctive sub-group. Both these findings are consistent with plant-grazer and prey-predator relationships for these species observed (Jesse, 2001). Nevertheless, it is also possible to note some contradictions within these arrangements, for instance, the green algae *Ulva* sp. was not integrated with the other algae, and the trochidae *C. trochiformis* and its predator were not within a single group (Fig. 3a,b). The Q -resemblance shows a more realistic pattern according to personal observations. At 40 % of dissimilarity the cluster dendrogram revealed two extreme groups for the seagrass meadows and mud habitats. The sand-gravel and sand habitats represent a transition zone between seagrass bed and mud habitat (Fig. 4a,b). These results are corroborated by ANOSIM which significantly separated the four habitats (Global R: 0.998, $p < 0.0001$). It is important to point out that both MDS-plots (R/Q -resemblance) had a “excellent” goodness of fit with a stress of 0.001 and 0.005 respectively (sensu Kruskal, 1964). Based on these results of the multivariate analysis, the univariate analysis of average biomass was carried out by habitat and the entire area.

Univariate patterns

Seasonal biomass pattern of the species in each habitat

Seagrass habitat. Only the biomass of the scallop *A. purpuratus* was found to significantly differ between seasons, with highest values in winter and spring (Table 2A). However, this species suffered two commercial extractions between spring and summer (1996-1997).

Sand-gravel habitat. *A. purpuratus*, *C. polyodon*, *P. barbiger*, and *Ch. chamissoi*, *Ulva* sp. and other Rodophytas biomass varied significantly between seasons. *A. purpuratus*, *C. polyodon* and the algae presented highest biomass values during spring (Table 2B). It is important to point out that *A. purpuratus*, *C. polyodon*, and *Ch. chamissoi* suffered commercial extractions between winter and summer.

Sand habitat. *X. cassidiformis* (snail), *C. polyodon* and *C. coronatus* biomass significantly differed between seasons (Table 2C). *X. cassidiformis* and *C. polyodon* were harvested during the study period.

Mud habitat. *C. coronatus* and *C. porteri* biomass were found to differ between seasons. For the remainder species no significant differences were found (Table 2D).

The outcomes of statistical power of the tests (*a posteriori* case) show high probabilities of type II error for all species where the rejection of the null hypothesis failed. The qualitative analysis showed different patterns of biomass between seasons (Table 2A-D).

Seasonal biomass pattern of the species in the whole area

Figs. 5a,b,c show the biomass distribution for *A. purpuratus*, *Tegula* sp. and *Mulinia* sp. Significant seasonal differences were not detected. However, each species presented a different temporal pattern, with lowest biomass values of *A. purpuratus*, *Tegula* sp. and *Mulinia* sp. in summer, winter and spring respectively. Significant differences between winter and the other seasons were found for *X. cassidiformis* and *C. trochiformis* (Fig. 5d,e). For the tunicate *P. chilensis* this decrease was not statistically significant in comparison to the other seasonal periods, even though its biomass decreased in summer (Fig. 5f). The qualitative analysis showed that the biomass patterns of these species were dissimilar between seasons.

For seastars *M. gelatinosus*, *L. magallanica* and *H. helianthus* biomass did not statistically differ between seasons (Fig. 6a,b,c). Unfortunately, the probability of type II error was relatively high for the three analysis (0.53, 0.78 and 0.75 respectively). However, the qualitative tendencies showed dissimilar biomass patterns between seasonal periods.

C. polyodon and *C. porteri* biomass differed statistically between winter-spring in comparison to other seasons (Fig. 7a,c). Both species showed a different biomass pattern with respect to the highest and lowest abundance. Average *C. coronatus* biomass was not found to differ seasonally (Fig. 7b). Fig. 7d shows the abundance pattern of *P. barbiger*. Highest biomass were found in autumn and differed significantly from other seasons. *Taliepus* sp. biomass did not significantly differ between seasons (Fig. 7e). Both species presented a different seasonal biomass pattern.

The seasonal biomass patterns of *Ch. chamissoi* and the remaining red algae were similar, with highest value in spring, differing from other seasons (Fig. 8a,b). *Ulva* sp. presented a different biomass pattern with maximum values in summer and autumn, which did not differ significantly. Both values differed significantly in regard to average biomass of winter and spring (Fig. 8c).

Seasonal biomass pattern by habitat and whole area

Fig. 9a shows that the average biomass pattern in the seagrass meadows did not significantly differ between seasons. Highest and lowest biomass values were found in winter and summer, respectively. The total biomass of the sand-gravel habitat showed a different seasonal pattern when compared to seagrass, and the highest abundance was detected in spring, differing significantly from other seasons (Fig. 9b). Seasonal biomass distribution of the sand habitat was found to be similar with the one observed in seagrass, although, seasonal variations were not significant (Fig. 9c). Highest average biomass of the mud and sand-gravel habitats was found in spring differing significantly from the rest of the year (Fig. 9d). Temporal biomass distribution were qualitatively dissimilar for all habitat types.

Fig 10. Shows the accumulative average biomass pattern for the whole study area. Highest and lowest average biomass values were detected in spring and winter respectively, but statistically this difference was not significant.

In often situations the statistical tests failed to reject the null hypothesis with a low power. Assuming the sampling design, $\alpha = 0.05$, and a power of 0.80 fixed, the optimum sample size could be estimated for each species (Table 1).

Productivity

Table 3 shows the magnitudes of production and biomass by species and habitat and for the whole area as obtained analytically and from literature reports. In the more structured and complex habitat (sand-gravel), epifauna contributed 81.94% to the total secondary productivity. In seagrass, its contribution was 12.20%, in sand 4.79 %, and in mud 1.09 %. The mussel *Mulinia* sp. performed the highest production of the entire system (Table 3), but was not considered for the calculations described above, because this mussel inhabits only a narrow strip along the beach, which is proportionally small in comparison to the rest of the sand habitat.

Discussion

Based on the results, it seems that two factors are most influential for the biomass dynamics of the species considered: the fishery activities on *A. purpuratus*, *C. polyodon*, *X. cassidiformis* and *Ch. chamissoi*, and the migration behaviour of not exploited decapods such as *C. coronatus* and *C. porteri* (Jesse, 2001). Any other biotic factors such as primary production –coupled to upwelling dynamic-, reproduction and recruitment cycles did not seem to be relevant for the annual biomass pattern. An exceptional case are the macroalgae, which strongly depend on the environmental conditions (e.g. light and temperature) of each season.

The sand-gravel habitat concentrated the highest biomass and production of the entire system, which may be explained by its structural complexity. The high complexity of this habitat arises from its abiotic substrate factors such as number and size of the stones, but also from biotic factors such as the microhabitats offered by different macroalgae and by *Pyura chilensis*. In this context, it should be noted that other species (microepifauna was not assessed in the present work) as well as recruits of *A. purpuratus*, *Tegula* sp., *C. trochiformis*, *C. polyodon*, *P. barbiger* and *Taliepus* spp. were always found to co-occur with the algae and *P. chilensis* (Jesse, 2001).

It is widely reported that seagrass beds rank among the most productive ecosystems in nature (e.g. Ott, 1981; Frankovich & Fourqurean, 1997; Ziegler & Benner, 1999 and reference therein) supporting different species associations of epiphyta (e.g. Tomasko & Lapointe, 1991; Frankovich & Fourqurean, 1997), benthic invertebrates (infaunal and epifaunal associations) (e.g. Connolly, 1997; Reusch, 1998; Edgar, 1999a; Rose et al., 1999) and fishes (e.g. Bell et al., 1987; Ferrell & Bell, 1991; Edgar, 1999b). In our study area, the seagrass beds of *H. tasmanica* also constitute a complex habitat. However, compared to sand-gravel, it seems to offer optimum conditions to other the species or groups of organisms such as microepifauna, epiphytas, infauna, fishes, among others (González, 1992). It is very important to stress that this habitat also offered an optimum refuge for recruits of *A. purpuratus*, *C. polyodon* and *Taliepus* spp. (Jesse, 2001). This function as nursery ground has widely been reported for other seagrass beds around the world (e.g. Thayer et al., 1984; Eckman, 1987; Edgar, 1999a,b).

In the sand and mud habitat, an interesting decapod guild could be observed, which preferentially feeds on the infauna (Jesse, 2001). Crabs of this guild are known to migrate towards deeper waters, probably due to the high temperatures during summer (Arntz & Fahrbach, 1986; Wolff pers. comm. 2000) and/or to depletion of food after an intensive depredation during winter and spring (Jesse, 2001). In the sand habitat, especially in the

nearshore beach area, the clam *Mulinia* sp. contributes most to the total invertebrate biomass and production of the entire habitat and whole area. It may be explained by the sediment properties (fine sand and high matter content) which characterise the southern end beaches of Tongoy Bay. These sediments offer optimum conditions for deposit feeders as *Mulinia* sp., preventing filter-feeders species (McLusky et al., 1975; Whitlatch, 1977; Whitlatch, 1981; Wilson & Shelley, 1986; Long & Lewis, 1987; Skilleter, 1992), such as its eventual competitor the clam *Mesodesma donacium* which dominates along the remainder beaches of the bay characterised by opposite sediment conditions (Ortiz & Stotz, 1996). Moreover, *Mulinia* sp. is an unexploited bivalve species, which is protected by the local fisherman, who consider it as a possible future resource.

It is difficult to compare our results with the biomass of other species in other places, principally due to the different environmental conditions, habitat characteristics and different sampling methods. According to the literature of comparable ecosystems (Mannino & Montagna, 1997; DrGas et al., 1998; Taylor, 1998; Wilson, 1999) it seems, however, that our estimations of biomass of the dominant crabs and bivalve species is for above those given in other reports. Nevertheless, the biomass of decapods particularly in seagrass meadows was lower compared to other temperate seagrass bed (Edgar, 1999b).

Some statistical tests failed to reject the null hypothesis (H_0) with low magnitudes of power. For these the optimum sample size needed to maximise the robustness of the tests were estimated. This analysis showed that in most cases a twice as large sample size had to be taken. Only for *P. chilensis*, *Tegula* sp. and *Mulinia* sp. this quantity of samples could be obtained. For the remainder populations, particularly the seastar, an increase of the size of sample unit may be recommended for further studies in comparable benthic communities. It is important to point out that for the red algae *Ch. chamissoi* the *a priori* estimations of effect size improved considerably the robustness of the test of hypothesis (Table 1). Based on our experience, we suggest to apply the statistical power analysis: *a priori* and *a posteriori* cases by which it is possible to improve the reliability of a sampling program (under hypothesis) and to assess the robustness of the statistical tests. In those situations when a lower power is detected, it suggests that a qualitative analysis of the kind presented here should be performed, because under this circumstances rigorous conclusions are unjustified.

Frequently, scientists aim to construct seasonal models of trophic interactions within an ecosystem, to account for the expected seasonal dynamics of the biomass of –and flow between– dominant species. However, based on our results of seasonal biomass pattern for each species, within each habitat and the entire area, this approach does not seem advantageous. Our results suggest that a steady-state model using mean annual values for each habitat and the whole area would be the best choice.

The development of mathematical models seem to be a useful strategy for the assessment of the impacts of multifishery activities and different policy options for an adaptive management (Walters & Korman, 1999; Walters et al., 1999; Castilla, 2000). Some possible management polices with unknown effects on the natural system may be: (1) the elimination of predators of important resources (e.g. seastars and decapods species), (2) the support of any policy to increase the abundance of target species (e.g. MacKenzie, 1970; Kassner & Malouf, 1982; Kennedy, 1989; Whitlatch & Osman, 1994; Stotz, 1997), and (3) the introduction of desirable commercial species, among others.

The current study constitutes a first contribution to the assessment of biomass and production of exploited populations and their trophically related species in the study area. Further studies must be focused on the quantification of trophic flows, as well as on other ecological interactions (e.g. competition, mutualism, comensalism, amensalism, etc.). Lastly,

the ecological fitness (or *health* -sensu Raport, 1998) of the benthic ecosystem seems to be assured, because the fisherman of Puerto Aldea apply a species-specific exploitation regime principally on two resources (*A. purpuratus* and *Ch. chamissoi*), but also protect this area against further exploitation by neighbouring fisher communities. These measures have been successfully to avoid the over-exploitation of the natural stocks.

Conclusions

Based our results we suggest that only the harvest activity and the migratory behaviour of the unexploited decapods are the principal factors that would explain the seasonal biomass dynamic. The seasonal changes of biomass were unexpectedly small for the entire study area, the habitats and also for the most single species. These results justify the development of “average” annual models for each community and whole area, by which it is possible to assess the impact of alternative management scenarios on the global properties of the systems. We suggest also to perform the *a priori* and *a posteriori* power analysis by which the reliability of the sampling program and the robustness of the statistical test are improved.

Acknowledgements

We would like to thank the anonymous reviewers for critical evaluation of this manuscript.

Literature Cited

- ABRAMS, P., 1991: Strengths of indirect effects generated by optimal foraging. *Oikos*, 62: 167-176.
- ACUÑA, E., MORAGA, J. & URIBE, E., 1989: La zona de Coquimbo: un sistema nerítico de alta productividad. *CPPS Rev Pacífico Sur*, Número especial, 145-157.
- ALHEIT, J. & BERNAL, P., 1994: Effects of physical and biological changes on the biomass yield of the Humboldt Current ecosystem. In: K. Sherman, L. Alexander & B. Gold (Eds.), *Large marine ecosystems: Stress mitigation and sustainability*. AAAS Publications. USA: 53-68.
- ARNTZ, W. & E. FAHRBACH, 1986: El Niño experimento climático de la naturaleza 1a. Ed. Fondo de Cultura Económica, México, 312.
- BELL, J., WESTOBY, M. & STEFFE, S., 1987: Fish larvae settling in seagrass: do they discriminate between beds of different leaf density?. *J. Exp. Mar. Biol. Ecol.*, 111: 133-144.
- BERRIOS, M., PACHECO, A. & OLIVARES, J., 1985: Análisis de refracción de olas en sistemas de bahías de la IV Región de Coquimbo, Chile. Informe Final. Depto. Biología Marina, Universidad Católica del Norte, Sede Coquimbo: 76.
- BILLICK, I. & CASE, T., 1994: Higher order interactions in ecological communities: what are they and how can they be detected?. *Ecology*, 75(6): 1529-1543.
- BOX, G., 1953: Non-normality and test on variances. *Biometrika*, 40: 318-335.
- BREY, T., 1990: Estimating productivity of macrobenthic invertebrates from biomass and mean individual weight. *Meeresforsch.*, 32:329-343.
- BROWN, A. & A. MCLACHLAN, 1990: *Ecology of Sandy Shores*. Elsevier. Amsterdam: 433.
- BUSCHMANN, A., 1992: Algal communities of a wave-protected intertidal rocky shore in southern Chile. In: U. Seeliger (Ed.), *Coastal Plant Communities of Latin America*. Academic press Inc., San Diego: 91-104.

- BUSTAMANTE, R. & CASTILLA, J.C., 1987: The shellfishery in Chile: an analysis of 26 years of landings (1960-1985). *Biología Pesquera* (Chile), 16:79-97.
- CASTILLA, J.C., 1981: Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile-Central. II. Depredadores de alto nivel trófico. *Medio Ambiente* (Chile), 5: 190-215.
- CASTILLA, J.C., 2000: Roles of experimental marine ecology in coastal management and conservation. *J. Exp. Mar. Biol. Ecol.*, 250: 3-21.
- CASTILLA, J.C. & MORENO, C., 1982: Sea urchin and *Macrocystis pyrifera*. Experimental test of their ecological relations in southern Chile. In: J.M. Lawrence (Ed.), *International Echinoderm Conference, Tampa Bay*. Balkema, Rotterdam: 257-263.
- CASTILLA, J.C., GUÍÑEZ, R., ALVARADO, J., PACHECO, C. & VARAS, M., 2000: Distribution, population structure, population biomass and morphological characteristics of the Tunicate *Pyura stolonifera* in the Bay of Antofagasta, Chile. *P.S.Z.N.: Marine Ecology*, 21(2): 161-174.
- CLARKE, K. & WARWICK, R., 1994: Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, UK: 144.
- CLARKE, K., WARWICK, R. & BROWN, B., 1993: An index showing breakdown of seriation, related to disturbance, in a coral-reef assemblage. *Mar. Ecol. Prog. Ser.*, 102: 153-160.
- CONNOLLY, R., 1997: Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. *Hydrobiologia*, 346: 137-148.
- DANERI, G., DELLAROSSA, V., QUIÑONES, R., JACOB, B., MONTERO, P. & Ulloa, O., 2000: Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Mar. Ecol. Prog. Ser.*, 197: 41-49.
- DAY, R. & QUINN, G., 1989: Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.*, 59(4): 433-463.
- DRGAS, A., RADZIEJEWSKA, T., & WARZOCHA, J., 1998: Biomass size spectra of near-shore shallow-water benthic communities in the Gulf of Gdansk (southern Baltic Sea). *P. S. Z. N.: Marine Ecology*, 19(3): 209-228
- ECKMAN, J., 1987: The role of hydrodynamic in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *J. Exp. Mar. Biol. Ecol.*, 106: 165-191.
- EDGAR, G., 1999a: Experimental analysis of structural versus trophic importance of seagrass beds. I. Effects on macrofaunal and meiofaunal invertebrates. *Vie et Milieu*, 49(4): 239-248.
- EDGAR, G., 1999b: Experimental analysis of structural versus trophic importance of seagrass beds. II Effects on fishes, decapods and cephalopods. *Vie et Milieu*, 49(4): 249-260.
- FATH, B. & PATTEN, B., 1999: Review of the foundations of network environ analysis. *Ecosystems*, 2: 167-179.

- FERREL, D. & BELL, J., 1991: Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Mar. Ecol. Prog. Ser.*, 72: 15-24.
- FRANKOVICH, T. & FOURQUREAN, W., 1997: Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Mar. Ecol. Prog. Ser.*, 159: 37-50.
- FUENTES, I., 1988: Desarrollo y morfología externa comparada de larvas y post-larvas de *Mesodesma donacium* y *Mulinia* sp. (Bivalvia: Mactracea) cultivadas en laboratorio. Tesis de Pregrado y Título de Biólogo Marino. Universidad Católica del Norte, Chile.
- GONZÁLEZ, S., 1992: *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog y comunidad asociada en el norte de Chile. Tesis de Licenciatura, Universidad Católica del Norte, Facultad de Ciencias del Mar, Chile.
- GONZÁLEZ, S., STOTZ, W., TOLEDO, P., JORQUERA, M. & ROMERO, M., 1991: Utilización de diferentes microambientes del intermareal como lugares de asentamiento por *Fissurella* spp. (Gastropoda: Prosobranchia) (Palo Colorado, Los Vilos, Chile). *Rev. Biol. Mar. (Valparaíso, Chile)*, 26(2): 325-338.
- ILLANES, J., AKABOSHI, S. & URIBE, E., 1985: Efectos de la temperatura en la reproducción del ostión del norte *Argopecten purpuratus* en la Bahía de Tongoy durante el fenómeno El Niño 1982-83. *Invest. Pesq. (Chile)*, 32: 167-173.
- JARA, F. & MORENO, C., 1984: Herbivory and structure in a midlittoral rocky community: a case in southern Chile. *Ecology*, 65: 28-38.
- JARAMILLO, E., 1978: Zonación y estructura de la comunidad macrofaunística en playas de arena del sur de Chile (Mehuín, Valdivia). *Stud. Neotrop. Fauna Environm.*, 13: 71-92.
- JARAMILLO, E., 1982: Taxonomy, natural history and zoography of sand beach isopods from the coast of southern Chile. *Stud. Neotrop. Fauna Environm.*, 17: 175-194.
- JARAMILLO, E., 1987: Sandy beach macroinfauna from the Chilean coast: zonation patterns and zoogeography. *Vie et Milleu*, 37: 165-174.
- JARAMILLO, E., MCLACHLAN, A. & COETZEE, P., 1993: Intertidal zonation patterns of macroinfauna over a range of exposed sandy beaches in south-central Chile. *Mar. Ecol. Prog. Ser.*, 101: 105-118.
- JARAMILLO, E., DUGAN, J. & CONTRERAS, H., 2000: Abundance, tidal movement, population structure and burrowing rate of *Emerita analoga* (Anomura, Hippidae) at a dissipative and a reflective sandy beach in south central Chile. *P.S.Z.N.: Marine Ecology*, 21(2): 113-127.
- JESSE, S., 2001: Comparative ecology of sympatric brachyuran crab species in the shallow subtidal of the pacific coast of north Chile and their importance for the artisanal fishery in Puerto Aldea. PhD Dissertation, University of Bremen, Germany, 125 pp.
- KASSNER, J. & MALOUF, R., 1982: An evaluation of "spawner transplants" as a management tool in Long Island's hard clam fishery. *J. Shellfish Res.*, 2: 165-172.
- KENNEDY, V., 1989: The Chesapeake Bay oyster fishery: traditional management practices. In: J.F. Caddy (Ed.), *Marine Invertebrate Fisheries: Their Assessment and Management*. J Wiley and Sons, NY: 455-477.
- KRUSKAL, J., 1964: Multidimensional scaling by optimising goodness of fit to a nonmetric hypothesis. *Psychometrika*, 29: 1-27.

- LAWLOR, L., 1979: Direct and indirect effects of n-species competition. *Oecologia* (Berlin), 43: 355-364.
- LEVINS, R., 1974: The qualitative analysis of partially specified systems. *Ann. N.Y. Acad. Sci.* 231: 123-138.
- LONG, B. & LEWIS, J., 1987: Distribution and community structure of the benthic fauna of north shore of the Gulf of St. Lawrence described by numerical methods of classification and ordination. *Mar. Biol.*, 95: 93-101.
- MACKENZIE, C.L. Jr., 1970: Oyster culture in Long Island Sound, 1966-69. *Comm. Fish. Rev.*, 859: 27-40.
- MANNINO, A. & MONTAGNA, P., 1997: Small-scale spatial variation of macrobenthic community structure. *Estuaries*, 20(1): 159-173.
- MCLUSKY, B., NAIR, S., STIRLING, A. & BHARGAVA, R., 1975: The ecology of a central west Indian Beach, with particular reference to *Donax incarnatus*. *Mar. Biol.*, 30: 267-276.
- MENGE, B., 1995: Indirect effects in marine rocky intertidal interactions webs: patterns and importance. *Ecol. Monogr.*, 65(1): 21-74.
- MILLER, T., 1994: Direct and indirect species interactions in an early old-field plant community. *Am. Nat.*, 143(6): 1007-1025.
- MONTECINOS, V. & QUIROZ, D., 2000: Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30°). *Aquat. Sci.*, 62: 364-380.
- MORAGA, J. & OLIVARES, M., 1989: Oceanografía físico-química. In: Estudio repoblamiento de recursos bentónicos área piloto IV Región de Coquimbo. CORFO, IFOP: 395-414.
- MORENO, C. & JARAMILLO, E., 1983: The role of grazers in the zonation of intertidal macroalgae of the Chilean coast near Valdivia. *Oikos*, 41: 73-76.
- MORENO, C. & JARA, F., 1984: Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fuegian Islands, Chile. *Mar. Ecol. Prog. Ser.*, 15:99-107.
- MORENO, C. & SUTHERLAND, J., 1982: Physical and biological processes in a *Macrocystis pyrifera* community near Valdivia, Chile. *Oecologia* (Berlin), 55: 1-6.
- MORENO, C., REYES, A. & ASECIO, G., 1993: Habitat and movements of the recruits of *Concholepas concholepas* (Mollusca: Muricidae) in the rocky intertidal of southern Chile. *J. Exp. Mar. Biol. Ecol.*, 171: 51-61.
- MORENO, C., ASECIO, G., DUARTE, W. & MARIN, V., 1998: Settlement of the muricid *Concholepas concholepas* and its relationship with El Niño and coastal upwellings in southern Chile. *Mar. Ecol. Prog. Ser.*, 167: 171-175.
- OJEDA, P. & SANTELICES, B., 1984a: Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in Central Chile. *Mar. Ecol. Prog. Ser.*, 19: 83-91.
- OJEDA, P. & SANTELICES, B., 1984b: Invertebrate communities in holdfast of the kelp *Macrocystis pyrifera* from southern Chile. *Mar. Ecol. Prog. Ser.*, 16: 65-73.
- OLIVARES, M., 1988: Variación temporal de las condiciones oceanográficas en Bahía Herradura de Guayacán, Chile. *Biota* (Chile), 4:89-106.

- ORTIZ, M. & STOTZ, W., 1996: Distribución de juveniles recientemente asentados de *Mesodesma donacium* (Lamarck 1818) (Mollusca: Bivalvia: Mesodesmestidae) en tres bahías de la cuarta región: variables físicas y químicas que le caracterizan. Biol. Pesq. (Chile), 25: 27-40.
- OTT, J., 1981: Adaptive strategies at the ecosystems level: examples from two benthic marine systems. P.S.Z.N.: Marine Ecology, 2(2): 113-158.
- PACHECO, A., OLIVARES, J. & BERRIOS, M., 1987: Caracterización de calidad de agua y sedimentos en condiciones de invierno y verano en Bahía Tongoy. Informe final de proyecto Universidad Católica del Norte, Depto. De Biología Marina, Coquimbo, Chile.
- PAINE, R., 1980: Food webs: linkage, interaction strength and community infrastructure. J. Animal Ecol., 49: 667-685.
- PATTEN, B., 1981: Environs: the superniches of ecosystems. Amer. Zool., 21: 845-852.
- PATTEN, B., 1982: Environs: relativistic elementary particles for ecology. Am. Nat., 119(2): 179-219.
- PATTEN, B., 1985: Energy cycling in the ecosystem. Ecol. Model., 28: 1-71.
- RAPORT, D., 1998: Defining ecosystem health. In: D. RAPORT, R. COSTANZA, P. EPSTEIN, C. GAUDET & R. Levins (Eds.), Ecosystem Health. Blackwell Science, Inc. M.A.: 18-33
- REUSCH, TH., 1998: Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. Mar. Ecol. Prog. Ser., 167: 149-153.
- ROSE, C., SHARP, W., KENWORTHY, W., HUNT, J., LYONS, W., PRAGER, E., VALENTINE, J., HALL, M., WHITFIELD, P. & FOURQUREAN, J., 1999: Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Mar. Ecol. Prog. Ser., 190: 211-222.
- SANTELICES, B., 1981: Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile Central. I. Cinturones de macroalgas. Medio Ambiente (Chile), 5: 175-189.
- SANTELICES, B., 1989: Algas marinas de Chile. Distribución, ecología, utilización y diversidad. Ediciones Universidad Católica de Chile, Santiago, Chile.
- SANTELICES, B., 1990: Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr. Mar. Biol. Ann. Rev., 28: 177-276.
- SANTELICES, B., 1991: Littoral and sublittoral communities of continental Chile. In: D. Goodwall (Ed.), Ecosystems of the world. Elsevier: 347-369.
- SANTELICES, B. & OJEDA, P., 1984a: Effects of canopy removal on the understory algal community structure of coastal forest of *Macrocystis pyrifera* from southern America. Mar. Ecol. Prog. Ser., 14: 165-173.
- SANTELICES, B. & OJEDA, P., 1984b: Population dynamics of coastal forest of *Macrocystis pyrifera* in Puerto Toro, Isla Navarino, southern Chile. Mar. Biol. Prog. Ser., 14: 175-183.
- SKILLETER, G., 1992: Recruitment of cerithiid gastropods (*Rhinoclavis* spp.) in sediments at One Tree Reef, Great barrier Reef. J. Exp. Mar. Biol. Ecol., 156: 1-21.
- SOKAL, R. & ROHLF, F., 1995: Biometry. 3 ed. W. H. Freeman and Co. San Francisco: 878.
- STEEL, R. & TORRIE, H., 1988: Bioestadística: Principios y Procedimientos. 1a Ed. McGraw-Hill: 662.
- STOTZ, W., 1997: Las áreas de manejo en la Ley de Pesca y Acuicultura: Primeras experiencias y evaluación de la utilidad de esta herramienta para el recurso loco. Estud. Oceanol. (Chile), 16: 67-86.

- STOTZ, W. & GONZÁLEZ, S., 1997: Abundance, growth, and production of the sea scallop *Argopecten purpuratus* (Lamarck 1819): bases for sustainable exploitation of natural scallop beds in north-central Chile. *Fisheries Research*, 32: 173-183.
- STOTZ, W., DE AMESTI, P., MARTINEZ, D. & PEREZ, E., 1991: Lugares de asentamiento y desarrollo de juveniles tempranos de *Concholepas concholepas* (Bruguière 1789) en ambientes inter y submareales de la IV Región, Coquimbo, Chile. *Rev. Biol. Mar. (Valparaíso, Chile)*, 26(2): 339-350.
- TAYLOR, R., 1998: Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. *Mar. Ecol. Prog. Ser.*, 172: 37-51
- THAYER, G., BJORN DAL, K., OGDEN, J., WILLIAMS, S. & ZIEMAN, J., 1984: Role of larger herbivores in seagrass communities. *Estuaries*, 7: 351-376.
- TIKU, M., TAN, W. & BALAKRISHNAN, N., 1986: *Robust Inference*. Marcel Dekker: 321.
- TOMASKO, D. & LAPIONTE, B., 1991: Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Mar. Ecol. Prog. Ser.*, 159: 37-50.
- UNDERWOOD, A., 1981: Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.*, 19: 513-605.
- UNDERWOOD, A., 1997: *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press: 504.
- UNDERWOOD, A., 1999: Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *J. Exp. Mar. Biol. Ecol.*, 232: 125-140.
- VASQUEZ, J., 1991: Variables morfológicas y relaciones morfométricas de *Lessonia trabeculata* (Villouta & Santelices, 1986) en una población submareal del norte de Chile. *Rev. Chil. Hist. Nat.*, 64: 271-279.
- VASQUEZ, J., 1992: *Lessonia trabeculata*, a subtidal bottom kelp in northern Chile: A case study for a structural and geographical comparison. In: U. Seeliger (Ed.), *Coastal Plant Communities of Latin America*. Academic press Inc, San Diego: 77-89.
- VASQUEZ, J., 1993: Effects on the animal community of dislodgement of holdfasts of *Macrocystis pyrifera*. *Pacific Science*, 47: 180-184.
- VASQUEZ, J., 1995: Ecological Effects of Brown Seaweed Harvesting. *Bot. Mar.*, 38: 251-257.
- VASQUEZ, J. & CASTILLA, J.C., 1984: Trophical range and diet of *Luidia magallanica* in Beagle Channel, Southern Chile. *Puerto Toro. Medio Ambiente (Chile)*, 7: 47-51.
- VASQUEZ, J. & SANTELICES, B., 1984: Comunidades de macroinvertebrados en discos adhesivos de *Lessonia nigrescens* Bory (Phaeophyta) en Chile central. *Rev. Chil. Hist. Nat.*, 57:131-154.
- VASQUEZ, J. & SANTELICES, B., 1990: Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. *Hydrobiologia*, 204: 41-48.
- VASQUEZ, J., CASTILLA, J.C. & SANTELICES, B., 1984: Distributional patterns and diets of four species of sea urchins in a giant kelp forest (*Macrocystis pyrifera*) of Puerto Toro, Navarino Island, Chile. *Mar. Ecol. Prog. Ser.*, 19: 55-63.
- VILLOUTA, E. & SANTELICES, B., 1984: Estructura de la comunidad submareal de *Lessonia* (Phaeophyta, Laminariales) en Chile Norte y Central. *Rev. Chil. Hist. Nat.*, 57: 111-122.

- VILLOUTA, E. & SANTELICES, B., 1986: *Lessonia trabeculata* sp. nov. (Laminariales: Phaeophyta), a new kelp from Chile. *Phycologia*, 25: 81-86.
- WALTERS, C. & KORMAN, J., 1999: Cross-scale modelling of Ripirian ecosystem responses to hydrologic management. *Ecosystems*, 2: 411-421.
- WALTERS, C., PAULY, D. & CHRISTENSEN, V., 1999: Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems*, 2: 539-554.
- WARWICK, R. & CLARKE, K., 1993: Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Mar. Ecol. Prog. Ser.*, 92: 221-231.
- WEERAHANDI, S., 1995: ANOVA under unequal error variances. *Biometrics*, 51: 589-599.
- WHITLATCH, R., 1977: Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barnstable Harbor, Massachusetts. *Biol. Bull.*, 152: 275-294.
- WHITLATCH, R., 1981: Animal-sediment relationships in intertidal marine benthic habitats: some determinations of deposit-feeding species diversity. *J. Exp. Mar. Biol. Ecol.*, 53: 31-45.
- WHITLATCH, R. & OSMAN, R., 1994: A qualitative approach to managing shellfish populations: Assessing the relative importance of trophic relationships between species. *J. Shellfish. Res.*, 13(1): 229-242.
- WILSON, J. & SHELLEY, C., 1986: The distribution of *Nucula turgida* (Bivalvia: Protobranchia) from Dubling Bay, Ireland, and the effects of sediments organic content. *J. Mar. Biol. Assoc. U.K.*, 66: 119-130.
- WILSON, J., 1999: Population dynamics and energy budget for a population of *Donax variabilis* (Say) on an exposed South Carolina beach. *J. Exp. Mar. Biol. Ecol.*, 239: 61-83
- WISSINGER, S. & MCGRADY, J., 1993: Intraguild predation and competition between dragonfly larvae: direct and indirect effects on shared prey. *Ecology*, 74: 207-218.
- WOLFF, M., 1988: Spawning and recruitment in the Peruvian scallop *Argopecten purpuratus*. *Mar. Ecol. Prog. Ser.*, 42: 213-217
- WOLFF, M. & SOTO, M., 1992: Population dynamics of *Cancer polyodon* in La Herradura Bay, northern Chile. *Mar. Ecol. Prog. Ser.*, 85: 69-81.
- WOOTTON, T., 1994: Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology*, 75(1): 151-165.
- ZIEGLER, S. & BENNER, R., 1999: Nutrient cycling in the water column of a subtropical seagrass meadow. *Mar. Ecol. Prog. Ser.*, 188:51-62.

List of Tables and Figures

Table 1. Sample size (N), optimum sample after *a posteriori* power analysis (N'), size of sampling unit (m²) used at each habitat.

Table 2. Average biomass (g wet weight /m²) ± standard deviation for all species per habitat in each seasonal period. A. Seagrass beds, B. sand-grave, C. sand, and D. mud habitat. ANOVA and Statistical Power results.

Table 3. Average biomass (g wet weight/m²) ± standard deviation and production (g wet weight/m² year¹) for all species per habitat and whole area. Production values based on literature (in bold) and estimated by the allometric equation derived from Brey (1990) (in standard).

Fig. 1. (a) The main littoral types along of the Chilean coast: 1.= Dominated by exposed compact rocky shores; 2.= Dominated by exposed sandy shores; 3.= Mostly insular systems. (b) The principal bay systems of the IV Región of Coquimbo (Chile). (c) Study area of Puerto Aldea located at southern of Tongoy Bay.

Fig. 2. Hypothetical prey-predator and plant-grazer ecological relationships for the species and inhabit in each habitat. Target species in shaded circles.

Fig. 3. Species (*R*-mode) dendrogram and MDS-plot for the whole study area.

Fig. 4. Station (*Q*-mode) dendrogram and MDS-plot for the whole study area.

Fig. 5. Average biomass (g wet weight/m²) (\pm s.d) by season and annual for a) *A. purpuratus*, b) *Tegula* sp., c) *Mulinia* sp., d) *X. cassidiformis*, e) *C. trochiformis*, f) *P. chilensis*. ANOVA, SNK, and Power p-levels.

Fig. 6. Average biomass (g wet weight/m²) (s.d) by season and annual for a) *M. gelatinosus*, b) *L. magallanica*, c) *H. helianthus*. ANOVA and Power p-levels.

Fig. 7. Average biomass (g wet weight/m²) (s.d) by season and annual for a) *C. polyodon*, b) *C. coronatus*, c) *C. porteri*, d) *P. barbiger*, e) *Taliepus* sp. ANOVA, SNK, and Power p-levels.

Fig. 8. Average biomass (g wet weight/m²) (s.d) by season and annual for a) *Ch. chamissoi*, b) Rodophyta, c) *Ulva* sp. ANOVA and SNK p-levels.

Fig. 9. Total average biomass (g wet weight/m²) (s.d) by habitat and seasons. a) seagrass beds, b) sand-gravel, c) sand, and d) mud habitat. ANOVA, SNK, and Power p-levels.

Fig. 10. Total average biomass (g wet weight/m²) (s.d) for the whole area by season. ANOVA and Power p-levels.

Table 1. Summary of sample size (N), optimum sample size (N') after *a posteriori* power analysis, and size of sampling unit (m²) for each species by habitat.

Species	Habitats											
	Seagrass			Sand-Gravel			Sand			Mud		
	N	N'	Opt. Size (m ²)	N	N'	Opt. Size (m ²)	N	N'	Opt. Size (m ²)	N	N'	Opt. Size (m ²)
<i>Argopecten purpuratus</i>	~15	9	20	~15	14	20	~15	68	100	~15	18	100
<i>Meyenaster gelatinosus</i>	~15	37	100	~15	44	100	~15	44	100	~15	44	100
<i>Luidia magallanica</i>	~15	120	100	~15	44	100	~15	120	100	~15	120	100
<i>Heliaster helianthus</i>	15	68	100	15	44	100						
<i>Cancer polyodon</i>	~15	31	100	~15	18	100	~15	9	100	~15	18	100
<i>C. coronatus</i>							~15	12	100	~15	12	100
<i>C. porteri</i>										~15	15	100
<i>Paraxanthus barbiger</i>	15	44	100	15	9	100						
<i>Taliepus</i> sp.	15	31	100	15	31	100						
<i>Tegula</i> sp.				~60	120	0.25						
<i>Pyura chilensis</i>				~60	120	0.25						
<i>Calyptrea trochiformis</i>				~60	68	0.25						
<i>Xanthochorus cassidiformis</i>							~50	18	0.25			
<i>Mulinia</i> sp.							~9	18	0.25			
<i>Chondrocanthus chamissoi</i> *				~60	44 *	0.25						
<i>Ulva</i> sp.				~60	31	0.25						
Rodophyta				~60	68	0.25						

* *A priori* statistical power, with an effect size estimated of 0.25 from Stotz and González (unpubl. Data).

A sampling unit of 20 y 100m² means a transect of 10m x 2m and 50m x 2m respectively.

A sampling unit of 0.25m² means a cuadrate of 0.5x0.5m

Table 2. Biomass values (g wet weight/m²) (\pm standard deviation) for each species by habitat and season. ANOVA and Power probabilities.

BIOMASS (g wet weight / m ²)										
A. Seagrass Habitat										
Species	Seasons								ANOVA	Power
	Winter		Spring		Summer		Autumn			
<i>A. purpuratus</i>	238.61	\pm 107.63	158.94	\pm 95.24	93.46	\pm 49.37	143.18	\pm 68.69	sig. p < 0.05	
<i>M. gelatinosus</i>	26.6	\pm 21.18	22.97	\pm 20.35	13.42	\pm 11.1	18.92	\pm 15.87	no sig. p = 0.21	0.4
<i>L. magallanica</i>	0.91	\pm 2.04	0.6	\pm 2.32	0	\pm 0	0.39	\pm 1.53	no sig. p = 0.77	0.15
<i>H. helianthus</i>	0.77	\pm 1.6	0.26	\pm 0.68	0.54	\pm 1.22	0.38	\pm 0.8	no sig. p = 0.64	0.21
<i>C. polyodon</i>	17.09	\pm 13.32	14.62	\pm 9.79	10.84	\pm 11.81	9.18	\pm 6.29	no sig. p = 0.18	0.45
<i>P. barbiger</i>	1.07	\pm 2.45	0.25	\pm 0.67	0.45	\pm 0.76	0	\pm 0	no sig. p = 0.32	0.32
<i>Taliepus sp.</i>	0.95	\pm 0.85	1.77	\pm 1.28	1.24	\pm 0.98	1.86	\pm 1.49	no sig. p = 0.12	0.45
B. Sand-gravel habitat										
Species	Seasons								ANOVA	Power
	Winter		Spring		Summer		Autumn			
<i>A. purpuratus</i>	82.2	\pm 72.7	136.3	\pm 164.1	23.7	\pm 15.27	49.69	\pm 32.19	sig. p < 0.05	
<i>M. gelatinosus</i>	53.18	\pm 48.65	35.97	\pm 23.14	41.08	\pm 29.96	56.83	\pm 42.01	no sig. p = 0.38	0.32
<i>L. magallanica</i>	3.97	\pm 4.84	1.06	\pm 2.17	3.47	\pm 5.64	3.43	\pm 5.43	no sig. p = 0.32	0.32
<i>H. helianthus</i>	0.26	\pm 0.69	0.39	\pm 0.81	0.8	\pm 1.27	0.26	\pm 1.02	no sig. p = 0.39	0.32
<i>C. polyodon</i>	32.86	\pm 13.09	32.75	\pm 25.75	15.99	\pm 10.56	20.8	\pm 12.08	sig. p < 0.05	
<i>P. barbiger</i>	20.8	\pm 11.23	9.91	\pm 6.51	40.98	\pm 29.91	45.41	\pm 26.91	sig. p < 0.05	
<i>Taliepus sp.</i>	2.5	\pm 2.34	1.78	\pm 2.71	0.92	\pm 1.31	1.36	\pm 1.88	no sig. p = 0.22	0.45
<i>Tegula sp.</i>	421.36	\pm 370.7	541.28	\pm 535.79	476.22	\pm 771.38	651.82	\pm 759.21	no sig. p = 0.20	0.47
<i>P. chilensis</i>	216.53	\pm 233.81	237.51	\pm 353.24	185.36	\pm 268.2	275.42	\pm 217.78	no sig. p = 0.33	0.47
<i>C. trochiformis</i>	122.92	\pm 190.52	120.9	\pm 266.43	221.84	\pm 417.89	311.95	\pm 487.09	sig. p < 0.05	
<i>Ch. chamissoi</i>	90.3	\pm 112.14	1368.49	\pm 1931.94	793.33	\pm 564.93	38.7	\pm 75.48	sig. p < 0.05	
<i>Rodophyta</i>	17.19	\pm 30	220.17	\pm 698.79	68.75	\pm 106.93	81.82	\pm 80.58	sig. p < 0.05	
<i>Ulva sp.</i>	1.77	\pm 7.08	5.13	\pm 17.07	25.15	\pm 53.98	23.77	\pm 34.94	sig. p < 0.05	
C. Sand habitat										
Species	Seasons								ANOVA	Power
	Winter		Spring		Summer		Autumn			
<i>A. purpuratus</i>	42	\pm 42.41	53.23	\pm 58.17	34.19	\pm 17.26	51.67	\pm 47.09	no sig. p = 0.61	0.21
<i>M. gelatinosus</i>	13.94	\pm 21.47	12.14	\pm 22.52	20.02	\pm 23.06	23.09	\pm 16.91	no sig. p = 0.45	0.32
<i>L. magallanica</i>	0.3	\pm 1.18	0.42	\pm 1.36	0.9	\pm 2.11	0.82	\pm 1.91	no sig. p = 0.71	0.13
<i>C. polyodon</i>	33.72	\pm 17.22	19.58	\pm 13.2	10.52	\pm 10.77	8.81	\pm 8.5	sig. p < 0.05	
<i>X. cassidiformis</i>	27.02	\pm 40.1	11.48	\pm 25.63	4.51	\pm 5.51	3.54	\pm 4.87	sig. p < 0.05	
<i>Mulinia sp.</i>	3063.04	\pm 2417.01	2551.29	\pm 951.31	4998.55	\pm 2791.28	4026.56	\pm 3163.03	no sig. p = 0.19	0.45
<i>C. coronatus</i>	4.2	\pm 5.88	2.96	\pm 3.22	0.2	\pm 0.59	0.24	\pm 0.57	sig. p < 0.05	
D. Mud habitat										
Species	Seasons								ANOVA	Power
	Winter		Spring		Summer		Autumn			
<i>A. purpuratus</i>	0.74	\pm 1.77	7.71	\pm 10.44	2.35	\pm 3.16	4.53	\pm 6.1	no sig. p = 0.02	0.71
<i>M. gelatinosus</i>	0.99	\pm 3.74	0.77	\pm 2.06	2.15	\pm 4.28	0.29	\pm 0.57	no sig. p = 0.43	0.32
<i>L. magallanica</i>	0.52	\pm 1.16	0.82	\pm 1.74	0	\pm 0	0.37	\pm 1.05	no sig. p = 0.67	0.13
<i>C. polyodon</i>	5.77	\pm 5.48	4.11	\pm 4.26	12.85	\pm 13.54	5.88	\pm 6.52	no sig. p = 0.02	0.71
<i>C. coronatus</i>	4.39	\pm 4.05	8.75	\pm 5.06	3.6	\pm 1.87	8.73	\pm 4.53	sig. p < 0.05	
<i>C. porteri</i>	26.98	\pm 23.05	42.94	\pm 26.36	12.61	\pm 29.11	15.92	\pm 17.17	sig. p < 0.05	

Table 3. Annual biomass (g wet weight/m²) (\pm standard deviation) and production values for each species by habitat and whole area. Production magnitudes calculated analytically (in bold) and from literature source (in standard).

WHOLE AREA						
Biomass (g wet weight / m ²)						
Production (g wet weight / m ² year -1)						
Species	Habitats					TOTAL
	Seagrass	Sand-Gravel	Sand	Mud		
<i>A. purpuratus</i>	147.31 \pm 89.57	71.54 \pm 96.26	45.33 \pm 43.45	3.76 \pm 6.59	63.7 \pm 84.69	
	306.4	148.8	94.29	7.82	132.5	
<i>M. gelatinosus</i>	20.48 \pm 17.83	46.76 \pm 37.35	17.3 \pm 21.07	1.08 \pm 3.08	21.58 \pm 28.42	
	24.59	56.11	20.76	1.3	25.9	
<i>L. magallanica</i>	0.63 \pm 1.96	2.98 \pm 4.74	0.61 \pm 1.66	0.58 \pm 1.34	1.13 \pm 2.92	
	0.44	2.09	0.43	0.41	0.9	
<i>H. helianthus</i>	0.49 \pm 1.12	0.43 \pm 0.97			0.46 \pm 1.05	
	0.26	0.23			0.24	
<i>C. polyodon</i>	12.93 \pm 10.82	25.6 \pm 17.74	17.48 \pm 15.61	7.35 \pm 9.02	15.7 \pm 15.18	
	13.96	27.65	18.88	7.94	16.96	
<i>P. barbiger</i>	0.59 \pm 1.54	29.28 \pm 25.27			16.87 \pm 23.89	
	1.12	55.63			28.37	
<i>Taliepus</i> sp.	1.45 \pm 1.21	1.64 \pm 2.15			1.55 \pm 1.74	
	2.18	2.46			2.32	
<i>Tegula</i> sp.		520.6 \pm 629.41			520.6 \pm 629.41	
		1160.94			1160.94	
<i>P. chilensis</i>		228.46 \pm 272.82			228.46 \pm 272.82	
		733.36			733.36	
<i>C. trochiformis</i>		192.95 \pm 364.08			192.95 \pm 364.08	
		158.22			158.22	
<i>Ch. chamissoi</i>		564.8 \pm 1135.1			564.8 \pm 1135.1	
<i>Rodophyta</i>		95.68 \pm 358.92			95.68 \pm 358.92	
<i>Ulva</i> sp.		13.71 \pm 34.59			13.71 \pm 34.59	
<i>X. cassidiformis</i>			9.74 \pm 22.64		9.74 \pm 22.64	
			14.61		14.61	
<i>Mulinia</i> sp.			3676.9 \pm 2553.8		3676.9 \pm 2553.8	
			8456.89		8456.89	
<i>C. coronatus</i>			1.8 \pm 3.58	6.35 \pm 4.61	4.02 \pm 4.69	
			2.7	9.53	6.11	
<i>C. porteri</i>				23.67 \pm 26.49	23.67 \pm 26.49	
				11.84	11.84	
Total production	12.20%	81.94%	4.79%	1.07%	100%	

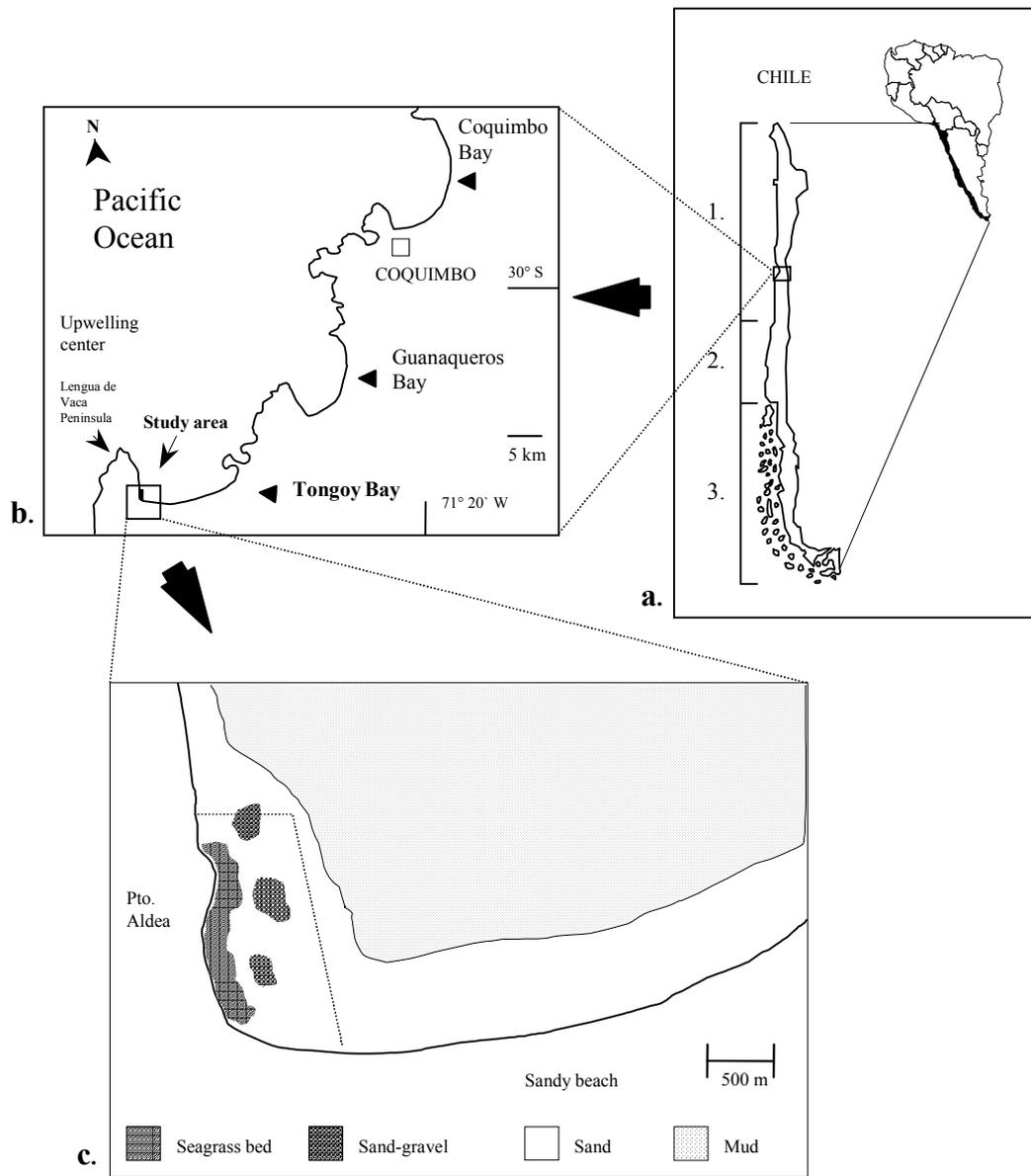


Fig. 1

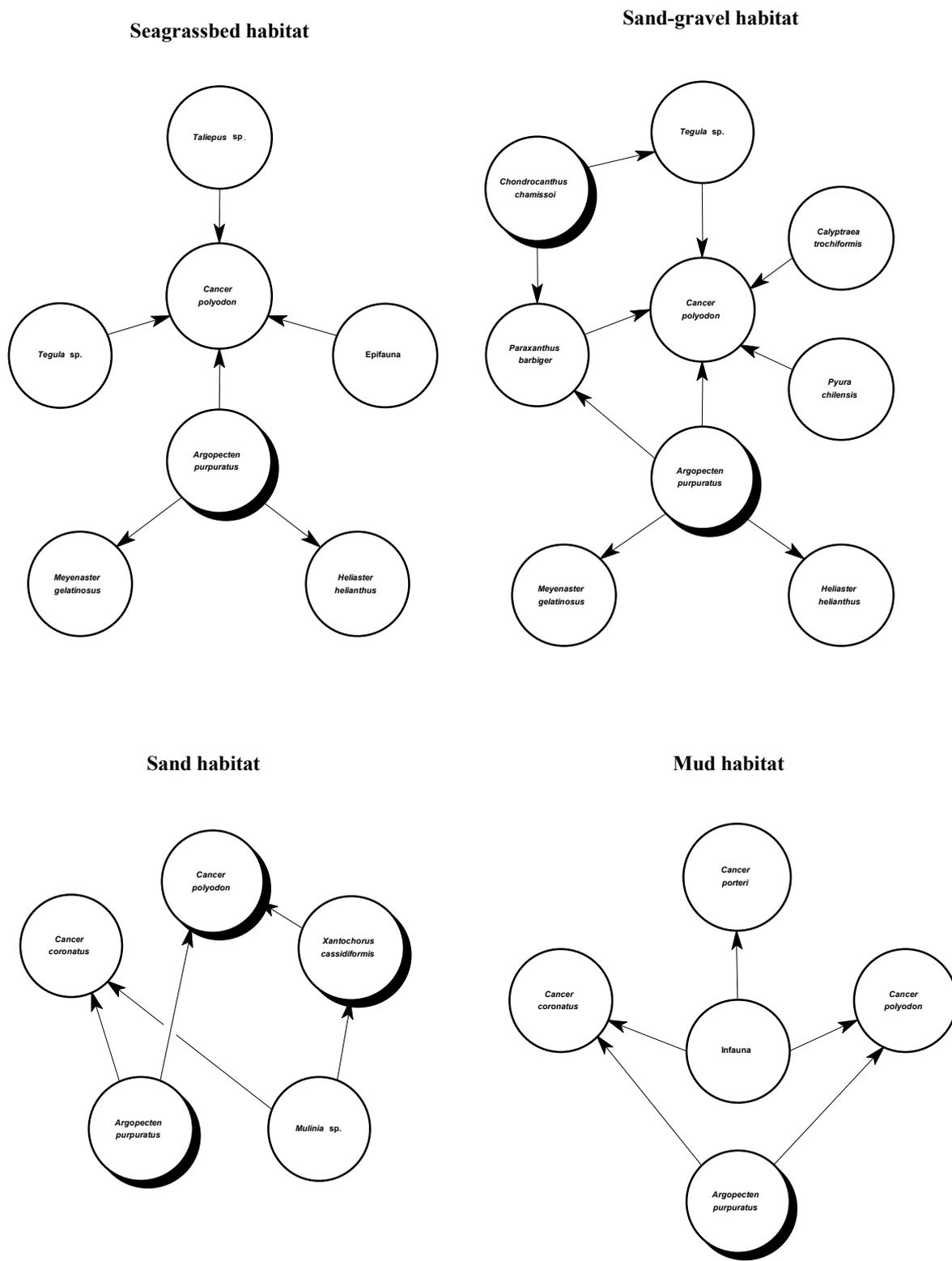


Fig. 2

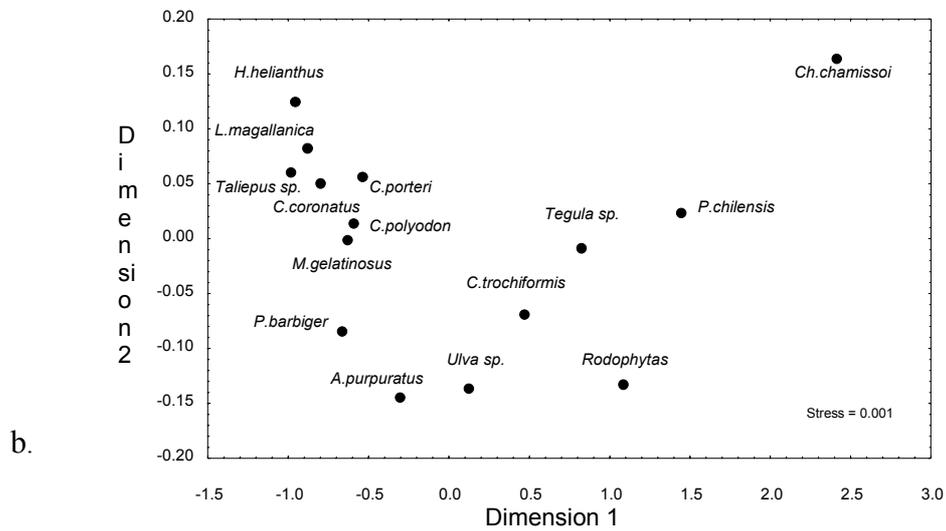
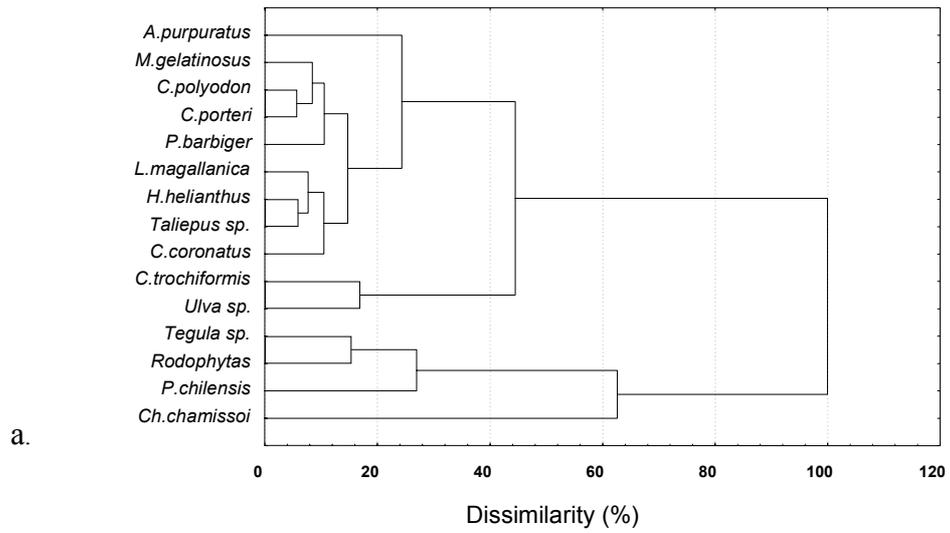


Fig. 3

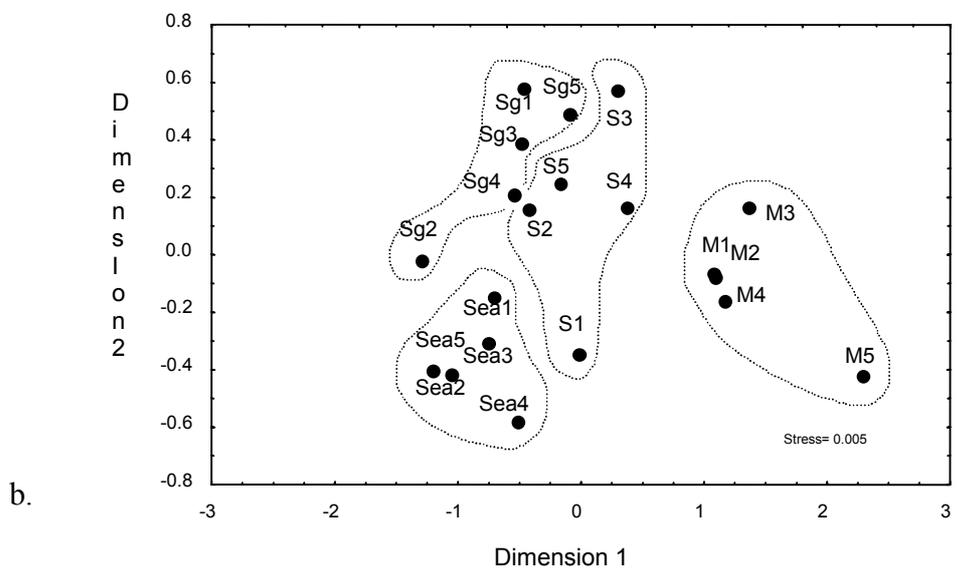
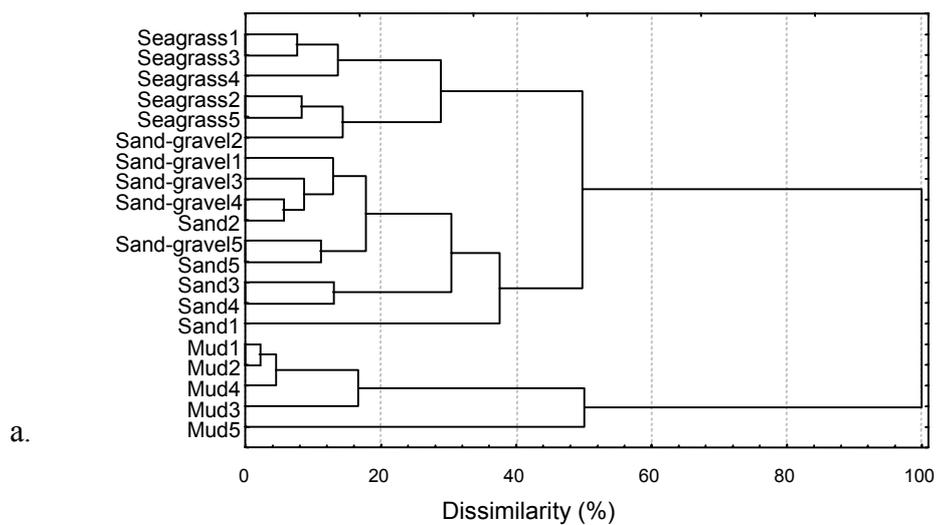


Fig. 4

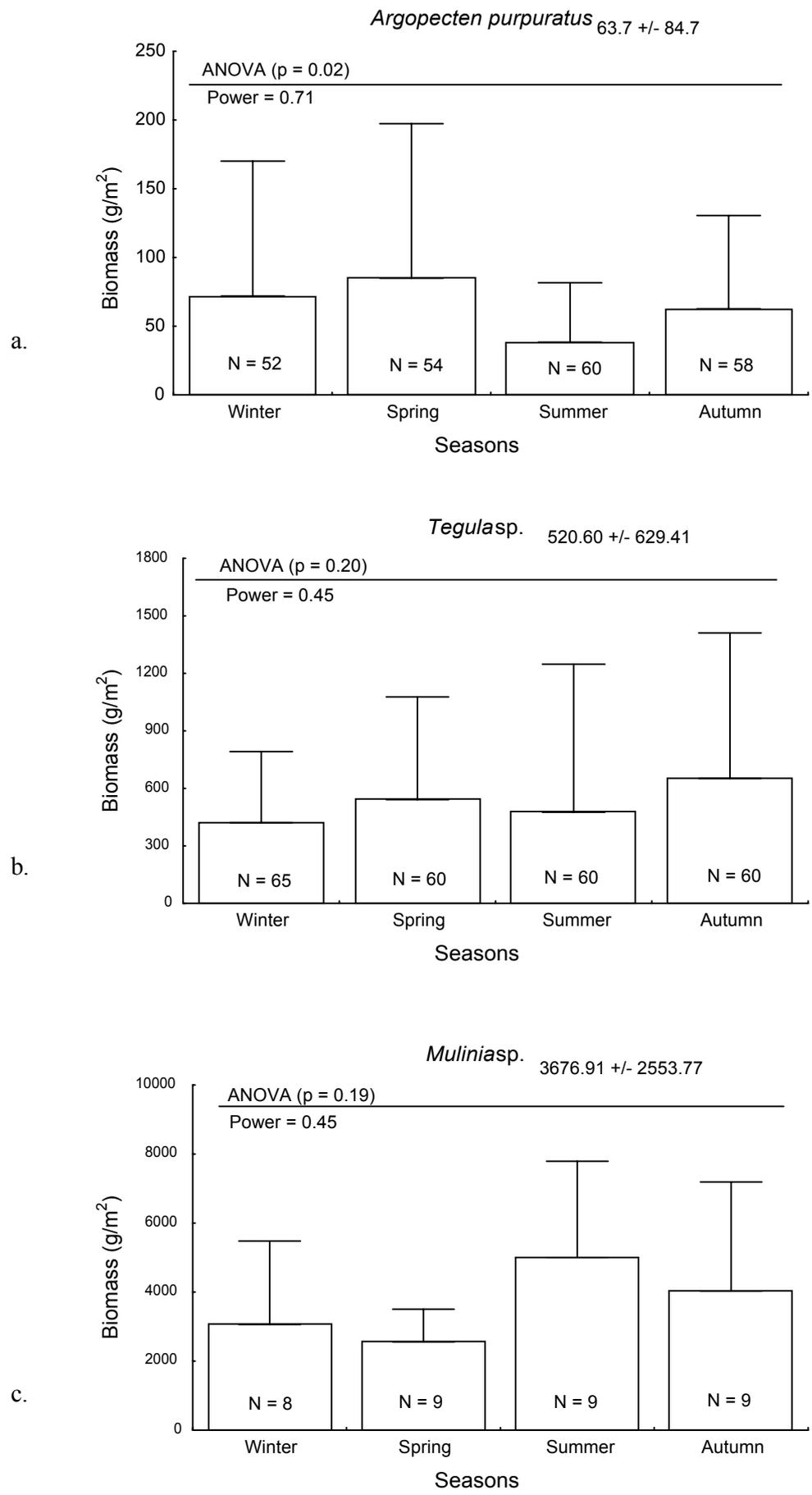


Fig. 5

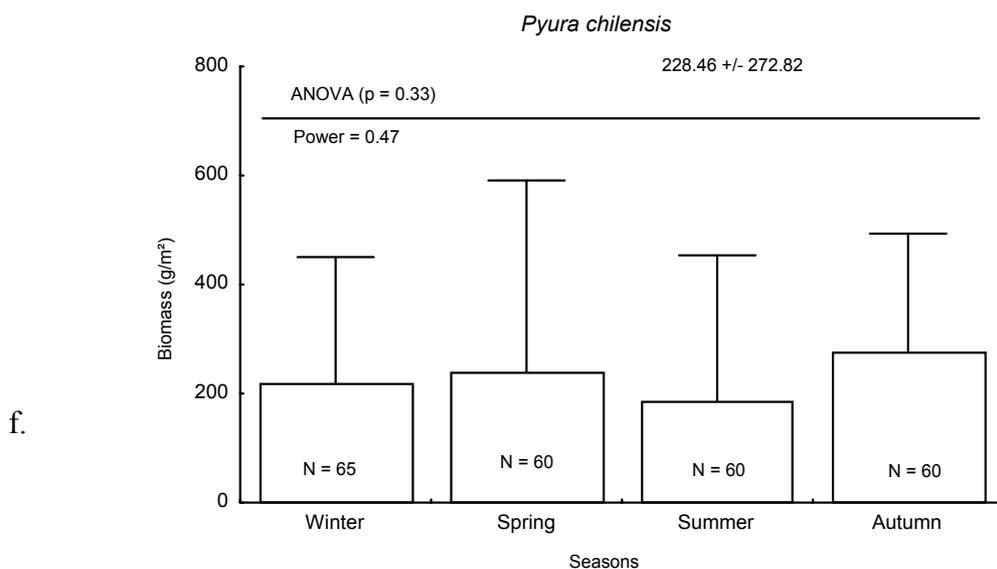
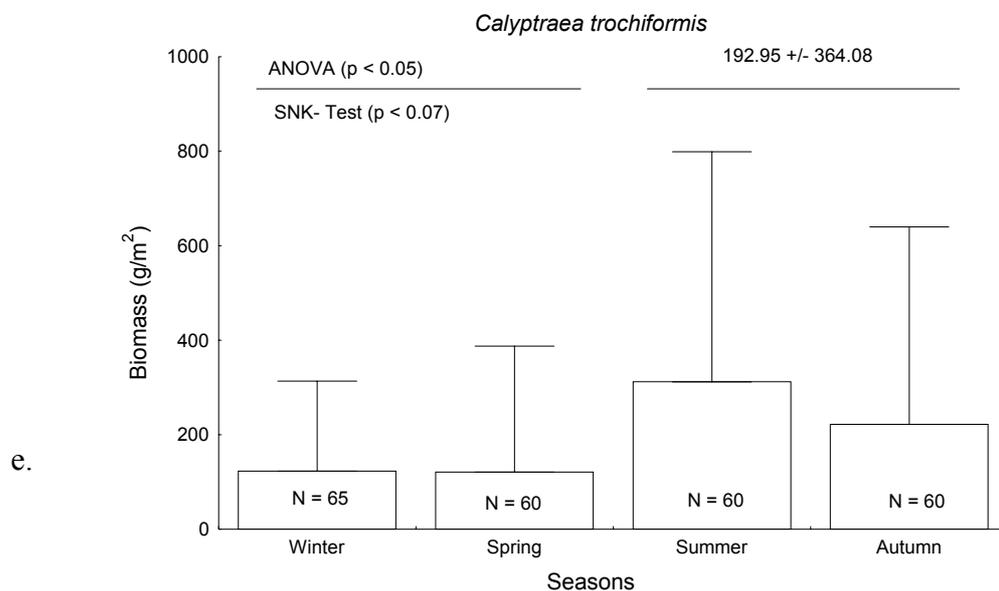
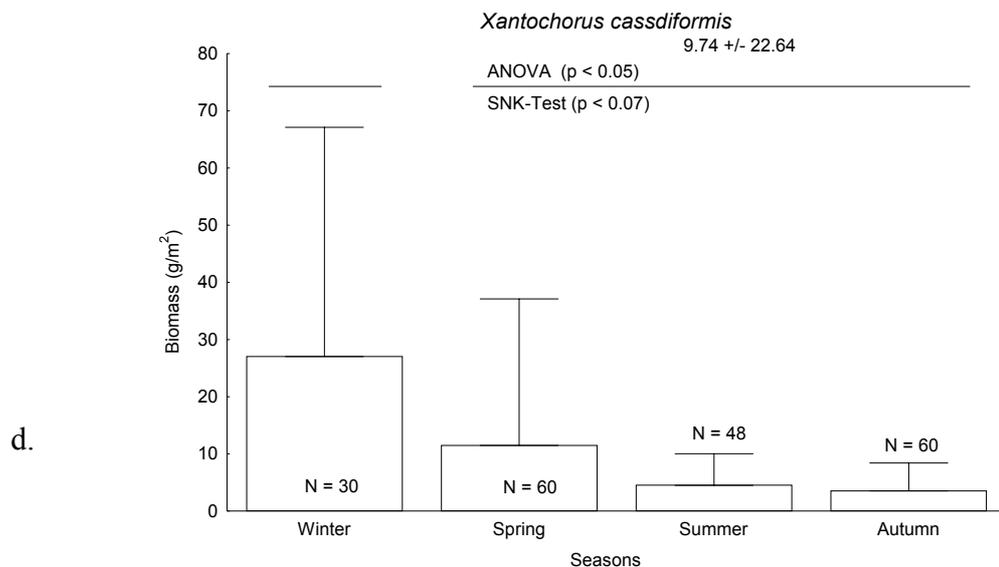


Fig. 5 continuation

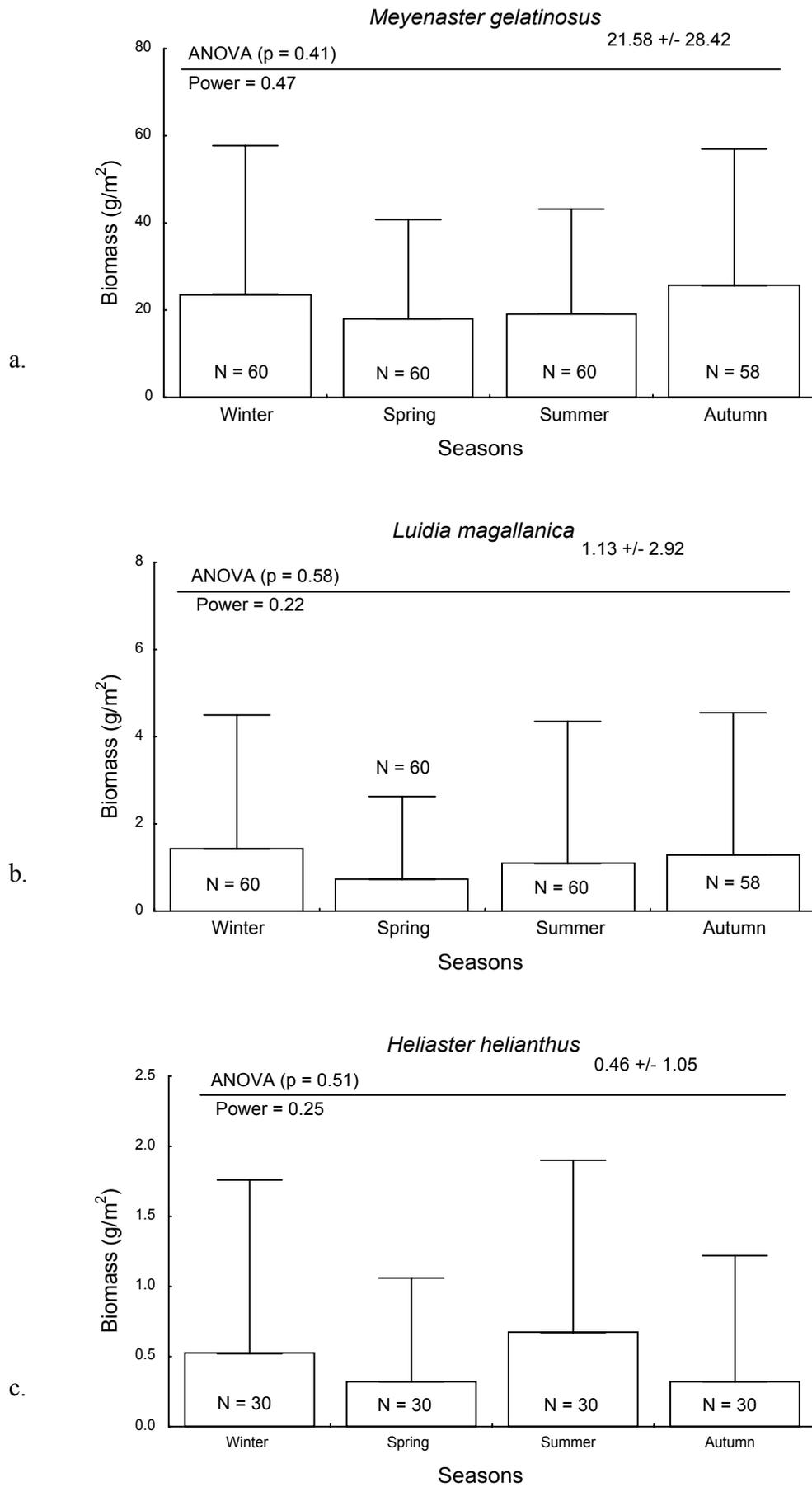


Fig. 6

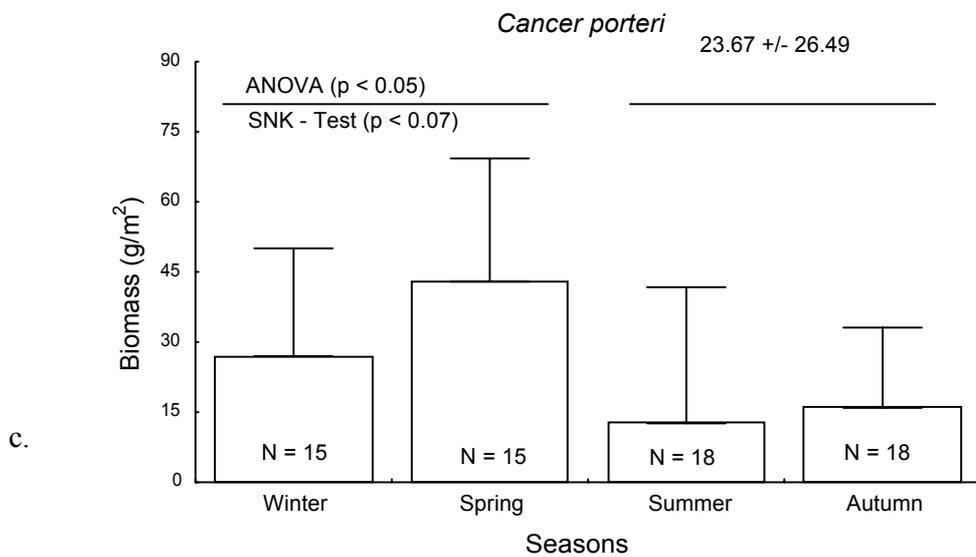
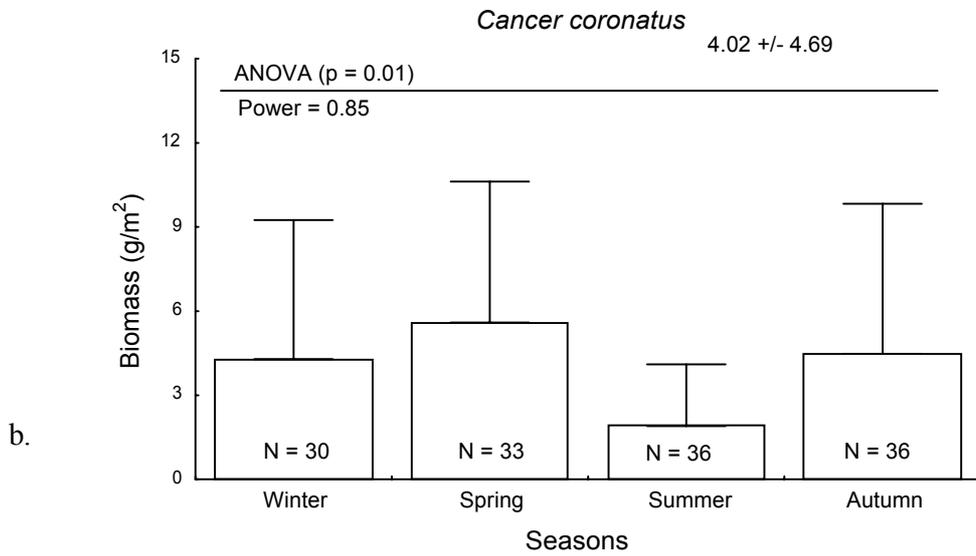
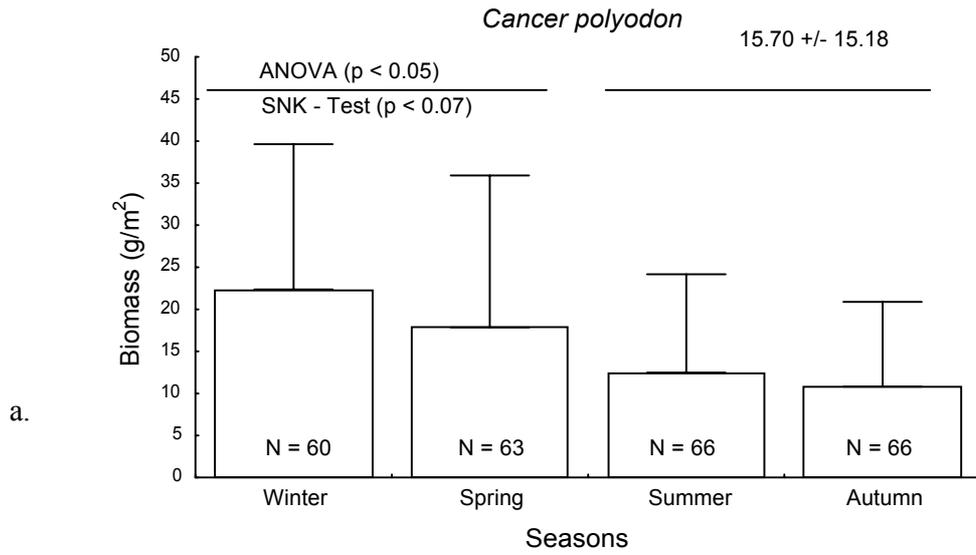


Fig. 7

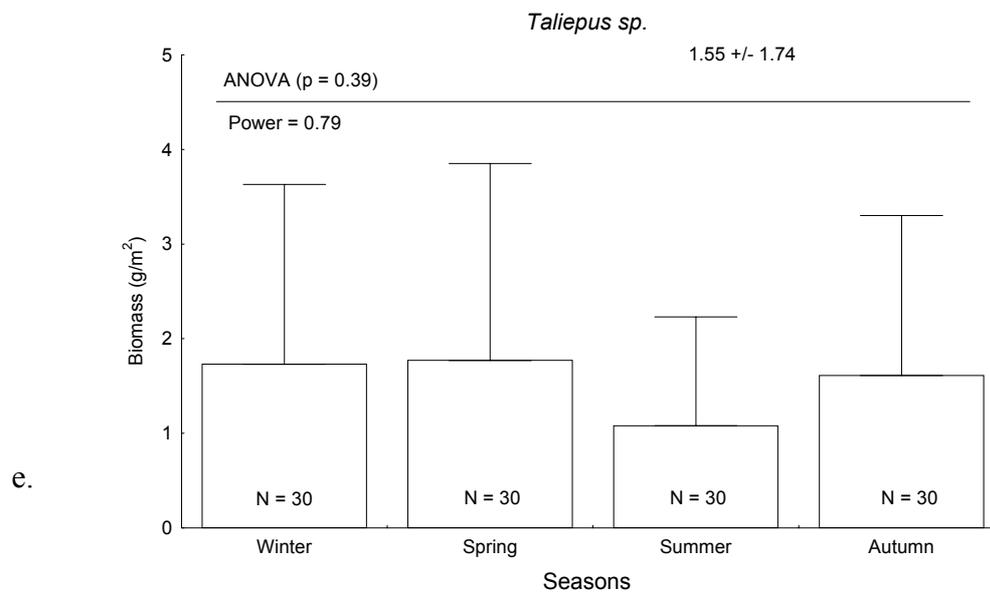
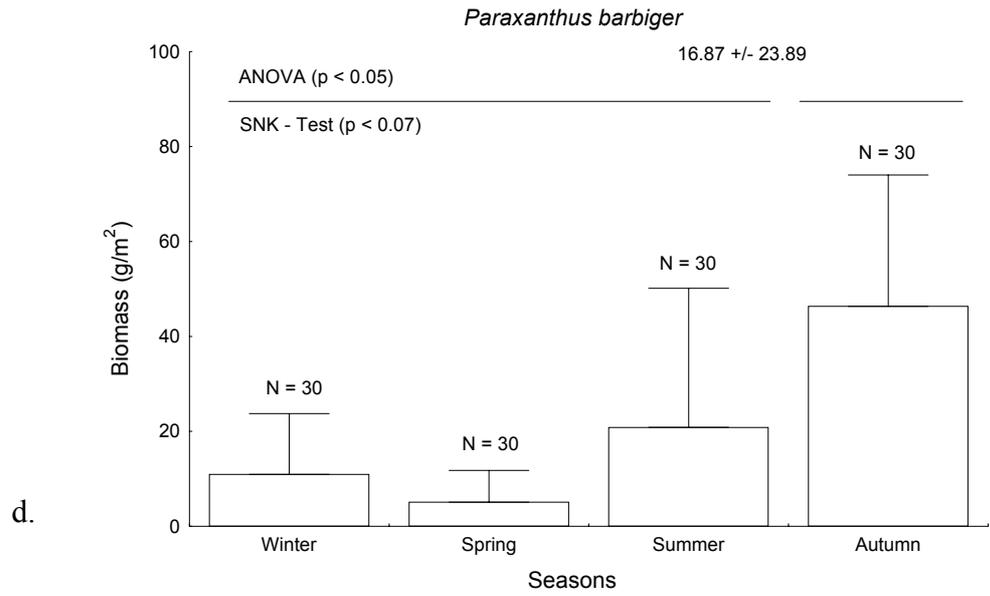


Fig. 7
continuation

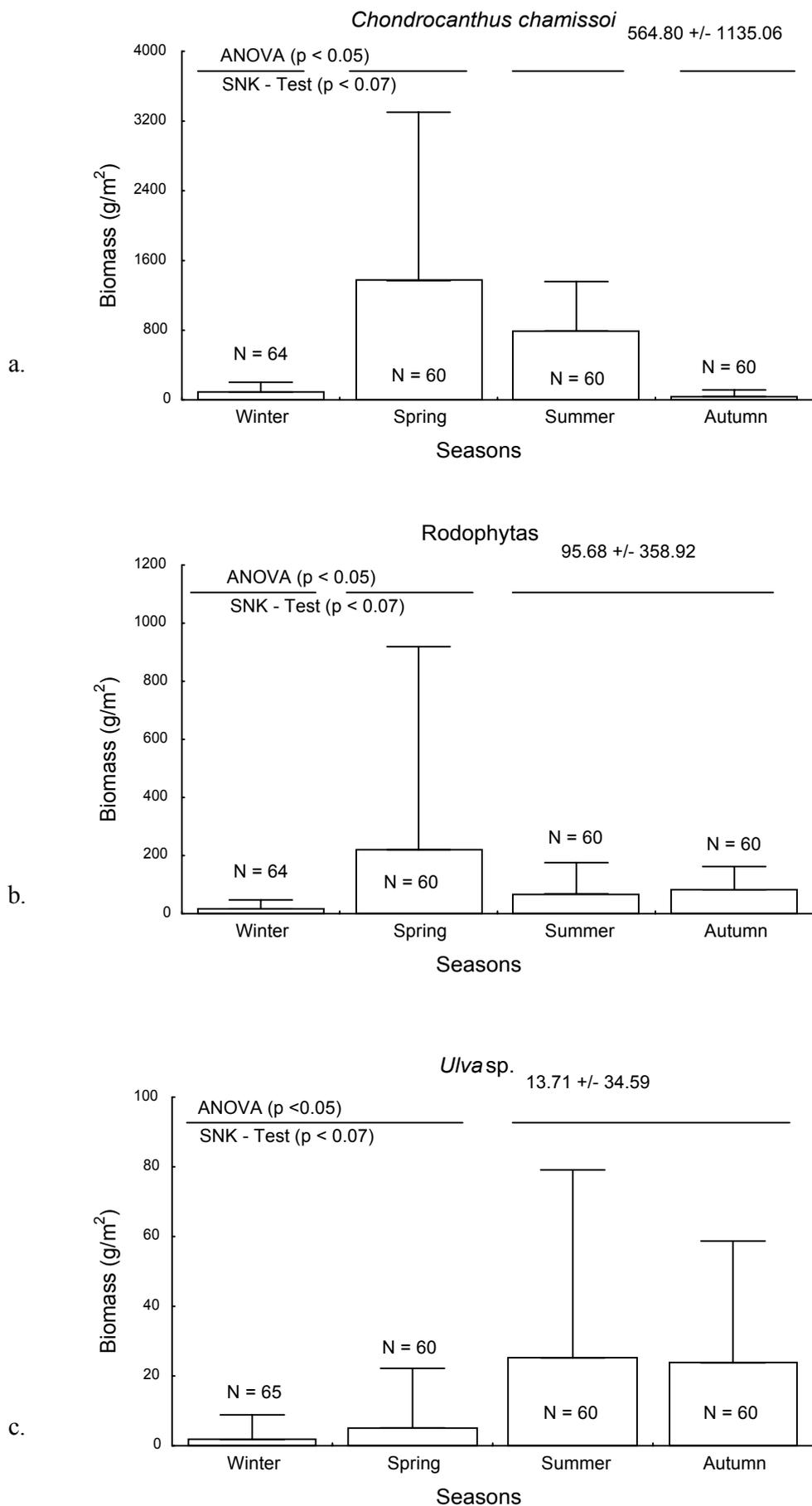


Fig. 8

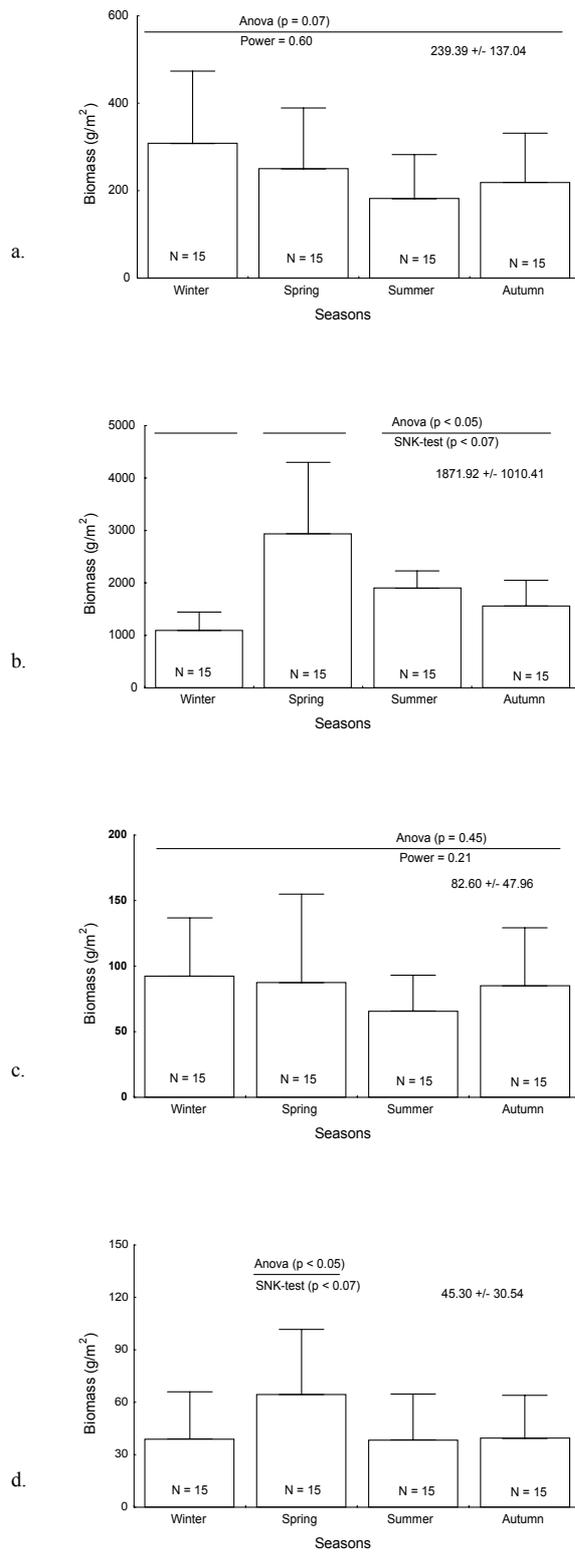


Fig. 9

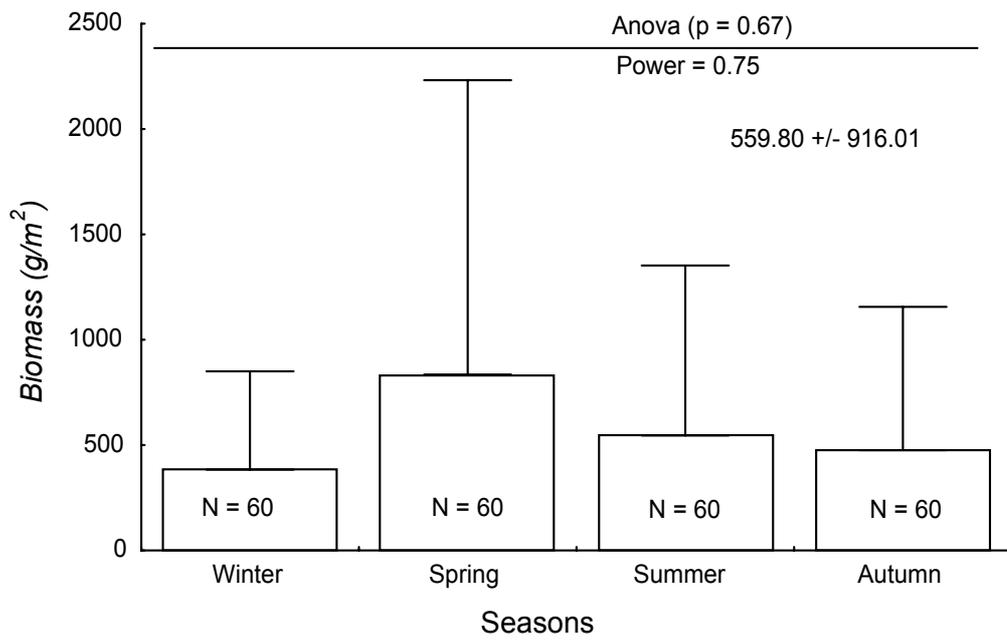


Fig. 10

5. Chapter II

“Observations in the feeding behaviour of the asteroid *Meyenaster gelatinosus* as response to changes in abundance of the scallop *Argopecten purpuratus* in benthic systems of northern Chile”

¹Marco Ortiz, ¹Sandra Jesse, ²Wolfgang Stotz & ¹Matthias Wolff

¹Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@zmt.uni-bremen.de; jesse@zmt.uni-bremen.de). Fax: +49 (0) 421 238 00 30.

²Grupo de Ecología y Manejo, Universidad Católica del Norte, Casilla 117, Coquimbo, Chile.

Key words: *Argopecten*, feeding-niche breath, prey spectrum, Ivlev index, management polices, subtidal communities.

2001

The first author developed the conceptual frame of this paper. The first and second author carried out the sampling programme. Data processing, analysis and interpretation were conducted by the first author. The first version of this work was written by the first author and it was improved with the cooperation of the other co-authors.

Abstract

Between winter 1996 and autumn 1997, the prey spectrum and feeding behaviour of the sea star *Meyenaster gelatinosus* (Meyen, 1834) and the seasonal abundance of the dominant benthic macrofauna were analysed in: (1) a shore-fringing seagrass meadow and (2) an adjacent sand-gravel benthic system of Tongoy Bay (central-north Chile). Of 524 sea stars collected, 130 (25%) had food in their stomachs and were feeding on the scallop *Argopecten purpuratus* (Lamarck, 1819), snails *Calytraea trochiformis* (Born, 1778), *Tegula luctuosa* (Orbigny, 1841), and *T. eryomphala* (Jones, 1844), and small epifauna constituted by the polyplacophora *Chiton* spp., gastropods such as *Nassarius gayi* (Kiener, 1835), *Nucula pisum* (Sowerby, 1835), *Turritella cingulata* (Sowerby, 1825) and *Mitrella unifasciata* (Sowerby, 1832). The scallop *A. purpuratus* suffered an intensive commercial harvest during the study period which decreased significantly its abundance in both habitats. As a response in the feeding behaviour of *M. gelatinosus* the following observations were made: (1) before harvesting started, *A. purpuratus* constituted the principal prey for *M. gelatinosus* in the seagrass habitat, whereas in the sand-gravel the above mentioned four prey types were equally distributed in its diet; (2) after harvesting, the frequency of occurrence of the scallop decreased in the stomachs of the sea star in the seagrass but was substituted by the group of small epifauna; (3) the breadth of the feeding-niche of the sea star increased, however, indicating that *M. gelatinosus* became a more generalist feeder as the scallop decreased in abundance. In the sand-gravel habitat, the diet composition remained unaltered, but *M. gelatinosus* showed an inverse tendency, specialising on the scallop; (4) *M. gelatinosus* increased its feeding preferences on *A. purpuratus* in both habitats when the abundance of the scallop declined as proved by the Ivlev index; and (5) *M. gelatinosus* feeds on a wide size-range (4 to 14 cm) of the scallop with a marked preference for larger size classes. Our results confirm, in part, the observations of local fishermen of Puerto Aldea regarding the possible negative impact of *M. gelatinosus* on the standing stock of the commercially exploited scallop.

Introduction

It is widely accepted that the structure of intertidal communities is not only determined by physical (disturbances) processes, but also largely by biological ones (predation and competitive interactions) (e.g. Connell 1961; Dayton 1971; Menge 1976, 2000; Lubchenco 1978; Lubchenco and Menge 1978; Underwood 1980; Underwood et al. 1983). Sea stars as top predators exert relevant impacts on these systems, and some of them are considered keystone species (sensu Paine 1966, 1974). Even though, many studies had to be carried out to prove the keystone-species hypothesis in different coastal ecosystems, most of these works have been addressed exclusively to intertidal communities (e.g. Phillips 1976, 1977; Branch 1978; Phillips and Castori 1982; Paine et al. 1985; Tokeshi et al. 1989; Arrontes and Underwood 1991; Espoz and Castilla 2000). Few investigations addressed subtidal communities and the role of these species therein. Most of them were essentially designed to estimate the effects of the sea star species on single prey species such as whelks, clams or scallops (e.g. Anger et al. 1977; Dayton et al. 1977; Barbeau and Scheibling 1994a,b; Arsenault and Himmelman 1996; Rochette et al. 1996; Barbeau et al. 1998; Morissette and Himmelman 2000).

The asteroid *Meyenaster gelatinosus* is one of the dominant predators inhabiting benthic systems along the central-north Chilean coast (Madsen 1956; Stotz

2001 per. comm.), including the Tongoy Bay (Wolff and Alarcón 1993) and the management area of Puerto Aldea (Ortiz et al. in prep.) (Fig. 1). Dayton et al. (1977) described the feeding behaviour of *M. gelatinosus* from communities of central-south Chile where it inhabits exposed rocky shores. Due to the fact that *M. gelatinosus* occurs sympatrically with the economically important scallop *Argopecten purpuratus*, the fishermen of Puerto Aldea have suggested the implementation of a management policy that intends to decrease the abundance of this “undesired” asteroid. Stotz and González (1997) proposed some guidelines for the development of a sustainable harvest strategy for the population of *A. purpuratus* in this management area based on the population dynamic of the scallop. However, the proposed strategy does not take into account its ecological linkages to other populations.

The sea stars are non-visual and slow-moving predators that seek for food by chemoreception or chance of encounters (Sloan and Campbell 1982). Stephens and Krebs (1986) proposed models by which it is possible to estimate prey size preference for generalised predator-prey combinations. These models have already been used for other marine species (e.g. Juanes 1992 and reference therein). One of these models predicts that the average size of the prey consumed by a sympatric predator would be biased towards small sizes. Based on this theoretical prediction, we may expect that, if the sea star *M. gelatinosus* feeds on the scallop *A. purpuratus*, it would largely select small individuals.

Between June 1996 (winter) and May 1997 (autumn) a study was carried out to estimate the dynamics of abundance and production of dominant macrofauna species inhabiting the benthic community of Puerto Aldea. During the study period, *A. purpuratus* suffered two intensive harvest (September of 1996 and December-January of 1996-97), which reduced its biomass significantly (ca. 50%) (Ortiz et al. submitted). The changes of scallop biomass due to harvesting may be considered as a natural, not replicated experiment. Therefore, the objectives of this study were: (1) to describe the prey spectrum of *M. gelatinosus* before and after fishing on the scallop, (2) to estimate the relative importance of *A. purpuratus* in its diet, (3) to determine if *M. gelatinosus* behaves as a generalist or specialist feeder of *A. purpuratus*, and (4) to assess in part the generalised sympatric predator-prey hypothesis for *M. gelatinosus* and *A. purpuratus*.

Material and Methods

Description of the study area

The study was carried out in Tongoy Bay (30°15'S – 71°31'W) in the IV Region (Coquimbo, Chile) (Fig. 1). The benthic area of Puerto Aldea corresponds to one of the 168 territorial use rights for fisheries (management areas) established along the coastal Chilean ecosystems (Castilla 2000). The management areas are assigned to fishermen associations for the planning of sustainable manipulations of the systems in order to increase the productivity of valuable resources. In the study area, four different habitats can be recognised: (1) seagrass meadows from 0 to 4 m depth, (2) sand-gravel between 4 and 10 m, (3) sand flats between 10 and 14 m, and (4) mud flats > 14 m depth. A complete description of these habitats was done by Jesse (2001) and Ortiz et al. (in prep.). The entire Tongoy Bay and particularly the subtidal benthic system of Puerto Aldea are protected from the prevailing south-west winds by Lengua de Vaca peninsula. The upwelling center near to Punta de Vaca (Acuña et al. 1989; Daneri et al. 2000; Montecino and Quiroz 2000) is one of the most important of northern Chile and supplies nutrients to the ecosystem and prevents the establishment

of a stable thermocline during summer. Temperature of bottom water ranges between 13°C and 17°C between winter and summer respectively (Jesse 2001).

Sampling design

The analysis of the food spectrum of *M. gelatinosus* was done in two habitats, the seagrass meadows composed exclusively of *Heterozostera tasmanica* (Martens ex Ascher) and the adjacent area constituted by sand and gravel. It has been widely reported that seagrass meadows support different species associations of epiphytes (e.g. Tomasko and Lapointe 1991; Frankovich and Fourqurean 1997), benthic invertebrates (infaunal and epifaunal associations) (e.g. Connolly 1997; Reush 1998; Edgar 1999a; Rose et al. 1999) and fish (e.g. Bell et al. 1987; Ferrell and Bell 1991; Edgar 1999b). Additionally, it serves as a nursery area for many invertebrate species (Thayer et al. 1984; Eckman 1987; Edgar 1999b, Jesse 2001).

The seasonal biomass variation (between winter 1996 and autumn 1997) of *M. gelatinosus*, *A. purpuratus*, the gastropods *Calyptraea trochiformis*, *Tegula luctuosa* and *T. euryonphala* was determined in both habitats at 5 randomly chosen stations, taking 3 random samples per station for *M. gelatinosus* and *A. purpuratus* and 20 samples for *C. trochiformis*, *Tegula* sp. and the other species. All samples were collected by means of HOOKA diving. Table 1 summarises the number of samples taken per season and the size of each sample unit. The preys of *M. gelatinosus* were determined *in situ* (daylight), as the sea star spreads out its stomach enveloping the prey, which allows easy recognition of its food. The sampling of abundance of preys and the food items of *M. gelatinosus* was simultaneously done. Additionally, predator and prey sizes were registered.

Statistical analysis

The Bartlett and Hartley's tests were used to evaluate the normality of data and Cochran's test to assess the homogeneity of variances (Underwood 1981, 1997). When non-normality and heterogeneity were significant ($p < 0.005$), the square root or logarithmic transformation of data (\log_{10} data) was applied (Sokal and Rohlf 1995; Underwood 1981, 1997), satisfying the assumptions of the statistical test. The lower p-level ($p < 0.005$) was used because parametric tests are robust with non-normality of data and non-severe heterogeneity of variance (Box 1953; Tiku et al. 1986; Underwood 1981, 1997; Weerahandi 1995). When the assumptions for parametric test were satisfied, t-test and one-way ANOVAs were applied with $p < 0.05$. In cases of statistical significance the post hoc analysis Student-Newman-Keuls was used (Steel and Torrie 1988; Underwood 1981, 1997) with $p < 0.07$ (Type I error), according to the adjustment recommended by Day and Quinn (1989). *A posteriori* statistical power analysis was calculated in those situations where the null hypothesis was not rejected.

Two analysis were used to estimate the feeding behaviour (generalist and specialist) of *M. gelatinosus*. The breadth of feeding-niche (B) was calculated with respect to frequency (%) of occurrence in terms of biomass of each prey item (sensu Levins 1968), as follow;

$$B = \frac{1}{\sum_{i=1}^n p_i^2}, \quad (1)$$

where, p_i denotes the wet weight proportion of the prey species i related to the total prey biomass consumed by the sea star, and n is the total number of different prey species. This index ranges from 1, when the predator concentrates its feeding on a

single species (specialisation), to values >1 where the different preys are consumed in similar proportions (generalisation). The electivity or preference of *M. gelatinosus* for a particular prey was estimated by Ivlev's index (E) (Krebs 1989), which relates the proportion (%) of the prey item in the diet with the relative abundance of the prey in the environment as follow:

$$E_i = \frac{v_i - n_i}{v_i + n_i}, \quad (2)$$

where,

v_i = % of species i in the diet of predator, and

n_i = % of species i in the environment.

This index ranges from positive to negative values for the preferred and the avoided preys, respectively.

Results

Of 524 individuals of *M. gelatinosus* examined, only 130 (~25%) were feeding on different prey species. Besides of *A. purpuratus*, the gastropods *Calyptraea trochiformis* (Born 1778), *Tegula luctuosa* and *T. euryomphala* (grouped like *Tegula* sp.), smaller gastropods such as *Nassarius* sp., *Nucula* sp., *Turritella* sp. and *Mitrella* sp., and the polyplacophora *Chiton* spp. (grouped like small epifauna) were preyed upon (Table 1). It is important to indicate that these species present different inhabit behaviours. The scallop is highly mobile compared to *Tegula* sp. and small epifauna, whereas the gastropod *C. trochiformis* is semi-sessile.

Fig. 2 shows the relative diet composition (%) of *M. gelatinosus* for each habitat before and after harvesting of *A. purpuratus*. Before harvesting (winter-spring 1996), the scallop was the principal prey for the asteroid only in the seagrass habitat (55.5%), whereas in the sand-gravel habitat no specific preference for a prey item was observed. However, this situation changed radically after the harvesting period in summer 1997. In the seagrass, the importance of the scallops declined (27.3%), instead the sea star preyed more upon the small epifauna. In the sand-gravel habitat all preys presented a relatively homogeneous occurrence (Table 2).

Fig. 3a illustrates that *A. purpuratus* is consumed by larger individuals of *M. gelatinosus*, whereas smaller sea star feed on *C. trochiformis*, *Tegula* sp. and small epifauna (Fig. 3b,c,d), statistical significance was found (ANOVA, $p < 0.05$; SNK, $p < 0.07$) (Fig. 4). Only smaller individuals of *A. purpuratus* (< 3.0 cm) do not suffer depredation from *M. gelatinosus* (Fig. 5). However, the sea star seems to concentrate its feeding on the scallops of ca.10 cm wide-length. Fig. 6a shows the significant decrease in biomass (ANOVA, $p < 0.05$; SNK, $p < 0.07$) of *A. purpuratus* in both habitats as consequence of the harvesting activities. Nevertheless, the sea star did not show significant changes in biomass per habitat as a response to the decline in scallop abundance. Only a significant difference between habitats was detected (ANOVA, $p < 0.05$; SNK, $p < 0.07$) (Fig. 6b). In regard to the other prey species, *C. trochiformis* presented significant seasonal differences in biomass (t-test, $p < 0.05$) (Fig. 6c), whereas *Tegula* sp. remained relatively constant (t-test, $p = 0.80$), nonetheless, a rigorous conclusion does not seem justified due to the low power calculated (Power = 0.50). For the species grouped as small epifauna, information of seasonal changes in abundance was not available, but it is known that the abundance of small epifauna is considerably higher in the sand-gravel than the seagrass habitat (González 1992, León 2000).

Table 2 summarises the breath of feeding-niche (B) and the Ivlev indices calculated before and after fishing on the scallops. The index of niche breath showed that in the seagrass meadow *M. gelatinosus* changed from a specialist to a generalist feeder as the biomass of *A. purpuratus* is decreased, while in the sand-gravel habitat an inverse tendency was observed. The Ivlev index indicated that in both habitats the preference of *M. gelatinosus* for *A. purpuratus* increased independently from significant changes in the scallop abundance. For the other prey species, the electivity index presented an inverse pattern.

Discussion

The present study described the food items and the feeding spectrum of a dominant sea star predator in a subtidal system of the north-central Chilean coast constituted of seagrass and sand-gravel. Although a high number of sea star was observed during the study period, no juveniles (< 5 cm) could be found. Thus generalisations of *M. gelatinosus* feeding behaviour refer to the adult population only. The absence of juveniles may be related to a recruitment failure (Tokeshi et al. 1989), or because they inhabit other microhabitats (crevices, hollows, fissures). The observed one modal distribution of *M. gelatinosus* seems to be a generalised pattern for sea stars independent of the species and habitat where they occur (Menge 1972; Yamagushi 1975; Anger et al. 1977; Dayton et al. 1977; Town 1980; Scheibling 1980; Penney and Griffiths 1984; Tokeshi et al. 1989; Barbeau and Scheibling 1994a).

The wide variety of prey items found in the stomachs suggest a general ability of the sea stars species to access different resources (Feder 1959; Paine 1966; Anger et al. 1977; Dayton et al. 1977; Tokeshi 1989), which holds also for *M. gelatinosus* in the subtidal systems of Tongoy Bay. However, some starfish species prefer a particular type of prey, as shown by Anger et al. (1977); Dayton et al. (1977); Tokeshi (1989) and for *M. gelatinosus* in this study. However, we cannot generalise on th preferences because feeding would be highly dependent on habitat structure and prey availability.

Our results show that before scallop abundance declined significantly due to harvest, the sea star consumed preferentially *A. purpuratus* only in the seagrass habitat. This may be explained by scallop dominance in the seagrass, and therefore may reflect opportunistic feeding behaviour rather than true preference. After fishing, the small epifauna replaced the scallop in the diet of the sea star, which could be taken as a behavioural response of sea star to changes in the prey availability. Nevertheless, large individuals of *M. gelatinosus* feed preferentially on *A. purpuratus*, in comparison to smaller ones that consume other prey items. This would suggest some type of difficulty for sea stars to feed on scallops, possibly due to a large handling time which increases the chance of scallops to escape (Barbeau and Scheibling 1994a). Scallops are highly mobile in comparison to other prey species. However, further studies should be conducted to estimate the energetic content of the prey species to assess an eventual energetic explanation for the pattern feeding observed. Likewise, the fact that only small size-class scallops (< 3.0 cm) were not consumed by the sea star may be explained by natural escape (favoured by bottom currents) and/or low energetic content. Our results suggest that the generalised hypothesis referring to a predator's preference for small size of preys could not be verified for *M. gelatinosus* and *A. purpuratus*. However, it should be taken into account that the current study describes field observations, where other biological (intra-/inter-specific

competition) and physical factors (bottom currents) may also influence the feeding behaviour of the sea star.

While the diet composition of *M. gelatinosus* seems to reflect directly the environmental food/prey supply, the feeding-niche breadth and the Ivlev indexes revealed unexpected values. Based on the breadth of feeding-niche index, the significant depletion of *A. purpuratus* (by harvest) would be in itself a stimulus strong enough for the sea star to change its behaviour from a generalist to a specialist feeder in the sand-gravel habitat. The Ivlev index indicated an increase of preference for the prey *A. purpuratus* in both habitats. These results show that *M. gelatinosus* would be eventually a facultative specialist predator under certain circumstances. This finding has as yet not been reported for subtidal sea star species, possibly due to the difficulty to conduct experiments where changes in abundance of preys are needed.

These results confirm, in part, the notion of fishermen of Puerto Aldea that *M. gelatinosus* may exert a significant negative impact upon the abundance and production of the commercially important scallop *A. purpuratus*. Nevertheless, further investigations should address to the following aspects: (1) the quantification of the consumption rate of the sea star and, (2) the determination of the energetic content of the preyed species to assess the hypothesis that the preference for scallops could be a consequence of its comparatively higher energetic contents.

References

- Acuña E, Moraga J, Uribe E (1989) La zona de Coquimbo: un sistema nerítico de alta productividad. CPPS Rev Pacífico Sur, N° especial: 145-157
- Anger K, Rogal U, Schreiber G, Valentin C (1977) In-situ investigations on the echinoderm *Asterias rubens* as a predator of soft-bottom communities in the western Baltic Sea. Helgoländer wiss Meeresunters 29: 439-459
- Arrontes J, Underwood AJ (1991) Experimental studies on some aspects of the feeding ecology of the intertidal starfish *Patiriella exigua*. J Exp Mar Biol Ecol 148: 255-269
- Arsenault DJ, Himmelman JH (1996) Size-related changes in vulnerability to predators and spatial refuge use by juvenile Iceland scallops *Chlamys islandica*. Mar Ecol Prog Ser 140: 115-120
- Barbeau MA, Scheibling RE (1994a) Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magallanicus* (Gmelin)). J Exp Mar Biol Ecol 180: 103-136
- Barbeau MA, Scheibling RE (1994b) Temperature effects on predation of juvenile sea scallops [*Placopecten magallanicus* (Gmelin)] by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say). J Exp Mar Biol Ecol 182: 27-47
- Barbeau MA, Scheibling RE, Hatcher BG (1998) Behavioural responses of predatory crabs and sea stars to varying density of juvenile sea scallops. Aquaculture 169 (1-2): 87-98
- Bell J, Westoby M, Steffe S (1987) Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? J Exp Mar Biol Ecol 111: 133-144
- Box G (1953) Non-normality and test on variances. Biometrika 40: 318-335
- Branch GM (1978) The responses of South African patellid limpets to invertebrate predators. Zool Afr 13: 221-232

- Castilla JC (2000) Roles of experimental marine ecology in coastal management and conservation. *J Exp Mar Biol Ecol* 250: 3-21
- Connell J (1961) Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol Monogr* 31: 61-104
- Connolly R (1997) Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. *Hydrobiologia* 346: 137-148
- Daneri G, Dellarossa V, Quiñones R, Jacob B, Montero P, Ulloa O (2000) Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Mar Ecol Prog Ser* 197: 41-49
- Day R, Quinn G (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecol Monogr* 59(4): 433-463
- Dayton PK (1971) Competition, disturbance and community organisation: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr* 41: 351-389
- Dayton PK, Rosenthal R, Mahen L, Antezana T (1977) Population structure and foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its preys. *Mar Biol* 39: 361-370
- Eckman J (1987) The role of hydrodynamic in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *J Exp Mar Biol Ecol* 106: 165-191
- Edgar G (1999a) Experimental analysis of structural versus trophic importance of seagrass beds. I. Effects on macrofaunal and meiofaunal invertebrates. *Vie et Milieu* 49(4): 239-248
- Edgar G (1999b) Experimental analysis of structural versus trophic importance of seagrass beds. II. Effects on fishes, decapods and cephalopods. *Vie et Milieu* 49(4): 249-260
- Espoz C, Castilla JC (2000) Escape responses of four Chilean intertidal limpets to seastars. *Mar Biol* 137: 887-892
- Ferrel D, Bell J (1991) Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Mar Ecol Prog Ser* 72: 15-24
- Frankovich T, Fourqurean W (1997) Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Mar Ecol Prog Ser* 159: 37-50
- González S (1992) *Heterozostera tasmanica* (Martens en Aschers) den Hartog y comunidad asociada en el norte de Chile. Tesis de Licenciatura, Universidad Católica del Norte, Facultad de Cs del Mar, Chile.
- Jesse S (2001) Comparative ecology of sympatric brachyuran crab species in the shallow subtidal of the Pacific coast of north Chile and their importance for the artisanal fishery Puerto Aldea. PhD Dissertation, University of Bremen, Germany, 125 pp.
- Juanes F (1992) Why do decapod crustaceans prefer small-sized molluscan prey?. *Mar Ecol Prog Ser* 87: 239-249
- Krebs Ch J (1989) *Ecological methodology*. Harper & Row, NY, 654 pp
- León R (2000) Relaciones tróficas del *Cancer polyodon* (Poepping 1936). Tesis para obtener el título de Biólogo Marino, Universidad Católica del Norte, sede Coquimbo, Chile.

- Levins R (1968) Evolution in changing environments. Princeton University Press, Princeton, 120 pp
- Lubchenco J (1978) Species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am Nat* 112: 23-39
- Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. *Ecol Monogr* 59: 67-94
- Madsen FJ (1956) Asteroid. Reports of the Lund University Chile expedition 1948-1949. *Acta Univ. Lund. (N°2)* 67: 1-53
- Menge BA (1976) Organisation of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol Monogr* 46: 355-393
- Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J Exp Mar Biol Ecol* 250: 257-289
- Montecinos V, Quiroz D (2000) Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30°). *Aquat Sci* 62: 364-380
- Morissette S, Himmelman JH (2000) Decision of the asteroid *Leptasterias polaris* to abandon its prey when confronted with its predator, the asteroid *Asterias vulgaris*. *J Exp Mar Biol Ecol* 252: 151-157
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65-75
- Paine RT (1974) Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93-120
- Paine RT, Castilla JC, Cancino J (1985) Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zeland and Washington State. *Am Nat* 125: 679-691
- Phillips DW (1976) The effect of a species-specific avoidance response to predatory starfish distribution of two gastropods. *Oecologia* 23: 83-94
- Phillips DW (1977) Avoidance and escape responses of the gastropod mollusc *Olivella biplicata* (Sowerby) to predatory asteroids. *J Exp Mar Biol Ecol* 28: 77-86
- Phillips DW, Castori P (1982) Defensive responses to predatory seastars by two specialist limpets, *Notoacmaea insessa* (Hinds) and *Collisella instabilis* (Gould), associated with marine algae. *J Exp Mar Biol Ecol* 59: 23-30
- Reush TH (1998) Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. *Mar Ecol Prog Ser* 167: 149-153
- Rochette R, McNeil JN, Himmelman JH (1996) Inter-and-intra-population variations in the response of the whelk *Buccinum undatum* to the predatory asteroid *Leptasterias polaris*. *Mar Ecol Prog Ser* 142: 193-201
- Rose C, Sharp W, Kenworthy W, Hunt J, Lyons W, Prager E, Valentine J, Hall M, Whitefield P, Fourqurean J (1999) Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. *Mar Ecol Prog Ser* 190: 211-222
- Sokal R, Rohlf F (1995) Biometry. 3ed. Freeman and Co. San Francisco, 878 pp.
- Sloan NA, Campbell AC (1982) Perception of food. In: Echinoderm nutrition, pp 3-23. Jangoux M, Lawrence JM (Ed.), AA Balkema, Rotterdam.

- Steel R, Torrie H (1988) Bioestadística: principios y procedimientos. 1ed. McGraw-Hill, 662 pp.
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton.
- Stotz W, Gonzalez S (1997) Abundance, growth, and production of the sea scallop *Argopecten purpuratus* (Lamarck 1819): bases for sustainable exploitation of natural scallop beds in north-central Chile. Fish Res 32: 173-183
- Thayer G, Bjorndal K, Ogden J, Williams S, Ziemann J (1984) Role of larger herbivores in seagrass communities. Estuaries 7: 351-376
- Tiku M, Tan W, Balakrishnan N (1986) Robust Inference. Marcel Dekker, 321 pp
- Tokeshi M, Estrella C, Paredes C (1989) Feeding ecology of a size-structured predator population, the South American sun-star *Heliaster helianthus*. Mar Biol 100:495-505
- Tomasko D, Lapointe B (1991) Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. Mar Ecol Prog Ser 159: 37-50
- Underwood AJ (1980) The effects of grazing by gastropods and physical factors on the upper species of intertidal prosobranch gastropods. Oecologia 33: 185-202
- Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr Mar Biol Ann Rev 19: 513-605
- Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, 504 pp
- Underwood AJ, Denley EJ, Moran MJ (1983) Experimental analysis of the structure and dynamics of midshore rocky intertidal algal community. Oecologia 48: 221-233
- Weerahandi S (1995) ANOVA under unequal error variances. Biometrics 51: 589-599
- Wolff M, Alarcon E (1993) Structure of a scallop *Argopecten purpuratus* (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in northern Chile. J Shell Res 12(2): 295-304

List of Tables and Figures

- Table 1 Sampling design with sample size (N) and area of sampling unit (m²). List of prey species consumed by *M. gelatinosus*.
- Table 2 Abundance in percentage (%) and biomass (g wet weight/m²) of preys in each habitat and in the stomachs of *M. gelatinosus*. Feeding-niche breadth (B) and Ivlev indexes for each prey. (Note: the estimation of abundance of small epifauna is based on González (1992) and León (2000).
- Fig. 1 A. Main topographical types along the Chilean coast: 1.= dominated by exposed rocky shores, 2.= dominated by exposed sandy shores, 3.= mostly insular systems. B. Principal bay systems of the IV Region of Coquimbo, Chile. C. Study area of Puerto Aldea located at southern of Tongoy Bay.
- Fig. 2 Occurrence (%) of preys in stomachs of *M. gelatinosus* in the seagrass and the sand-gravel habitats before and after fishing on the scallop *A. purpuratus*.
- Fig. 3 *M. gelatinosus* population size structure and the size of individuals during feeding activities on: a.) *A. purpuratus*, b.) *C. trochiformis*, c.) *Tegula* sp. and d.) Small Epifauna.

Fig. 4 Average (\pm standard deviation) of length (cm) of the sea star *M. gelatinosus* which were observed feeding. (Number of individuals of *M. gelatinosus* feed on each prey item).

Fig. 5 *A. purpuratus* size structure and size of individuals consumed by *M. gelatinosus*.

Fig. 6 Average biomass (\pm standard deviation) of: a.) *A. purpuratus*, b.) *M. gelatinosus*, c.) *C. trochiformis*, and d.) *Tegula* sp., by habitat and during winter-spring and summer-autumn (before/after fishing on *A. purpuratus*). Small letters above the bars indicate where significant differences were detected after SNK test (similar letters indicate no differences).

Table 1. Sampling design with sample size (N) and area of the sampling unit (m²).
List of prey species consumed by *M. gelatinosus*.

Species	Habitats			
	Seagrass		Sand-Gravel	
	N	Size (m ²)	N	Size (m ²)
<i>Argopecten purpuratus</i>	15	20	15	20
<i>Megenaster gelatinosus</i>	15	100	15	100
<i>Calyptrea trochiformis</i>	*		60	0.25
<i>Tegula lucruosa</i> and <i>T. euryomphala</i> grouped like <i>Tegula</i> sp.	**		60	0.25
<i>Chiton</i> sp., <i>Nassarius</i> sp., <i>Nucula</i> sp., <i>Turritela</i> sp., and <i>Mitrella</i> sp. grouped like Small Epifauna	**		**	

A sampling unit of 20 y 100m² means a transect of 10m x 2m and 50m x 2m respectively.

A sampling unit of 0.25m² means a cuadrate of 0.5x0.5m

* Personal estimations (Ortiz pers. obs)

** Abundance data taking from literature (González 1992, León 2000).

Table 2. Abundance in percentage (%) and biomass (g wet weight) of preys in each habitat and in the stomach of *M. gelatinosus*. Feeding-niche breath and Ivlev indexes for each prey. (Note: the estimation of abundance of small epifauna is based on González (1992) and León (2000).

Habitats					
Seagrass					
Before fishing	Abundance of prey in	% in stomachs	g ww	Breath of the feeding	Ivlev index
Item	environment g ww (%)	(N)		niche (B)	
<i>Argopecten purpuratus</i>	190.8(47.3)	55.5(15)	2229.5	0.95	0.08
<i>Calyptrea trochiformis</i>	< 3.0(0.65)	29.6(8)	42.87	0.0004	0.96
<i>Tegula</i> sp.	< 190.0(47.1)	3.7(1)	2.91	0.000002	-0.85
Small epifauna	< 20.0(4.95)	11(3)	9.3	0.00002	0.38
				1.05	
After fishing					
Item					
<i>A. purpuratus</i>	118.31(35.71)	27.3(3)	293.25	0.31	0.13
<i>C. trochiformis</i>	< 3.0(0.9)	9.1(1)	201.74	0.15	0.82
<i>Tegula</i> sp.	< 190.0(57.35)	9.1(1)	10.63	0.0004	-0.73
Small epifauna	< 20.0(6.04)	54.5(6)	16.6	0.0012	0.8
				2.17	
Sand-gravel					
Before fishing					
Item					
<i>A. purpuratus</i>	107.32(11.48)	22.8(13)	1352.9	0.53	0.33
<i>C. trochiformis</i>	121.95(13.05)	31.5(18)	451.49	0.059	0.41
<i>Tegula</i> sp.	478.92(51.23)	21.8(12)	13.84	0.00005	0.4
Small epifauna	~226.6(24.24)	23.9(14)	43.4	0.0005	-0.0007
				1.69	
After fishing					
Item					
<i>A. purpuratus</i>	35.77(3.26)	22.8(8)	693.17	0.66	0.75
<i>C. trochiformis</i>	266.89(24.33)	25.7(9)	96.75	0.013	0.03
<i>Tegula</i> sp.	564.02(51.41)	31.4(11)	42.32	0.0024	-0.24
Small epifauna	~226.6(21.0)	20.1(7)	21.7	0.00064	-0.02
				1.48	

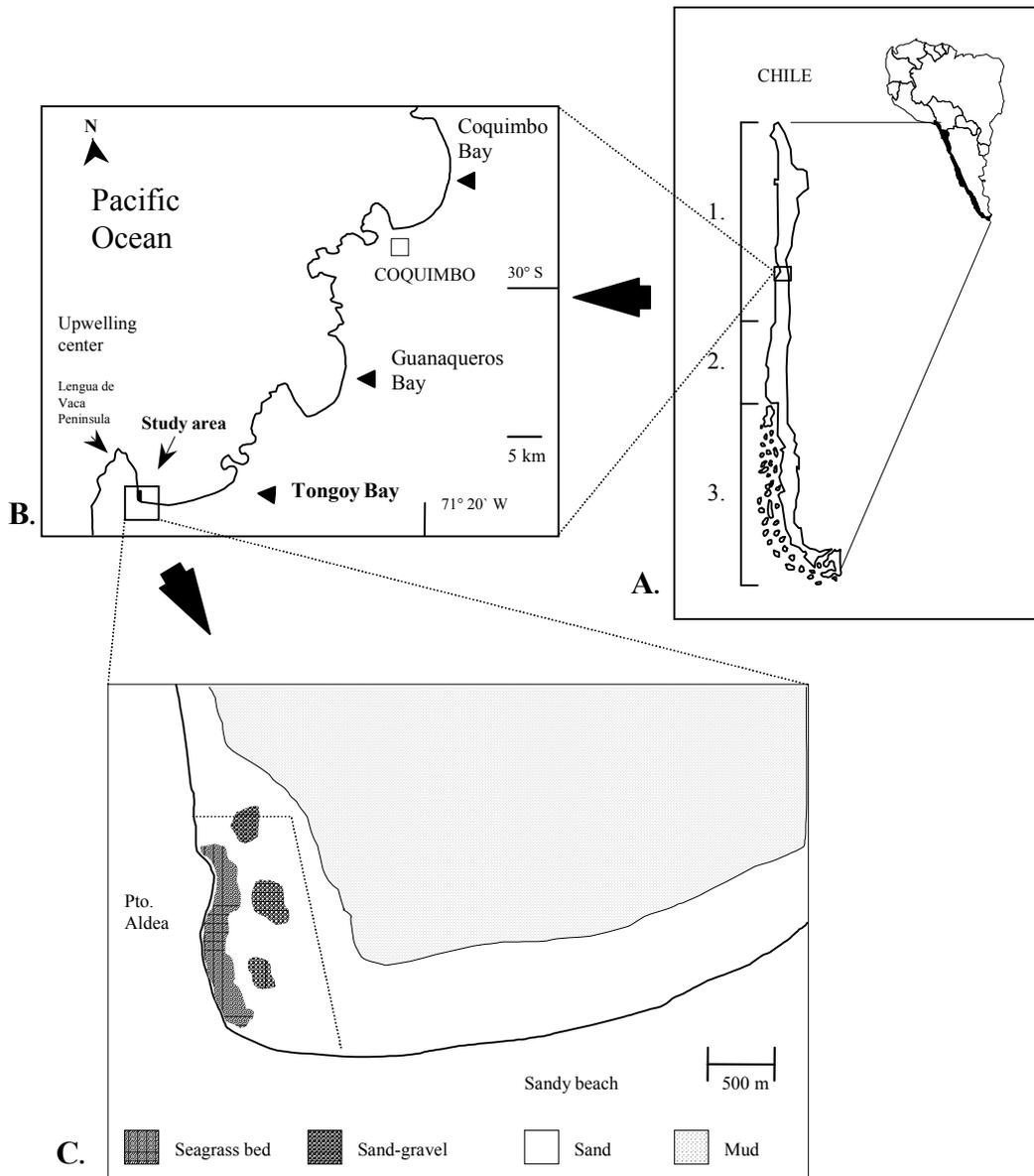


Fig. 1

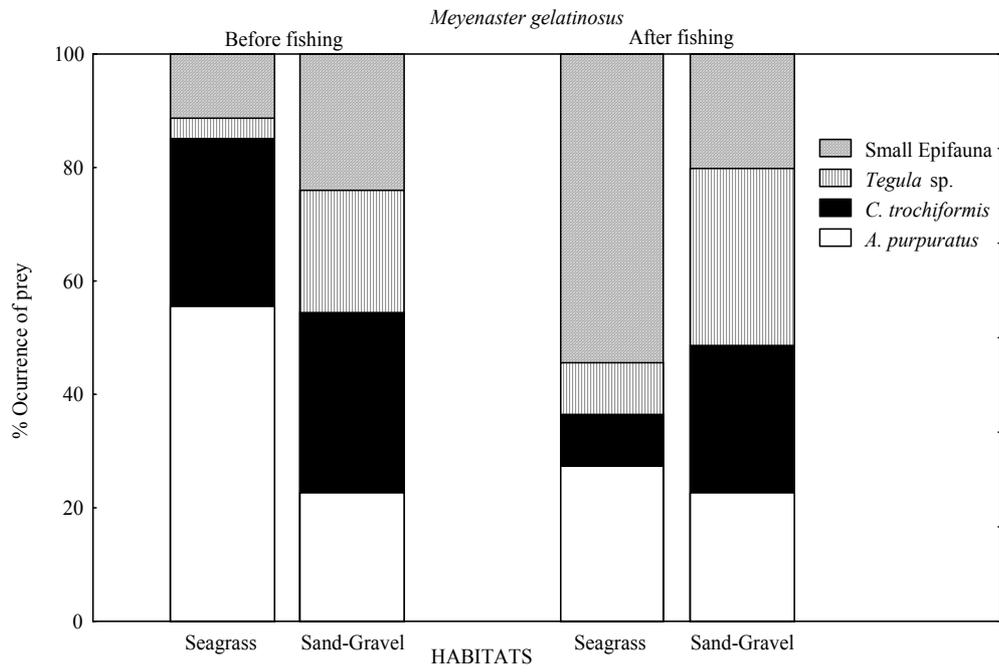


Fig. 2

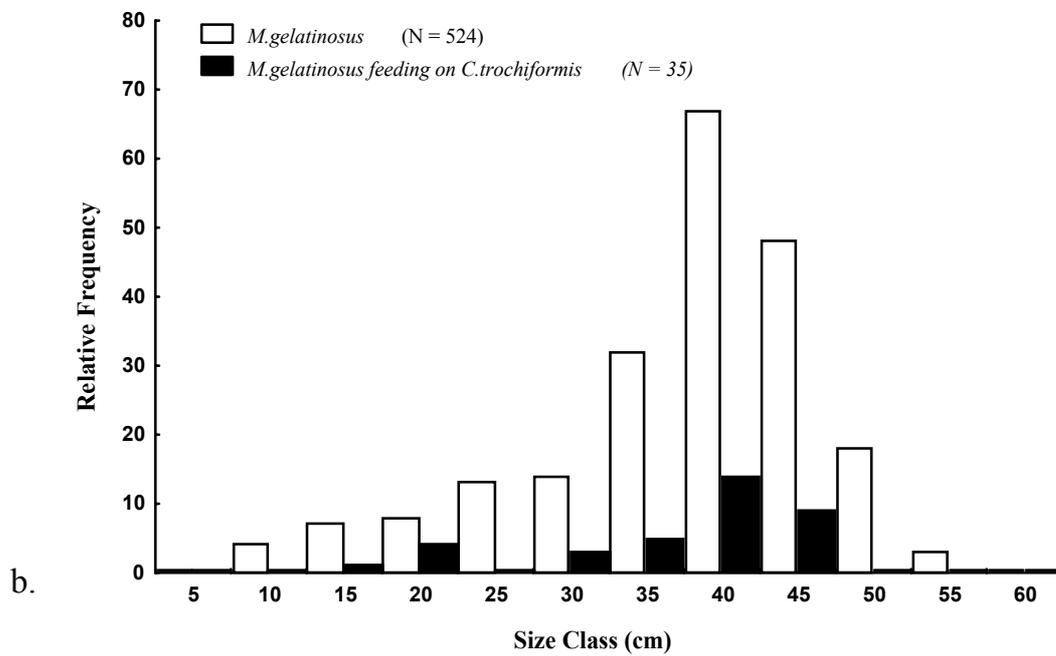
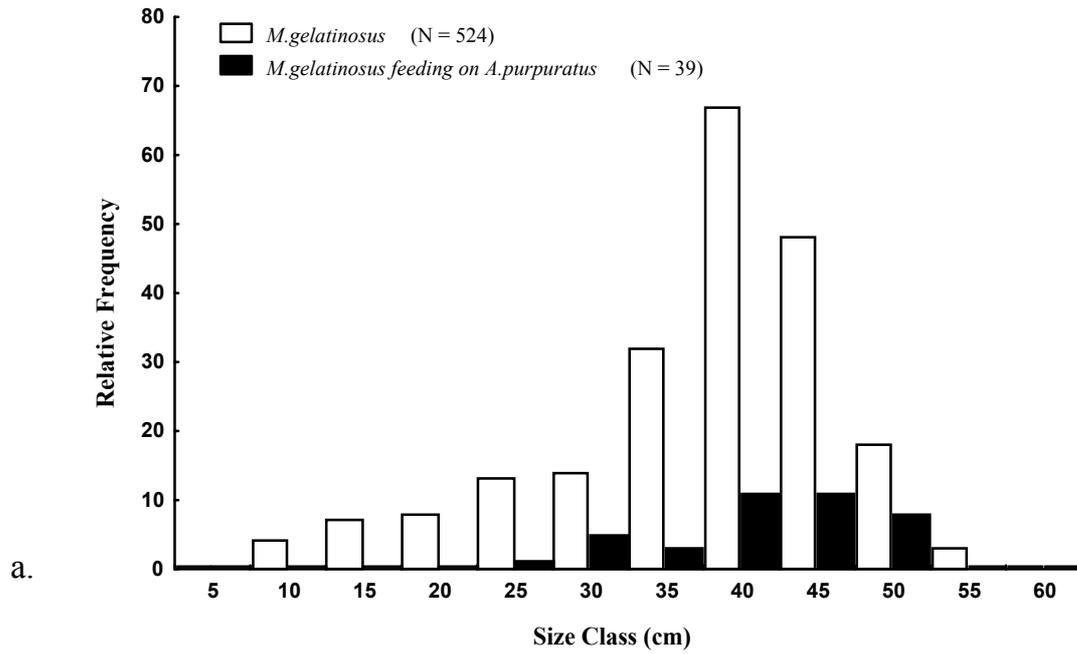


Fig. 3

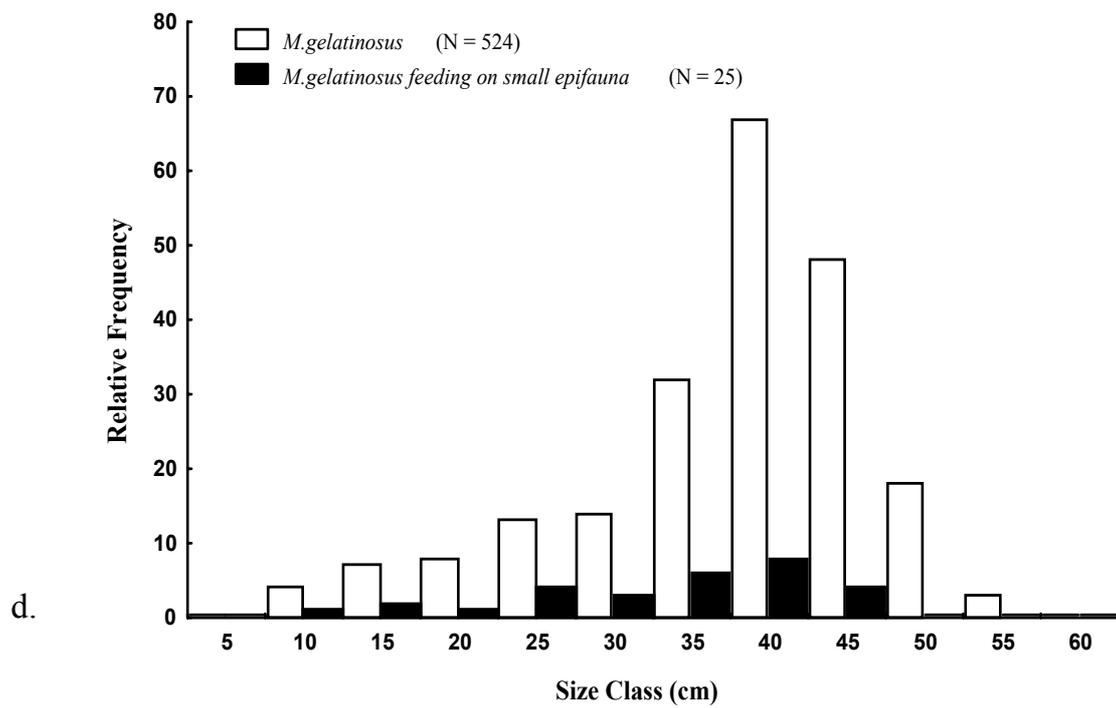
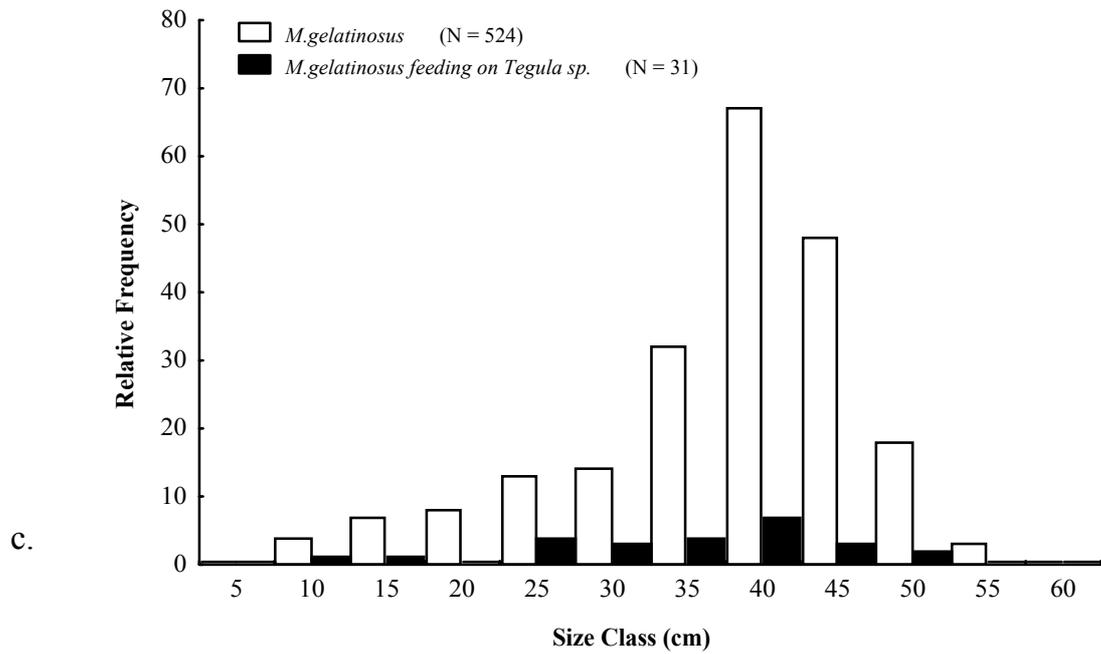


Fig. 3
continuation

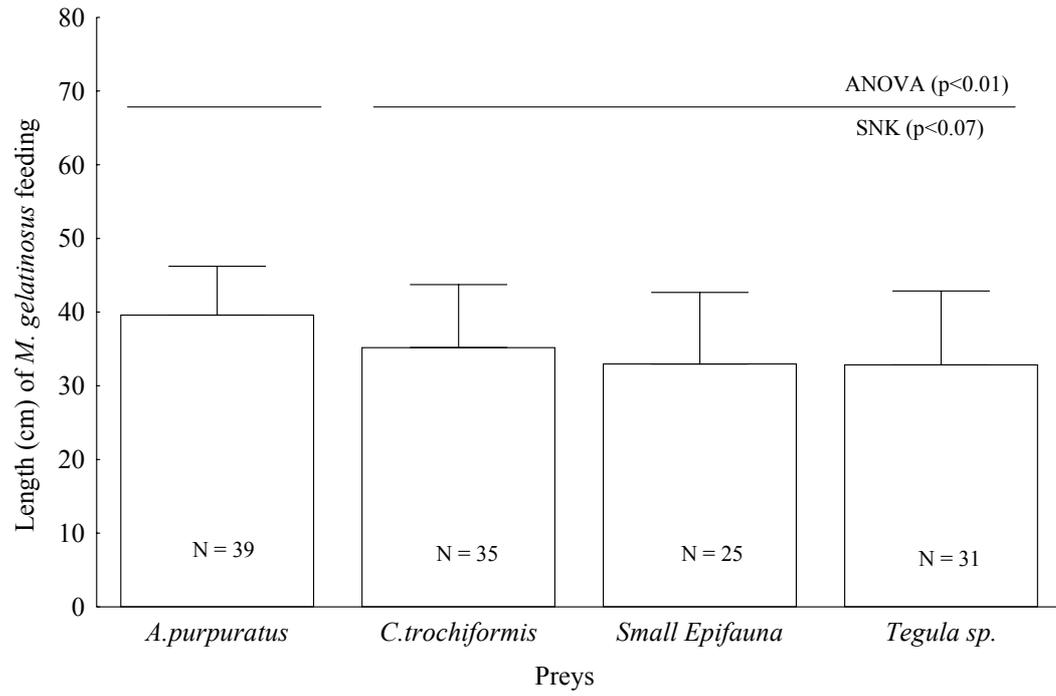


Fig. 4

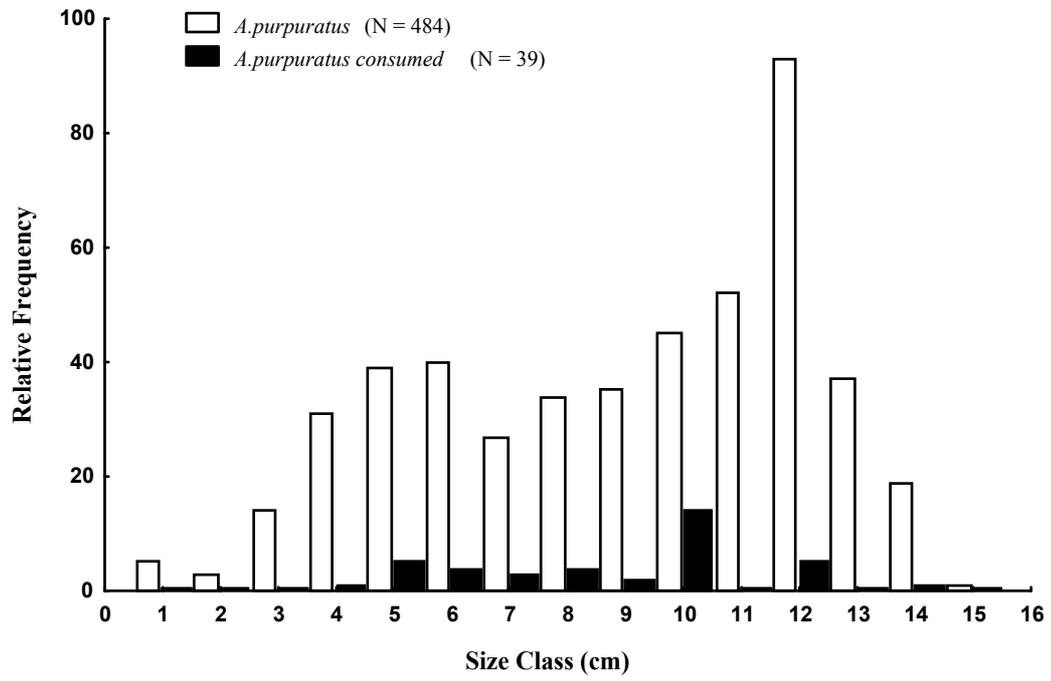


Fig. 5

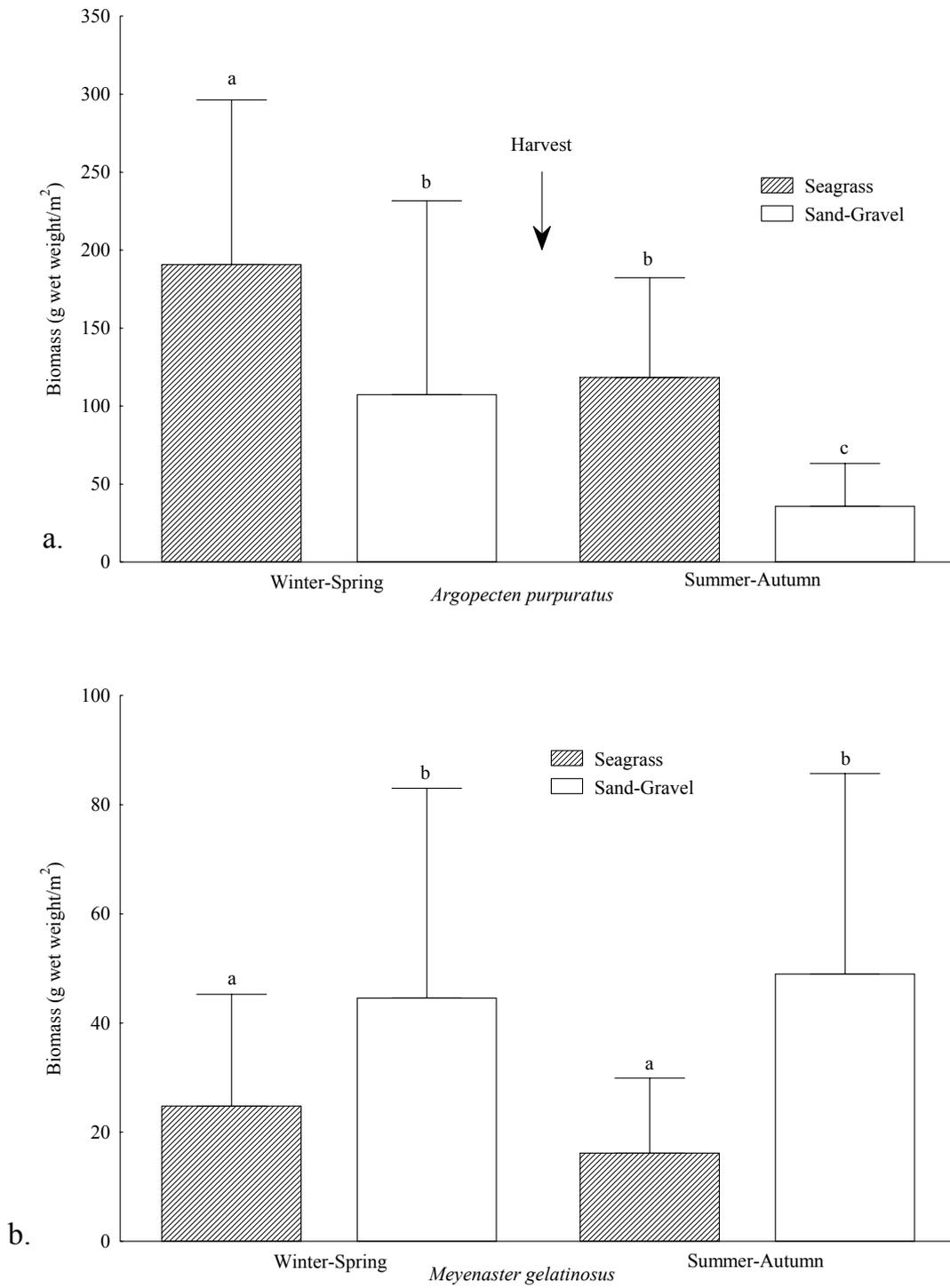


Fig. 6

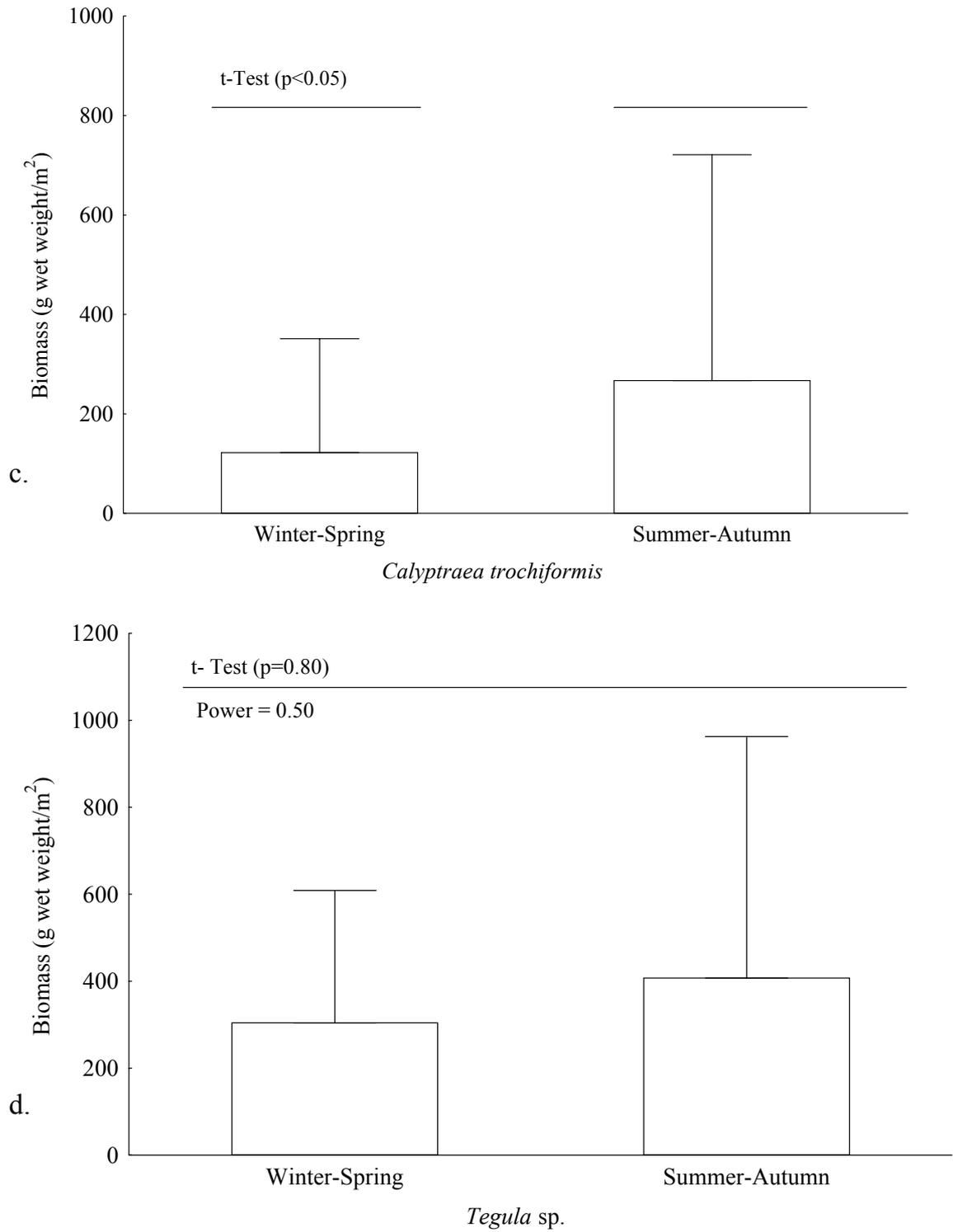


Fig. 6
continuation

6. Chapter III

“Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and assessment of management strategies”

Marco Ortiz & Matthias Wolff

Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@zmt.uni.bremen.de & mwolff@zmt.uni-bremen.de). Fax: + 49 (0) 421 238 00 30.

Key word: benthic habitats, biomass balance, ecosystem structure, management, network analysis, upwelling systems.

2001

The original idea for this publication was developed by the first author. The last version of this contribution was possible after intensive intellectual discussions with the co-author.

Abstract: Steady-state trophic flow models of four benthic communities (seagrass, sand-gravel, sand and mud habitats) were constructed for a subtidal area in Tongoy Bay (Chile). Information of biomass, catches, food spectrum and dynamics of the commercial and non-commercial populations was used and the ECOPATH II software of Christensen and Pauly (1992a) was applied. The sea star *Meyenaster gelatinosus* and the crabs *Cancer polyodon*, *C. porteri* and *Paraxanthus barbiger* were found to be the most prominent predators in the benthic system. The scallop *Argopecten purpuratus* as well as other bivalves represented the principal secondary producers in the seagrass, sand-gravel and sand habitats, while the Infauna dominated the mud habitat. The highest total biomass and system throughput (33579.3 t/km²/year) was calculated for the sand-gravel habitat. The sand habitat had a negative net system production due to the amount of primary production imported from deeper waters to satisfy the food requirements of the large beach clam (*Mulinia* sp.) populations. The mean trophic level of the fishery varied between 2.06 (sand-gravel) and 3.92 (sand) reflecting the fact that the fishery concentrates on primary producers (i.e. algae and filter feeding), and on top predators (i.e. snails and crabs). Fishery is strongest in sand-gravel habitat, where annual catches amount to 122.05 g/m². Low values of the relative Ascendency (*A/C*) (from 27.4 to 32.7 %) suggest that the systems analysed are immature and highly resistant to external perturbations. Manipulations of the input data for the exploited species suggest that seagrass and sand-gravel habitats have a potential for a ~3 times higher than the present production of scallops and the red algae *Chondrocanthus chamissoi*. Results of Mixed Trophic Impacts analysis suggest that any management policy aimed at a man-made increase in the standing stocks of *A. purpuratus* and *Ch. chamissoi* in seagrass and sand-gravel habitats, and a removal of the seastar *M. gelatinosus* in the seagrass habitat appears justified.

1. Introduction

Quantitative assessment of energy-matter flows in complex marine ecosystems has important implications for the understanding of the ecological processes and the prediction of ecosystem functions in response to environmental and anthropogenic impacts (Gaedke, 1995). Likewise, a theoretical evaluation of policy options and the design of an adaptive management for multispecies fisheries (Walters and Hilborn, 1978; Hilborn et al., 1995; Walters and Korman, 1999; Walters et al., 1999; Castilla, 2000) can also be based on these assessments. Nevertheless, the dynamics and regulation of food webs can only be understood if processes occurring at the species or guild level are simultaneously considered with those acting upon the entire ecosystem. The scallop *Argopecten purpuratus* and the red macroalgae *Chondrocanthus chamissoi* suffer an intensive harvest from fishermen of Puerto Aldea (Tongoy Bay, Chile) (Fig. 1). While community interactions for both species (e.g. depredation, competence, commensalism, among others) were studied (Stotz and González, 1994; Marahrens, 1995; Jesse, 2001; Ortiz et al. in prep.), there is still a lack of studies on the large scale effects of both fisheries on the entire community. Management strategies for *A. purpuratus* and *Ch. chamissoi* that have recently been developed (Stotz and Gonzalez, 1994, 1997), are just based on the population dynamics of both species. The principal shortcoming of such single species approaches is to consider the populations as being isolated from their biological (ecological interactions) and abiotic environments (physical factors) (Levins and Lewontin, 1980; Levins and Wilson, 1980; Patten, 1997; Levins, 1998). The reductionistic character of these abstractions seems to be the principal reason for the frequent failure of management policies aimed at the conservation of commercial species and their ecosystems (Larkin, 1977; Hilborn et al., 1995; Patten, 1997; Roberts, 1997; Walters et al., 1999).

The first bay-scale trophic model within the SE Pacific upwelling system of northern Chile was developed by Wolff (1994) using the ECOPATH II software (Christensen

and Pauly, 1992a). Pelagic and benthic compartments were simultaneously considered and the model allowed to evaluate the responses of the ecosystem to the input of unnatural amounts of suspended scallop cultures and to fishery activities on several invertebrate species (e.g. scallops, clams, decapods, macroalgae, etc). Additionally, sustainability assessment were done considering both human activities. Even though Wolff (1994) arrived at some relevant conclusions about the ecological mechanisms operating at different trophic levels and about global network properties of the ecosystem (sensu Ulanowicz, 1986, 1997), he integrated with his bay-scale approach over different systems habitats (subsystems). In the present article, therefore, a finer scale of distinguishable habitats situated in the management area of Puerto Aldea (Fig. 1) is chosen. In this small management area there are four distinct habitats, within which the principal valuable populations the scallop *Argopecten purpuratus* and the red algae *Chondrocanthus chamissoi* are trophically linked to other benthic species. Hence, any global management policy should have different impacts in each habitat. Under these constrains, the objective of the present work is to construct trophic mass-balance models one for each subsystem (habitat) and one for the whole benthic area (combined habitats) of Puerto Aldea. Based on these models the behaviour of components under different management scenarios will be assessed. This study follows recommendations of May (1974), Paine (1980, 1984) and Hall and Raffaelli (1993) according to which the stability of a system would be increased if the food webs are organised into subsystems. Likewise, the strategy followed here is based on research findings of Jesse (2001) in the same study area, who concluded that the eventual development of management polices for crabs species must be habitat-specific, and that crabs species should be treated as single species compartments due to important intraspecific differences. The models use annual biomass averages since Ortiz et al. (in prep.) found that seasonal biomass variations were insignificant in all habitats and in the whole area. This study is the first attempt to construct trophic models at the small scale of benthic habitats in the Chilean coastal ecosystems and addresses the following questions: (1) How is the biomass distribution and biomass flow structure in each habitat type?; (2) What are the principal benthic predators in each habitat, their consumption rates and prey items?; (3) Is it possible to recognise and quantify redundancy, that is, several species of similar trophic roles (sensu Lawton, 1994), in the system?; (4) What is the carrying capacity of each habitat in terms of food availability for target species and predators?; (5) Which are the species most likely affected by different management scenarios?; (6) How sustainable are different management strategies?

ECOPATH II represents a steady-state modelling approach in which the system compartments are balanced by consumption and exports. It combines the approach of Polovina (1984) to estimate the biomass and food consumption of the ecosystem elements (species or groups) with Ulanowicz's (1986, 1997) network analysis of flows among elements of the system for the calculation of ecosystem indices. These indices are the Total System Throughput (T), Ascendency (A), Development Capacity (C), and A/C ratio. Throughput describes the size or vigor of a system and it represents a measure of its activity or metabolism. The Ascendency integrates both size and organisation of the systems, and organisation refers to the number and diversity of interactions between its components. The Development Capacity quantifies the upper limit to Ascendency and the A/C ratio describes the degree of maximum specialisation that is actually realised in the system (Ulanowicz and Mann, 1981; Jarre et al., 1991; Baird and Ulanowicz, 1993; Costanza et al., 1998). Another important index is the redundancy which quantifies the multiplicity of parallel flows between any two arbitrary compartments of the system (sensu Ulanowicz, 1986, 1997). These indices have been widely used to describe and compare a variety of ecosystems of different sizes, geographical locations and complexities (Baird and Ulanowicz, 1989; Baird et al., 1991; Ulanowicz and Wulff, 1991; Christensen and Pauly, 1993; Wolff, 1994; Wolff et al., 1996,

1998, 2000; Monaco and Ulanowicz, 1997; Rocha et al., 1998; Jarre-Teichmann and Christensen, 1998; Niquil et al., 1999; Heymans and Baird, 2000).

2. Material and Methods.

2.1. Subtidal benthic system of Puerto Aldea, Tongoy Bay.

The four habitats modelled are located in the management area of Puerto Aldea, Tongoy Bay (30°15`S – 71°31`W) IV Región of Coquimbo, Chile (Fig. 1). This management area corresponds to one of 168 of such along the Chilean coast that are assigned to fishermen organizations (Castilla, 2000) to maximise, within sustainable boundaries, the production of commercial resources in a self-responsible way. In this area can be distinguish the following habitats: (1) seagrass meadows from 0 to 4 m depth, (2) sand-gravel between 4 and 10 m, (3) sand between 10 and 14 m, and (4) mud > 14 m depth (Fig. 1).

Tongoy bay and the study area protected from the prevailing south-westerly winds of the Lengua de Vaca peninsula. Near Punta Lengua de Vaca lies an important upwelling centre (Acuña et al., 1989; Daneri et al., 2000; Montecinos and Quiroz, 2000), which supplies nutrients to the ecosystem and prevents the establishment of a stable thermocline during summer through permanent intrusions of upwelling water to the bay. Bottom water temperature ranges between 13°C and 17°C in winter and autumn respectively (Jesse, 2001).

2.2. Basic modeling approach

The energy budgets for each habitat and for the whole study area were determined using the ECOPATH II software, which for each trophic group (species considered in this study) uses a set of linear equations (one for each group or specie i in the system) (Christensen and Pauly, 1992a) in order to balance the flows in- and out of the compartment.

The basic equation can be expressed as:

$$\frac{dB_i^*}{dt} = P_i - (B_i \cdot M2_i) - P_i \cdot (1 - EE_i) - EX_i \quad (1)$$

where,

*	= at steady-state (= 0)	
P_i	= the production of i	(g/m ² year ¹)
B_i	= the biomass of i	(g/m ²)
$M2_i$	= the depredation mortality of i	(year ⁻¹)
EE_i	= the ecotrophic efficiency of i	(%)
$1 - EE_i$	= the other mortalities of i	(year ⁻¹)
EX_i	= the export of i	(g/m ² year ¹)

Therefore, the total production by a group or species i is balanced by predation from other groups ($B_i \cdot M2_i$) by non-depredation losses ($P_i \cdot (1 - EE_i)$) and losses to other systems (e.g. sedimentation and fishery). The production can be more conveniently estimated from the production/biomass ratio (P/B) and the average annual biomass (B), which is expressed as ($P_i = B_i \cdot P/B_i$). Predation mortality depends of the activity of the predator and it can be expressed as the sum of consumption by all predators j preying upon specie i i.e.:

$$(B_i \cdot M_i) = B_j \cdot \frac{Q_j}{B_j} \cdot \frac{D_{ji}}{C_{ji}} \quad (2)$$

where,

$\frac{Q_j}{B_j}$ = consumption/biomass ratio of the predator j (year⁻¹), and

$\frac{D_{ji}}{C_{ji}}$ = fraction of the prey i in the average diet of predator j .

Two of the parameters B , P/B and EE must be set initially for each species (or groups), the remaining can be computed by the program. Particularly for some lower-trophic level species, EE is sometimes changed by the program, even though P or P/B are treated initially as unknowns. Q/B of a compartment (or species) can also be calculated by the model (if treated as an unknown) in initial parametrization, if information is available on the amount of prey entering the compartment.

2.3. Selection of model compartments

The selection and definition of the model compartments (populations) was based on the information of direct trophic interactions between the target species and the other important macrofauna species of the system (Stotz and González, 1994; Marahrens, 1995; Jesse, 2001; Ortiz in prep.). All available information of biomass (B) (Ortiz et al. in prep.), catches, turnover rates (P/B), consumption rates (Q/B) and ecological efficiencies (EE) was assembled from own studies and the literature and is summarised in Table 1. Estimates of biomass and productivity for many invertebrate species were obtained during winter 1996 and autumn 1997 by Jesse (2001) and Ortiz et al. (in prep.). The large epifauna compartment includes the large crabs species *Hepatus chilense*, *Platymera gaudichaudi*, *Gaudichaudia gaudichaudia* (Jesse, 2001), the group of small epifauna is comprised of the molluscs *Turritela* spp., *Fissurella* spp. *Chiton* spp. *Nasarius* spp. *Mitrella* spp., *Linucula* spp., and the infauna compartment includes polychaeta and other buried bivalves (León, 2000).

2.4. Determination of food item, construction of diet matrix.

For the sea stars *M. gelatinosus* and *H. helianthus* the identification of food items was assessed *in situ* for each seasonal period from winter 1996 to autumn 1997 (Ortiz in prep.). For the crabs *P. barbiger* and *Taliepus* sp. an identification of stomach contents was conducted during winter and summer of 1996-97 respectively. For the crabs *C. polyodon*, *C. coronatus*, *C. porteri*, and snails *X. cassidiformis* and *Tegula* sp. published information was used (Jara, 1996; León, 2000; Jesse, 2001; Olivares in prep.). The diet matrix for each habitat and total area (Table 2) shows that many benthic groups are considered to feed to a certain extend on the microbial film (bacteria) which is considered as food source for molluscs filter-feeders (Prieur et al., 1990), deposit-feeders (infauna) (Kemp, 1986; Plante et al., 1989; Grossmann and Reichardt, 1991; Plante and Mayer, 1994; Epstein, 1997; Plante and Shriver, 1998), zooplankton (Rieper, 1982; King et al., 1991; Epstein, 1997), and equinodermata (Findlay and White, 1983).

2.5. Balancing the model

The first step was to verify whether the model outputs were realistic, that is, to check if the Ecological Efficiency (EE) was < 1.0 for all compartments. $EE > 1.0$ are inconsistent as not more biomass can be used than produced by a compartment. If inconsistency was detected, the B values (averages) were lightly adjusted within the confidence limits (standard deviation) given by Ortiz et al. (in prep.). P/B values were adjusted for the sea star species. If further inconsistencies were detected, the food matrix was adjusted slightly, due to the fact that the initial values of the diet matrix were considered semi-quantitative data only. As a second step, Gross Efficiency (GE) and R/B values were checked for their consistency by comparing them with the literature data as the missing Q/B , P/B values were calculated by the program (Table 3).

2.6. Assessment of management policies

The effects of the following three management strategies for each habitat were assessed by different runs of the ECOPATH II program: (1) increase of (artificial) biomass or production of scallops *A. purpuratus*, (2) increase of (artificial) biomass or production of the red algae *Ch. chamissoi*; and (3) decrease (artificial removal) of the undesirable predator sea star *M. gelatinosus*. The input data were manipulated by increase and decrease of biomass for commercial and undesirable species respectively. The resulting values calculated by the program on the Ecotrophic Efficiency (*EE*) and Gross Efficiency (*GE*) were registered. Furthermore, the direct and indirect impacts of these management strategies on the communities were evaluated by the Mixed Trophic Impact routine (Ulanowicz and Puccia, 1990). This routine of ECOPATH II allows to estimate the direct and indirect effect on the remainder compartments as response to the impact of a perturbation on a particular population or group of the system.

3. Results and Discussion

3.1. Balancing the model and evaluation of the compartment parameters

The “balanced” models for each habitat and for the whole area are shown in Fig. 2. The boxes are arranged along the y-axis as a function of the estimated trophic level and the box area is proportional to the square root of the biomass. Table 3 summarises the input values for the final run and those values that were calculated by the program. The principal modifications during the balancing procedure were done with the diet matrix for each habitat and the whole area.

The *R/B* values for all compartment estimated by the program are close to the values proposed by Schwinghamer et al. (1986). Likewise the *R/A* estimates for gastropods and bivalves are close to those given in Huebner and Edwards (1981) and Humphreys (1979) respectively. The *GE* values for bivalves and gastropods and for the other benthic compartments calculated by the program lie within the range described by Riisgard and Randløv (1981) and Mann (1982) respectively (Table 3). Despite the smaller scale of the here presented habitat (benthic) models compared to the larger scale model (pelagic and benthic) developed by Wolff (1994), our model estimates of *R/B*, *R/A*, and *GE* were very similar. During the balancing procedure the *Q/B* values for the sea star were changed from 0.6 to 1.2 which are lower than given by Wolff (1994).

3.2. Trophic flow structures and transfer efficiencies

In the seagrass and sand-gravel habitats, seagrass *H. tasmanica* and macroalgae, respectively, represented the most important primary producers in terms of biomass (ca. 61 and 53 % respectively). Whereas the scallop *A. purpuratus* and the infauna were the most relevant animal compartments in terms of biomass (90 and 65 g/m² respectively) and food intake respectively in the seagrass habitat (Fig. 2). In the sand-gravel habitat *Tegula* sp. (snail), *A. purpuratus*, *C. trochiformis* (snail), *P. chilensis* (tunicate) and the infauna were the most prominent compartments (150, 71.54, 70 and 60 g/m² respectively), reaching ~29 % of the total system biomass. In the sand habitat the bivalve *Mulinia* sp. and infauna were the most prominent compartments (55 % of system biomass). In the mud habitat infauna and small epifauna compartments concentrated ca. 53 % of the biomass (Fig. 2). Of the benthic predators, the sea star *M. gelatinosus* and the crab *C. polyodon* played a relevant role in the seagrass (20.5 and 10 g/m² respectively) and in the sand (17.3 and 17.48 g/m² respectively) in comparison to the other predators. In the sand-gravel habitat, *M. gelatinosus*, *P. barbiger* (crab) and *C. polyodon* dominated, reaching 46.76, 25.6 and 29.28 g/m² respectively. By

contrast, in the mud habitat, the crab *C. porteri* was the most prominent predator of the system (23.7 g/m^2) (Fig. 2).

Zooplankton is by far the most important “consumer” in all subsystems and in the combined model (Fig. 2, Table 3). The compartments seagrass, macroalgae, phytoplankton, and zooplankton have the lowest ecotrophic efficiencies, since an important part of their production would be not directly consumed in the systems and enters the detritus pool (Table 3).

Most of the transfer efficiencies estimated in all models ranked within the limits (10-20 %) commonly described in the literature (E.P. Odum, 1971; H.T. Odum, 1971; Barnes and Hughes, 1988; Baird and Ulanowicz, 1989; Wolff, 1994; Monaco and Ulanowicz, 1997; Heymans and Baird, 2000) (Table 4).

3.3. Ecosystem structure

As our models only represent interactions in the benthic domain, a comparisons with models of a larger scale (including pelagic and benthic compartment) is difficult.

System throughput (T) was highest in sand-gravel ($33579.3 \text{ t/km}^2/\text{year}$), followed by the sand, seagrass and mud habitats (Table 5A). Although the sand habitat had the lowest primary production, it ranked second in the total system throughput due to the fact that it accommodates at least two sub-habitats (beaches and deeper systems), and also as it imports large amounts of detritus (Table 2). For the combined model, T was estimated as $20593.9 \text{ t/km}^2/\text{year}$, close to the values reported by Wolff (1994) ($20834.9 \text{ t/km}^2/\text{year}$) for the entire bay ecosystem. The sand habitat had a negative net system production due to the large amount of primary production imported into the system from deeper waters to satisfy the food requirements of the beach clam *Mulinia* sp. (Table 5A). Fig. 3 illustrates that up to 90 % of the throughput (the “power” generated within the system, sensu E.P. Odum, 1971 and H.T. Odum, 1971) is reached from the trophic levels I to II and II to III in each habitat and the combined area. Whereas a comparison with T values of other ecosystem models seems problematic (see above), the fact that the sand-gravel habitat had a higher T estimate than that of the integrated Tongoy Bay model (Wolff, 1994) and that for the Peruvian open upwelling and Benguela systems (Jarre et al., 1991 and Heymans and Baird, 2000) respectively, is surprising at first sight. However, this habitat represents a small and highly heterogeneous systems with enormous biomass of primary producers, filter feeders and predators.

Each of the models possess a lower system omnivory index (OI), ranging from 0.139 to 0.313, when compared to other reported ecosystem models (Monaco and Ulanowicz, 1997). Thus, it appears that the food webs are relatively linear in topology (Table 5B). The mean trophic level of the fishery ranged from 2.06 to 3.92 in our models. The lowest value in the sand-gravel habitat is due to the fact that the fishery concentrates on macroalgae and filter-feeding species, while in the other habitats important resources are crabs and snails which feed higher in the food chain. The highest annual catch in the sand-gravel habitat (122.05 g/m^2) and the highest gross efficiency of the fishery (0.02 %) show the great importance of this habitat for the fishery (Table 5A).

The sand-gravel habitat shows the greatest development Capacity (C) (Table 5B). The Ascendency (A) is a key property of the network that quantifies both the aggregate intensity of process activities and the level of specificity with which processes occur (Ulanowicz, 1986, 1997). A ranked highest the sand-gravel followed by the sand, seagrass and mud habitats (Table 5B). A calculated for the whole system (25092.2 Flowbits) is near to the 26312.6 Flowbits reported by Wolff (1994). The relative Ascendency (A/C), a measure of system organisation and efficiency, is considered to be also an index of the maturity as well

as the systems's ability to withstand perturbations (Ulanowicz, 1986, 1997). A large decrease of the A_i/C_i (internal) ratio in regard to A/C indicates a strong dependency of such a system on a few dominant external connections as was suggested by Baird et al. (1991). Whereas, the A/C values estimated for each habitat were closed (from 27.4 to 32.7 %) to the value reported for the entire Tongoy Bay (32.6 %), the A_i/C_i values, however, were higher. The lower A/C values should suggest that the habitats and the whole system are immature and have a higher resistance against external perturbations, but the sand habitat should be the most resistant and less mature. The large differences between A_i/C_i and A/C of ca. 9 % in regard to 3.8 % reported by Wolff (1994), may be due to the fact that in all models just the benthic populations were considered. Likewise, it is expected that systems with a relatively high A_i/C_i ratio may be more stable with respect to internal perturbations of the food webs (e.g. habitat modifications). Based on the A_i/C_i ratios and pathway redundancy values, the mud and sand-gravel habitats would be the most resistant against perturbations (Table 5B). However, the A/C values should be carefully considered because Ascendency was found negatively correlated with maturity (Christensen, 1994, 1995).

For the ranking of the different model compartments in term of their contribution to overall system structure and function, Ulanowicz (1997) proposed to estimate the relative Ascendency of each group. In all models, phyto-zooplankton concentrated >40 %, followed by detritus (including bacterial film) ~35 %, filter-feeders ~15 %, macroalgae ~10 % and top predators ~0.5 %. This underlines the importance of plankton compartments in comparison with the benthic groups in each habitat and the combined system.

3.4. Assessment of management strategies

The effects of three different management scenarios on EE and GE were assessed. If scallop biomass was increased to ca. 300 g/m² (providing no other changes) flows in the seagrass system would eventually well balance, while that for the predator sea star *M. gelatinosus* a minimum of ~10 g/m² was tolerated by the model. In the sand-gravel habitat, the carrying capacity of the system for the scallop is also ca. 300 g/m² and for the macroalgae ca.1500 g/m², and the minimum tolerable biomass for the sea star was ~10 g/m². These carrying capacities for *A. purpuratus* in both habitats are close to the 360 g/m² registered during the last El Niño event 1997/98 by Stotz et al. (unpubl.). Under these maximum habitat capacities and with the fishery efficiencies maintained constant, the catches of *A. purpuratus* may be increased by ~15 and 37 % in the seagrass and sand-gravel habitat respectively, and by ~30 % for *Ch. chamissoi* in the sand-gravel habitat. No attempts were made to adjust the population's parameters and feeding behaviour of the predators and grazers of the systems as a response to these additions of biomass, because relevant information about adaptive responses was not available.

The Mixed Trophic Impact for the seagrass bed and the sand-gravel habitats are given in Fig. 4a,b. Even though the scallop *A. purpuratus* shows similar positive and negative impacts on the remainder compartment in both habitats, their magnitudes are quite different. An increase in the production of the scallop would cause a negative effect on itself, and a positive on the fisheries and its predators. Only in the seagrass habitat, *M. gelatinosus* would have a negative indirect effect on the fisheries. Hence, sea star removal seems adequate in the seagrass habitat (Fig. 4a). The macroalgae *Ch. chamissoi* showed positive effects upon grazers, fisheries and indirect effects upon carnivorous species. Nevertheless, it also shows negative direct effects on itself and the other macroalgae which may be explained by the intensive competitive relationships (e.g. light and space) as described for other macroalgae species in other Chilean littoral and sublittoral ecosystems (Santelices, 1982, 1991; Santelices and Ojeda, 1984; Vásquez, 1992, 1995). However, an increase in the production of *Ch.*

chamissoi may have larger positive direct effects on the fishery (Fig. 4b). Additional management policies such as an increase of production of *A. purpuratus* and *Ch. chamissoi* may be applied in seagrass and sand-gravel habitats. Finally, the effects of the seagrass *H. tasmanica* on the remaining compartments were also evaluated (Fig. 4a). This species showed weak impacts on the other species and groups, because the seagrass species would offer more structural than trophic functions for benthic species (Frankovich & Fourqurean, 1997; Reusch, 1998; Edgar 1999a,b; Rose et al. 1999, among others).

The current work represent a first attempt to model trophic flows within small benthic habitats of a management area in the SE Pacific upwelling system. While relevant properties of the food web networks for each habitat emerged, facilitating the assessment of some management strategies, further ecological studies should be focused on the following topics: (1) the quantification of the imports and exports of energy or matter especially in seagrass meadows and sand-gravel habitats which support an intensive harvest; (2) the exploration of the main function of the seagrass species: trophic vs. structural; (3) the evaluation of the relative contribution of bacteria and particulate and dissolved organic matter (POM, DOM) as food source of the filter-feeders, among others. We recommend to apply the here presented food web network modelling analysis to aid and assess any fishery strategy in other benthic management areas along the Chilean coast. Further dynamical simulation models should be developed by which predictions about resilience time and maximum sustainable yield under different fishing scenarios with bottom-up, mixed and top-down flow control mechanisms could be achieved.

Acknowledgements

References

- Acuña, E., Moraga, J., Uribe, E., 1989. La zona de Coquimbo: un sistema nerítico de alta productividad. CPPS. Rev. Pacífico Sur, Número especial 145-157.
- Baird, D., Ulanowicz, R., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59(4), 329-364.
- Baird, D., Ulanowicz, R., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Mar. Ecol. Prog. Ser. 99, 221-237.
- Baird, D., Glade, J., Ulanowicz, R., 1991. The comparative ecology of six marine ecosystems. Philos. Trans. R. Soc. Lond. 333, 15-29.
- Barnes, R., Hughes, R., 1988. An introduction to marine ecology. Blackwell Scientific Publications, Oxford (2a Ed.), 351 pp.
- Castilla, JC., 2000. Roles of experimental marine ecology in coastal management and conservation. J. Exp. Mar. Biol. Ecol. 250, 3-21.
- Christensen, V., 1994. On the behaviour of some proposed goal functions for ecosystem development. Ecol. Model. 75/76, 37-49.
- Christensen, V., 1995. Ecosystem maturity –towards quantification. Ecol. Model. 77, 3-32.
- Christensen, V., Pauly, D., 1992a. ECOPATH II. a software for balancing steady-state ecosystems models and calculating network characteristics. Ecol. Model. 61, 169-185.
- Christensen, V., Pauly, D., 1992b. A guide to the ECOPATH II program (version 2.1) ICLARM Software 6. International Center for Living Aquatic Resources Management, Manila, Philippines, 72 pp.

- Christensen, V., Pauly, D., 1993. Flow characteristics of aquatic ecosystems. In: Christensen, V., Pauly, D. (Eds.), Trophic models of aquatic ecosystems. ICLARM Conf. Proc., 26, pp. 338-352.
- Costanza, R., Mageau, M., Norton, B., Patten, B., 1998. Predictors of Ecosystem Health. In: Raport, D., Costanza, R., Epstein, P., Gaudet, C., Levins, R. (Eds.), Ecosystem Health. Blackwell Science, Inc. M.A., pp. 241-250.
- Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P., Ulloa, O., 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. Mar. Ecol. Prog. Ser. 197: 41-49.
- Edgar, G., 1999a. Experimental analysis of structural versus trophic importance of seagrass beds. I. Effects on macrofaunal and meiofaunal invertebrates. Vie et Milieu 49(4), 239-248.
- Edgar, G., 1999b. Experimental analysis of structural versus trophic importance of seagrass beds. II. Effects on fishes, decapods and cephalopods. Vie et Milieu 49(4), 249-260.
- Epstein, S., 1997. Microbial food webs in marine sediments. I. Trophic interactions and grazing rates in two tidal flat communities. Microb. Ecol. 34, 188-198.
- Findlay, R., White, D., 1983. The effects of feeding by the sand dollar *Mellita quinquesperforata* (Leske) on the benthic microbial community. J. Exp. Mar. Biol. Ecol. 72, 25-41.
- Frankovich, T., Fourqurean, W., 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. Mar. Ecol. Prog. Ser. 159, 37-50.
- Gaedke, U., 1995. A comparison of whole-community and ecosystem approaches (biomass size distributions, food web analysis, network analysis, simulation models) to study the structure, function and regulation of pelagic food webs. J. Plankton Res. 6, 1273-1305.
- Grossmann, S., Reichardt, W., 1991. Impact of *Arenicola marina* on bacteria in intertidal sediments. Mar. Ecol. Prog. Ser. 77, 85-93.
- Hall, S., Raffaelli, D., 1994. Food Webs: theory and reality. Advances in Ecol. Res. 24: 187-239.
- Heymans, J., Baird, D., 2000. A carbon flow model and network analysis of the northern Benguela upwelling system, Namibia. Ecol. Modelling 126, 9-32.
- Hibbert, C., 1977. Energy relations of the bivalve *Mercenaria mercenaria* on an intertidal mudflat. Mar. Biol. 44, 77-84.
- Hilborn, R., Walters, C., Ludwig, D., 1995. Sustainable exploitation of renewable resources. Annu. Rev. Ecol. Syst. 26, 45-67.
- Huebner, J., Edwards, D., 1981. Energy budget of the predatory gastropod *Polinices duplicatus*. Mar. Biol. 61, 221-226.
- Humphreys, W., 1979. Production and respiration in animal population. J. Anim. Ecol. 48, 427-453.
- Jara, F., 1996. *Xanthochorus cassidiformis* (Gastropoda, Muricidea): a key predator in soft bottom communities from southern Chile. Proc. of the 4th ICMAM, J. Med. & Appl. Malacol. 8(1), 85.

- Jarre, A., Muck, P., Pauly, D., 1991. Two approaches for modelling fish stock interactions in the Peruvian Upwelling Ecosystem. ICES. Mar. Sci. Symp. 193, 171-184.
- Jarre-Teichmann, A., Christensen, V., 1998. Comparative modelling of trophic flows in four large upwelling ecosystems: global versus local effects. In: Durand, M.H., Cury, P., Mendelssohn, R., Roy, C., Bakun, A., Pauly, D. (Eds.), Global Versus Local Changes in Upwelling Systems. ORSTOM Editions, Paris, pp. 425-443.
- Jesse, S. 2001. Comparative ecology of sympatric brachyuran crab species in the shallow subtidal of the pacific coast of north Chile and their importance for the artisanal fishery in Puerto Aldea. PhD Dissertation, University of Bremen, Germany, 125 pp.
- Kemp, P., 1986. Direct uptake of detrital carbon by the deposit-feeding polychaeta *Euzonus mucronata* (Treadwell). J. Exp. Mar. Biol. Ecol., 99, 49-61.
- King, H., Sanders, R., Shotts, E., Porter, K., 1991. Differential survival of bacteria ingested by zooplankton from a stratified eutrophic lake. Limnol. Oceanogr. 36(5), 829-845.
- Larkin, P., 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106(1), 1-11.
- Lawton, J., 1994. What do species do in ecosystems? Oikos, 71, 367-374.
- León, R., 2000. Relaciones tróficas del *Cancer polyodon* (Poepping 1836). Tesis para obtener el título de Biólogo Marino, Universidad Católica del Norte, sede Coquimbo, Chile.
- Levins, R., 1998. The internal and external explanatory theories. Science as Culture 7(4), 557-582.
- Levins, R., Lewontin, R., 1980. Dialectics and reductionism in ecology. Synthese 43, 47-78.
- Levins, R., Wilson, M., 1980. Ecological theory and pest management. Ann. Rev. Entomol. 25, 287-308.
- Mann, K., 1982. Ecology of coastal waters. Studies in ecology 8, 322.
- Marahrens, M., 1995. Räuberbedingte sterblichkeit der kammuschel *Argopecten purpuratus* (L.) in der Bucht von Tongoy, Chile. Diplomarbeit. Mathematische-Naturwissenschaftliche Fakultät der Christian-Albrechts-Universität zu Kiel, 109 pp.
- May, R.T., 1974. Stability and complexity in model ecosystems. 2nd Edition. Monographs in Population Biology N° 6, Princeton University Press, N.J.
- Monaco, M., Ulanowicz, R., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. Mar. Ecol. Prog. Ser. 161, 239-254.
- Montecinos, V. Quiroz, D., 2000. Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30°). Aquat. Sci. 63, 364-380.
- Morioka, Y., Kitajima, Ch., Havashida, G., 1988. Oxygen consumption, growth, and calculated food requirement of the swimming crab *Portunus trituberculatus* in its early developmental stage. Bull. Japan. Soc. Sci. Fish. 54(7), 1137-1141.
- Niquil, N., Arias-González, J., Delesalle, B., Ulanowicz, R., 1999. Characterization of the planctonic food web of Takapoto Atoll lagoon, using network analysis. Oecologia 118, 232-241.

- Odum, E.P., 1971. Fundamentals of ecology. W. B. Saunders, Philadelphia, 574 pp.
- Odum, H.T. 1971. Environment, Power, and Society. John Wiley and Sons., N.Y. 331 pp.
- Paine, R., 1971. Energy flow in a natural population of the herbivorous gastropod *Tegula funebris*. Limnol. Oceanogr. 16, 86-98.
- Paine, R., 1980. Food webs: linkage, interaction strength and community infrastructure. The third Tansley Lecture. J. Animal Ecol. 49, 667-685.
- Paine, R., 1984. Some approaches to modelling multispecies systems. In: May, R. (Ed.), Exploitation of marine communities. Dahlem Konferenzen, Springer-Verlag, Berlin, pp. 191-207.
- Patten, B., 1997. Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. Ecol. Model. 100, 11-42.
- Plante, C., Mayer, L., 1994. Distribution and efficiency of bacteriolysis in the gut of *Arenicola marina* and three additional deposit feeders. Mar. Ecol. Prog. Ser. 109, 183-194.
- Plante, C., Shriver, A., 1998. Patterns of differential digestion of bacteria in deposit feeders: a test of resource partitioning. Mar. Ecol. Prog. Ser. 163, 253-258.
- Plante, C., Jumars, P., Baross, J., 1989. Rapid bacterial growth in the hindgut of a marine deposit feeder. Microb. Ecol. 18, 29-44.
- Polovina, J., 1984. Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3, 1-11.
- Prieur, D., Mével, G., Nicolas, J., Plusquellec, A., Vigneulle, M., 1990. Interactions between bivalve molluscs and bacteria in the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 28, 277-352.
- Reusch, Th., 1998. Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. Mar. Ecol. Prog. Ser. 167, 149-153.
- Rieper, M., 1982. Feeding preferences of marine harpacticoid copepods for various species of bacteria. Mar. Ecol. Prog. Ser. 7, 303-307.
- Riisgard, C., Randløv, A., 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar. Biol. 61, 227-234.
- Roberts, C., 1997. Ecological advice for the global fisheries crisis. TREE 12, 35-38.
- Rocha, G., Gasalla, M., Rossi-Wongtschowski, C., Soares, L., Pires-Vanin, A., Muto, E., Cergole, M., Aidar, E., Mesquita, H., Giancesella-Galvao, S., Vega-Pérez, L., Jarre-Teichmann, A., 1998. Quantitative model of trophic interactions in the Ubatuba Shelf System (Southeastern Brazil). Fishbyte, October-November, 25-32.
- Rose, C., Sharp, W., Kenworthy, W., Hunt, J., Lyons, W., Prager, E., Valentine, J., Hall, M., Whitfield, P., Fourqurean, J. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Mar. Ecol. Prog. Ser. 190, 211-222.
- Santelices, B., 1982. Bases biológicas para el manejo de *Lessonia nigrescens* en Chile central. Monografías Biológicas (Chile) 2, 135-150.

- Santelices, B., 1991. Littoral and sublittoral communities of continental Chile. In: Goodhall, D. (Ed.), Ecosystems of the world. Intertidal and Littoral Ecosystems. pp. 347-369.
- Santelices, B., Ojeda, P., 1984. Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. Mar. Ecol. Prog. Ser. 19, 73-82.
- Schwinghamer, P., Hargrave, B., Peer, D., Hawkins, C., 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar. Ecol. Prog. Ser. 31, 131-142.
- Stotz, W., González, S., 1994. Biodiversidad y pesca artesanal: Manejo experimental de recursos marinos bentónicos en la costa del centro-norte de Chile. Informe Final de Proyecto, Depto. de Biología Marina, Universidad Católica del Norte, Coquimbo, Chile.
- Stotz, W., González, S., 1997. Abundance, growth, and production of the sea scallop *Argopecten purpuratus* (Lamarck, 1819): bases for sustainable exploitation of natural scallop beds in north-central Chile. Fisheries Research 32, 173-183.
- Ulanowicz, R., 1986. Growth and development: Ecosystems phenomenology. Springer, N.Y., 203 pp.
- Ulanowicz, R., 1997. Ecology, the Ascendent Perspective. Complexity in Ecological Systems Series. Columbia University Press, N.Y., 201 pp.
- Ulanowicz, R., Puccia, Ch., 1990. Mixed trophic impacts in ecosystems. Ceonoses 5, 7-16.
- Ulanowicz, R., Wulff, F., 1991. Comparing ecosystem structures: the Chesapeake Bay and the Balthic Sea. In: Cole, J., Lovett, G., Findlay, S. (Eds.), Comparative Analysis of ecosystems, pattern, mechanism, and theories. Springer-Verlag, N.Y., pp. 140-166.
- Ulanowicz, R., Mann, K., 1981. Ecosystems under stress. In: Platt, K., Mann, K., Ulanowicz, R.(Eds.), Mathematical models in biological oceanography, The UNESCO Press, Paris, pp. 133-137.
- Vásquez, J., 1992. *Lessonia trabeculata*, a subtidal bottom kelp in northern Chile: a case study for structural and geographical comparison. In: Seeliger, U. (Ed.), Coastal Plant Communities of Latin America, Acad. Press, San Diego, pp. 77-89.
- Vásquez, J., 1995. Ecological effects of brown seaweed harvesting. Bot. Mar. 38, 251-257.
- Walters, C., Hilborn, R., 1978. Ecological optimization and adaptive management. Ann. Rev. Ecol. Syst. 9, 157: 188.
- Walters, C., Korman, J., 1999. Cross-scale modelling of riparian ecosystem responses to hydrologic management. Ecosystems 2, 411-421
- Walters, C., Pauly, D., Christensen, W., 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2, 539-554.
- Wolff, M., 1994. A trophic model for Tongoy Bay –a system exposed to suspended scallop culture (Northern Chile). J. Exp. Mar. Biol. Ecol. 182, 149-168.
- Wolff, M., Hartmann, H., Koch, V., 1996. A trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. Revista de Biología Tropical 44(3), 215-231.

Wolff, M., Koch, V., Chavarria, J., Vargas, J., 1998. A trophic flow model of the Golfo de Nicoya, Costa Rica. *Revista de Biología Tropical* 46(6), 63-79.

Wolff, M., Koch, V., Isaac, V., 2000. A trophic flow model of the Caeté mangrove estuary (North Brazil) with considerations for the sustainable use of its resources. *Estuarine, Coastal and Shelf Science* 50, 789-803.

List of Tables and Figures

Table 1. Benthic model compartment, populations and groups, and parameter values (Literature sources are also given). B = biomass (g wet weight/m²); C = catch; P/B = turnover ratio; Q/B = annual food consumption; UAF = unassimilated food.

Table 2. Prey-predator and plan-grazer matrix used for the ECOPATH II program. A. Seagrass beds habitat, B. Sand-gravel habitat, C. Sand habitat, D. Mud habitat, and E. combined benthic area.

Table 3. Parameter values entered (in bold) and estimated (standard) by ECOPATH II software. Explanation of symbols : B, P/B, Q/B, EE, and GE see Material and Methods section; FI = food intake; NE = net efficiency; R = respiration. A. Seagrass beds habitat, B. Sand-gravel habitat, C. Sand habitat, D. Mud habitat, and E. Combined benthic area.

Table 4. Transfer efficiencies for each level per habitat and whole benthic area.

Table 5 . A. Summary statistics after mass-balance process by ECOPATH II. B. Network flow indices. For more details and explanation see text and Christensen and Pauly (1992a).

Fig. 1. a) Main littoral types along the Chilean coast: 1.= dominated by exposed compact rocky shores, 2.= dominated by exposed sandy shores; 3.= mostly insular systems; b) The principal bay systems of the IV Region of Coquimbo (Chile); c) Study area of Puerto Aldea located at southern of Tongoy Bay.

Fig. 2. Trophic models for habitats and whole benthic system. The box size is proportional to the square root of the compartment (populations and groups) biomass. Biomass, (P/B) and (Q) are given. Seagrass beds habitat, Sand-gravel habitat, Sand habitat, Mud habitat, and combined benthic system.

Fig. 3. Lindeman pyramid of flows in each habitat and whole benthic system. The area of each discrete trophic level (indicated by roman numerals) is proportional to the throughput (total flow) at each level. The bottom compartment represents herbivore.

Fig. 4. Mixed trophic impacts (direct and indirect) as response to an increasing of *A. purpuratus* and *Ch. chamissoi*, and a decreasing of *M. gelatinosus*. a.) Seagrass habitat, and b.) Sand-gravel habitat.

Table 1. Benthic model compartment, populations and groups, and parameter values (Literature sources are also given). B = biomass (g wet weight/m²); C = catch; P/B = turnover ratio; Q/B = annual food consumption; UAF = unassimilated food.

Species / Groups	B ¹	C ²	P/B ³	Q/B ⁴	UAF ⁵	Literatura source
(1) <i>Meyenaster gelatinosus</i> (Whole area)	21.6	-	1.2	-	0.2	^{1,3} Ortiz et al. in prep.; ⁵ Christensen & Pauly (1992b).
Seagrass bed	20.5					
Sand-gravel	46.76					
Sand	17.3					
Mud	1.08					
(2) <i>Heliaster helianthus</i> (Whole area)	1.1	-	0.6	-	0.2	^{1,3} Ortiz et al. in prep.; ⁵ Christensen & Pauly (1992b).
Seagrass bed	0.5					
Sand-gravel	0.43					
(3) <i>Luidia magallanica</i> (Whole area)	1.3	-	0.7	-	0.2	^{1,3} Ortiz et al. in prep.; ⁵ Christensen & Pauly (1992b).
Seagrass bed	0.6					
Sand-gravel	2.98					
Sand	0.61					
Mud	0.58					
(4) <i>Cancer polyodon</i> (Whole area)	10.0	0.4	1.1	9.5	0.2	¹ Ortiz et al. in prep.; ² Ortiz in prep.; ³ Jesse, 2001; ⁴ Wolff (1994); ⁵ Morioka et al. (1988).
Seagrass bed	10.0					
Sand-gravel	25.6					
Sand	17.48					
Mud	7.35					
(5) <i>Cancer porteri</i> (Whole area)	3.5	-	0.5	4.5	0.2	¹ Ortiz et al. in prep.; ^{3,4} Jesse, 2001; ⁵ Morioka et al. (1988).
Mud	23.7					
(6) <i>Cancer coronatus</i> (Whole area)	2.5	-	1.8	9.5	0.2	¹ Ortiz et al. in prep.; ^{3,4} Jesse, 2001; ⁵ Morioka et al. (1988).
Sand	6.35					
Mud	6.35					
(7) <i>Paraxanthus barbiger</i> (Whole area)	4.0	-	1.95	9.9	0.2	¹ Ortiz et al. in prep.; ^{3,4} Jesse, 2001; ⁵ Morioka et al. (1988).
Seagrass bed	1.6					
Sand-gravel	29.28					
(8) Large Epifauna (Whole area)	5.5	-	1.25	9.5	0.2	¹ Ortiz et al. in prep.; ³ Jesse, 2001; ⁴ Wolff (1994); ⁵ Morioka et al. (1988).
Seagrass bed	2.2					
Sand-gravel	6.54					
Sand	6.0					
Mud	15.0					
(9) <i>Xanthochorus cassidiformis</i> (Whole area)	2.28	0.6	1.5	9.5	0.25	¹ Ortiz et al. in prep.; ² Ortiz in prep.; ³ Stotz unpubl.; ⁵ Huebner & Edwards (1981).
Sand	9.74					
(10) <i>Argopecten purpuratus</i> (Whole area)	55.0	16	2.08	5.5	0.3	¹ Ortiz et al. in prep.; ² Ortiz in prep.; ³ Stotz & González (1997); ⁴ Wolff (1994); ⁵ Hibbert (1977).
Seagrass bed	90.0					
Sand-gravel	71.54					
Sand	40.0					
Mud	4.0					
(11) <i>Taliepus</i> sp. (Whole area)	0.65	-	1.5	9.5	0.2	¹ Ortiz et al. in prep.; ^{3,4} Jesse, 2001; ⁵ Morioka et al. (1988).
Seagrass bed	1.3					
Sand-gravel	1.7					

(12) <i>Mulinia</i> sp. (Whole area) Sand	24.0 150.0	-	1.2	9.9	0.3	¹ Ortiz et al. in prep.; ² Stotz unpubl.; ⁴ Wolff (1994); ⁵ Hibbert (1977).
(13) <i>Calyptrea trochiformis</i> (Whole area) Sand-gravel	37.0 90.0	-	0.8	9.9	0.3	¹ Ortiz et al. in prep.; ² Stotz unpubl.; ⁴ Wolff (1994); ⁵ Hibbert (1977).
(14) <i>Tegula</i> sp. (Whole area) Sand-gravel	38.0 150.0	-	2.2	9.9	0.3	¹ Ortiz et al. in prep.; ² Stotz unpubl.; ⁴ Wolff (1994); ⁵ Paine (1971).
(15) <i>Pyura chilensis</i> (Whole area) Sand-gravel	20.0 70.0	-	3.2	11	0.3	¹ Ortiz et al. in prep.; ² Stotz unpubl.; ⁴ Wolff (1994); ⁵ Christensen & Pauly (1992b).
(16) Small Epifauna (Whole area) Seagrass bed Sand-gravel Sand Mud	18.0 29.5 20.0 43.0 21.0	-	3.7	12.5	0.25	¹ León (2000); ³ Ortiz et al. in prep.; ^{4,5} Wolff (1994).
(17) Infauna (Whole area) Seagrass bed Sand-gravel Sand Mud	60.0 65.0 60.0 104.5 96.0	-	4.4	14.5	0.3	¹ León (2000); ³ Ortiz et al. in prep.; ^{4,5} Wolff (1994).
(18) <i>Heterozostera tasmanica</i> (Whole area) Seagrass bed	110.0 450.0	-	-	-	0.2	¹ Ortiz et al. in prep.; ⁴ Christensen & Pauly (1992b)
(19) <i>Chondrocanthis chamissoi</i> (Whole area) Seagrass bed Sand-gravel Sand	78.6 5.5 564.8 3.0	11 4	-	-	0.2	¹ Ortiz et al. in prep.; ² Ortiz in prep.; ⁵ Christensen & Pauly (1992b).
(20) Rodophyta (Whole area) Seagrass bed Sand-gravel Sand	110.0 6.0 230.0 6.0	-	-	-	0.2	¹ Ortiz et al. in prep.; ⁵ Christensen & Pauly (1992b).
(21) <i>Ulva</i> sp. (Whole area) Seagrass bed Sand-gravel Sand	50.0 5.0 70.0 3.0	-	-	-	0.2	¹ Ortiz et al. in prep.; ⁵ Christensen & Pauly (1992b).
(22) Zooplankton (Whole area and habitats)	18	-	40	160	0.2	^{1,3,4} Wolff (1994); ⁵ Christensen & Pauly (1992b).
(23) Phytoplankton (Whole area and habitats)	28	-	250	-	0.2	^{1,3,4} Wolff (1994); ⁵ Christensen & Pauly (1992b).

Table 2. Prey-predator and plan-grazer matrix used for the ECOPATH II program. A. Seagrass beds habitat, B. Sand-gravel habitat, C. Sand habitat, D. Mud habitat, and E. combined benthic area.

Prey/Predator matrix

A. Seagrass Habitat

Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
(1) <i>M.gelatinosus</i>	0.02	0.03													
(2) <i>H.helianthus</i>	0.001	0.001													
(3) <i>L.magallanica</i>	0.001														
(4) <i>C.polyodon</i>				0.1											
(5) <i>P.barbiger</i>				0.03	0.01										
(6) <i>Taliepus</i> sp.				0.02											
(7) Large Epifauna				0.02	0.02		0.02								
(8) <i>A.purpuratus</i>	0.708	0.459		0.54	0.45		0.57								
(9) Small Epifauna	0.26	0.5		0.23	0.38	0.52	0.2		0.1						
(10) Infauna			0.9	0.05	0.05		0.2			0.5	0.05				
(11) <i>H.tasmanica</i>					0.05	0.3			0.15						
(12) <i>Ch.chamissoi</i>					0.01	0.06			0.02						
(13) Rodophyta					0.01	0.06			0.02						
(14) <i>Ulva</i> sp.					0.01	0.06			0.02						
(15) Zooplankton									0.05	0.15					
(16) Phytoplankton								0.85	0.05	0.15					0.95
(17) Bacteria	0.01	0.01	0.1	0.01	0.01		0.01	0.15	0.09	0.65					0.05

B. Sand-gravel Habitat

Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
(1) <i>M.gelatinosus</i>	0.02	0.02															
(2) <i>H.helianthus</i>	0.002	0.005															
(3) <i>L.magallanica</i>	0.01																
(4) <i>C.polyodon</i>				0.08													
(5) <i>P.barbiger</i>				0.08	0.1												
(6) <i>Taliepus</i> sp.				0.01													
(7) Large Epifauna				0.02	0.02		0.08										
(8) <i>A.purpuratus</i>	0.25	0.1		0.12	0.08		0.12										
(9) <i>C.trochiformis</i>	0.28	0.3															
(10) <i>Tegula</i> sp.	0.29	0.3		0.32	0.29		0.34										
(11) <i>P.chilensis</i>	0.11	0.23		0.15	0.17		0.15					0.08					
(12) Small Epifauna	0.02	0.02		0.05	0.05	0.05	0.06			0.02		0.01					
(13) Infauna			0.9	0.14	0.05		0.22					0.5	0.05				
(14) <i>Ch.chamissoi</i>					0.15	0.55				0.48		0.06					
(15) Rodophyta					0.04	0.35				0.3		0.03					
(16) <i>Ulva</i> sp.					0.03	0.05				0.05		0.04					
(17) Zooplankton											0.4	0.05	0.1				
(18) Phytoplankton								0.85	0.85		0.5	0.05	0.1				0.95
(19) Bacteria	0.02	0.02	0.1	0.03	0.02		0.03	0.15	0.15	0.15	0.1	0.18	0.75				0.05

Table 2 continuation

C. Sand Habitat														
Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14
(1) <i>M.gelatinosus</i>	0.03													
(2) <i>L.magallanica</i>	0.001													
(3) <i>C.polyodon</i>			0.11											
(4) <i>C.coronatus</i>			0.05	0.04										
(5) Large Epifauna			0.03		0.04									
(6) <i>X.cassidiformis</i>			0.05	0.04	0.05									
(7) <i>A.purpuratus</i>	0.349		0.15	0.1	0.1									
(8) <i>Mulinia</i> sp.			0.27	0.45	0.43	0.68								
(9) Small Epifauna	0.57		0.28	0.19	0.31	0.09			0.02					
(10) Infauna		0.9	0.01	0.1	0.02	0.18			0.64	0.05				
(11) <i>Ch.chamissoi</i>									0.01					
(12) Rodophyta									0.015					
(13) <i>Ulva</i> sp.									0.01					
(14) Zooplankton									0.05	0.15				
(15) Phytoplankton							0.85	0.85	0.05	0.15				0.95
(16) Bacteria	0.05	0.1	0.05	0.08	0.05	0.05	0.15	0.15	0.2	0.65				0.05

D. Mud Habitat										
Prey/Predator	1	2	3	4	5	6	7	8	9	10
(1) <i>M.gelatinosus</i>	0.02									
(2) <i>L.magallanica</i>	0.01									
(3) <i>C.polyodon</i>			0.1							
(4) <i>C.porteri</i>				0.1						
(5) <i>C.coronatus</i>			0.05		0.12					
(6) Large Epifauna			0.05			0.1				
(7) <i>A.purpuratus</i>	0.1		0.02		0.01	0.03				
(8) Small Epifauna	0.56		0.15	0.1	0.2	0.25		0.02		
(9) Infauna		0.9	0.3	0.5	0.48	0.45		0.65	0.05	
(10) Zooplankton			0.33					0.05	0.15	
(11) Phytoplankton							0.85	0.05	0.15	0.95
(12) Bacteria	0.31	0.1		0.3	0.19	0.17	0.15	0.23	0.65	0.05

Table 2 continuation

E. Total Area																						
Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
(1) <i>M.gelatinosus</i>	0.03	0.02																				
(2) <i>H.helianthus</i>	0.001	0.001																				
(3) <i>L.magallanica</i>	0.001																					
(4) <i>X.cassidiformis</i>					0.001		0.01		0.05													
(5) <i>C.polyodon</i>					0.1																	
(6) <i>C.porteri</i>						0.1																
(7) <i>C.coronatus</i>					0.02		0.1															
(8) <i>P.barbiger</i>					0.05			0.04														
(9) Large Epifauna					0.01				0.1													
(10) <i>A.purpuratus</i>	0.44	0.14			0.14		0.05	0.15	0.12													
(11) <i>Talipeus</i> sp.					0.01																	
(12) <i>Mulinia</i> sp.				0.49	0.09		0.08		0.1													
(13) <i>C.trochiformis</i>	0.2	0.2																				
(14) <i>Tegula</i> sp.	0.16	0.31			0.25			0.25	0.05													
(15) <i>P.chilensis</i>	0.089	0.239			0.09			0.09	0.02								0.08					
(16) mall Epifauna	0.069	0.08		0.09	0.079	0.07	0.189	0.12	0.25		0.1			0.02		0.02						
(17) Infauna			0.9	0.39	0.15	0.78	0.52	0.05	0.3								0.5	0.05				
(18) <i>H.tasmanica</i>								0.05			0.1			0.15		0.02						
(19) <i>Ch.chamissoi</i>								0.06			0.15			0.15		0.03						
(20) Rodophyta								0.04			0.35			0.45		0.04						
(21) <i>Ulva</i> sp.								0.13			0.3			0.2		0.03						
(22) Zooplankton																0.4	0.05	0.15				
(23) Phytoplankton										0.85		0.85	0.85			0.5	0.05	0.15				0.95
(24) Bacteria	0.01	0.01	0.1	0.03	0.01	0.05	0.05	0.02	0.01	0.15		0.15	0.15	0.03	0.1	0.18	0.65					0.05

Table 3. Parameter values entered (in bold) and estimated (standard) by ECOPATH II software. Explanation of symbols : B, P/B, Q/B, EE, and GE see Material and Methods section; FI = food intake; NE = net efficiency; R = respiration. A. Seagrass beds habitat, B. Sand-gravel habitat, C. Sand habitat, D. Mud habitat, and E. Combined benthic area.

Parameter entered and calculated by ECOPATH II

A. Seagrass Habitat

Species	C	B	P/B	Q/B	EE	GE	FI	NE	R/A	P/R	R/B
(1) <i>M.gelatinosus</i>	-	20.5	1.2	5	0.143	0.24	102.5	0.3	0.7	0.429	2.8
(2) <i>H.helianthus</i>	-	0.5	0.6	2.3	0.362	0.261	1.15	0.326	0.674	0.484	1.24
(3) <i>L.magallanica</i>	-	0.6	0.7	3	0.258	0.233	1.8	0.292	0.708	0.412	1.7
(4) <i>C.polyodon</i>	0.15	10	1.1	9.5	0.905	0.116	95	0.145	0.855	0.169	6.5
(5) <i>P.barbiger</i>	-	1.6	1.95	9.9	0.98	0.197	15.84	0.263	0.737	0.356	5.47
(6) <i>Taliepus</i> sp.	-	1.3	1.5	9.5	0.99	0.158	12.35	0.211	0.789	0.267	5.625
(7) Large Epifauna	-	2.2	1.25	9.5	0.973	0.132	20.9	0.164	0.836	0.197	6.35
(8) <i>A.purpuratus</i>	7.5	90	2.08	9.9	0.84	0.21	891	0.3	0.7	0.429	4.85
(9) Small Epifauna	-	29.5	3.7	12.5	0.944	0.296	368.75	0.395	0.605	0.652	5.675
(10) Infauna	-	65	4.4	14.7	0.857	0.299	955.5	0.428	0.572	0.747	5.89
(11) <i>H.tasmanica</i>	-	450	1.5	-	0.177	-	-	-	-	-	-
(12) <i>Ch.chamissoi</i>	0.01	5.5	6	-	0.269	-	-	-	-	-	-
(13) Rodophyta	-	6	5.5	-	0.269	-	-	-	-	-	-
(14) <i>Ulva</i> sp.	-	5	6	-	0.296	-	-	-	-	-	-
(15) Zooplankton	-	18	40	160	0.572	0.25	2880	0.313	0.688	0.455	88
(16) Phytoplankton	-	28	250	-	0.525	-	-	-	-	-	-
(17) Bacteria	-	-	-	-	0.166	-	-	-	-	-	-

B. Sand-gravel Habitat

Species	C	B	P/B	Q/B	EE	GE	FI	NE	R/A	P/R	R/B
(1) <i>M.gelatinosus</i>	-	46.76	1.2	5	0.145	0.24	233.8	0.3	0.7	0.429	2.8
(2) <i>H.helianthus</i>	-	0.43	0.6	2.3	0.187	0.261	0.99	0.326	0.674	0.484	1.24
(3) <i>L.magallanica</i>	-	2.98	0.7	3	0.122	0.233	8.94	0.292	0.708	0.412	1.7
(4) <i>C.polyodon</i>	0.15	25.6	1.1	9.5	0.977	0.116	243.2	0.145	0.855	0.169	6.5
(5) <i>P.barbiger</i>	-	29.28	1.95	9.9	0.868	0.197	289.87	0.263	0.737	0.356	5.475
(6) <i>Taliepus</i> sp.	-	1.7	1.5	9.5	0.969	0.158	16.15	0.211	0.789	0.267	5.625
(7) Large Epifauna	-	6.54	1.25	9.5	0.925	0.132	62.13	0.164	0.836	0.197	6.35
(8) <i>A.purpuratus</i>	7.5	71.54	2.08	9.9	0.841	0.21	708.25	0.3	0.7	0.429	4.85
(9) <i>C.trochiformis</i>	-	90	0.8	9.9	0.913	0.081	891	0.115	0.885	0.131	6.13
(10) <i>Tegula</i> sp.	-	150	2.2	9.9	0.934	0.222	1485	0.317	0.683	0.465	4.73
(11) <i>P.chilensis</i>	-	70	3.2	11	0.841	0.291	770	0.416	0.584	0.711	4.5
(12) Small Epifauna	-	20	3.7	12.5	0.971	0.296	250	0.395	0.605	0.652	5.675
(13) Infauna	-	60	4.4	14.7	0.924	0.299	882	0.428	0.572	0.747	5.89
(14) <i>Ch.chamissoi</i>	113.9	564.8	6	-	0.276	-	-	-	-	-	-
(15) Rodophyta	-	230	5.5	-	0.38	-	-	-	-	-	-
(16) <i>Ulva</i> sp.	-	70	6	-	0.227	-	-	-	-	-	-
(17) Zooplankton	-	19	40	160	0.54	0.25	3040	0.313	0.688	0.455	88
(18) Phytoplankton	-	36	250	-	0.526	-	-	-	-	-	-
(19) Bacteria	-	-	-	-	0.134	-	-	-	-	-	-

Table 3 continuation

C. Sand Habitat

Species	C	B	P/B	Q/B	EE	GE	FI	NE	R/A	P/R	R/B
(1) <i>M.gelatinosus</i>	-	17.3	1.2	5	0.145	0.24	86.5	0.3	0.7	0.429	2.8
(2) <i>L.magallanica</i>	-	0.61	0.6	2.3	0.245	0.261	1.4	0.326	0.674	0.484	1.24
(3) <i>C.polyodon</i>	0.05	17.48	1.1	9.5	0.972	0.116	166.06	0.145	0.855	0.169	6.5
(4) <i>C.coronatus</i>	-	6.35	1.8	9.5	0.958	0.189	60.33	0.237	0.763	0.31	5.8
(5) Large Epifauna	-	6	1.25	9.5	0.985	0.132	57	0.164	0.836	0.197	6.35
(6) <i>X.cassidiformis</i>	0.6	9.74	1.5	5.5	0.989	0.273	53.57	0.364	0.636	0.571	2.625
(7) <i>A.purpuratus</i>	0.99	40	2.08	9.9	0.849	0.21	396	0.3	0.7	0.429	4.85
(8) <i>Mulinia</i> sp.	-	150	1.2	9.9	0.854	0.121	1485	0.173	0.827	0.209	5.73
(9) Small Epifauna	-	43	3.7	12.5	0.914	0.296	537.5	0.395	0.605	0.652	5.675
(10) Infauna	-	104.5	4.4	14.7	0.99	0.299	1536.2	0.428	0.572	0.747	5.89
(11) <i>Ch.chamissoi</i>	-	3	6	-	0.299	-	-	-	-	-	-
(12) Rodophyta	-	6	5.5	-	0.244	-	-	-	-	-	-
(13) <i>Ulva</i> sp.	-	3	6	-	0.299	-	-	-	-	-	-
(14) Zooplankton	-	18	40	160	0.58	0.25	2880	0.313	0.688	0.455	88
(15) Phytoplankton	-	34	250	-	0.558	-	-	-	-	-	-
(16) Bacteria	-	-	-	-	0.259	-	-	-	-	-	-

D. Mud Habitat

Species	C	B	P/B	Q/B	EE	GE	FI	NE	R/A	P/R	R/B
(1) <i>M.gelatinosus</i>	-	1.08	1.2	5	0.083	0.24	5.4	0.3	0.7	0.429	2.8
(2) <i>L.magallanica</i>	-	0.58	0.7	2.3	0.133	0.304	1.33	0.38	0.62	0.614	1.14
(3) <i>C.polyodon</i>	0.05	7.35	1.1	9.5	0.888	0.116	69.82	0.145	0.855	0.169	6.5
(4) <i>C.porteri</i>	-	23.7	0.5	4.5	0.92	0.111	106.65	0.139	0.861	0.161	3.1
(5) <i>C.coronatus</i>	-	6.35	1.8	9.5	0.95	0.189	60.33	0.237	0.763	0.31	5.8
(6) Large Epifauna	-	15	1.25	9.5	0.955	0.132	142.5	0.164	0.836	0.197	6.35
(7) <i>A.purpuratus</i>	0.01	4	2.08	9.9	0.85	0.21	39.6	0.3	0.7	0.429	4.85
(8) Small Epifauna	-	21	3.7	12.5	0.999	0.296	262.5	0.395	0.605	0.652	5.675
(9) Infauna	-	96	4.4	14.7	0.974	0.299	1411.2	0.428	0.572	0.747	5.89
(10) Zooplankton	-	18	40	160	0.534	0.25	2880	0.313	0.688	0.455	88
(11) Phytoplankton	-	28	250	-	0.433	-	-	-	-	-	-
(12) Bacteria	-	-	-	-	0.223	-	-	-	-	-	-

Table 3 continuation

E. Whole Area											
Species	C	B	P/B	Q/B	EE	GE	FI	NE	R/A	P/R	R/B
(1) <i>M.gelatinosus</i>	-	21.6	1.2	5	0.146	0.24	108	0.3	0.7	0.429	2.8
(2) <i>H.helianthus</i>	-	1.1	0.6	2.3	0.169	0.261	2.53	0.326	0.67	0.484	1.24
(3) <i>L.magallanica</i>	-	1.3	0.7	3	0.12	0.233	3.9	0.292	0.708	0.412	1.7
(4) <i>C.polyodon</i>	0.4	10	1.1	9.5	0.92	0.116	95	0.145	0.855	0.169	6.5
(5) <i>C.porteri</i>	-	3.5	0.5	4.5	0.906	0.111	15.75	0.139	0.861	0.161	3.1
(6) <i>C.coronatus</i>	-	2.5	1.8	9.5	0.959	0.189	23.75	0.237	0.763	0.31	5.8
(7) <i>P.barbiger</i>	-	4	1.95	9.9	0.825	0.197	39.6	0.246	0.754	0.327	5.97
(8) Large Epifauna	-	5.5	1.25	9.5	0.913	0.132	52.25	0.164	0.836	0.197	6.35
(9) <i>X.cassidiformis</i>	0.6	2.28	1.5	5.5	0.986	0.273	12.54	0.364	0.636	0.571	2.625
(10) <i>A.purpuratus</i>	16	55	2.08	9.9	0.814	0.21	544.5	0.3	0.7	0.429	4.85
(11) <i>Taliepus</i> sp.	-	0.65	1.5	9.5	0.985	0.158	6.17	0.197	0.803	0.246	6.1
(12) <i>Mulinia</i> sp.	-	24	1.2	9.9	0.796	0.121	237.6	0.173	0.827	0.209	5.73
(13) <i>C.trochiformis</i>	-	37	0.8	9.9	0.747	0.08	366.3	0.115	0.885	0.131	6.13
(14) <i>Tegula</i> sp.	-	38	2.2	9.9	0.7	0.222	376.2	0.317	0.683	0.465	4.73
(15) <i>P.chilensis</i>	-	20	3.2	11	0.732	0.291	220	0.416	0.584	0.711	4.5
(16) Small Epifauna	-	18	3.7	12.5	0.81	0.296	225	0.395	0.605	0.652	5.675
(17) Infauna	-	60	4.4	14.7	0.861	0.299	882	0.428	0.572	0.747	5.89
(18) <i>H.tasmanica</i>	-	110	1.5	-	0.482	-	-	-	-	-	-
(19) <i>Ch.chamissoi</i>	114	78.6	6	-	0.383	-	-	-	-	-	-
(20) Rodophyta	-	110	5.5	-	0.321	-	-	-	-	-	-
(21) <i>Ulva</i> sp.	-	50	6	-	0.317	-	-	-	-	-	-
(22) Zooplankton	-	18	40	160	0.544	0.25	2880	0.313	0.688	0.455	88
(23) Phytoplankton	-	28	250	-	0.572	-	-	-	-	-	-
(24) Bacteria	-	-	-	-	0.163	-	-	-	-	-	-

Table 4. Transfer efficiencies for each level per habitat and whole benthic area.

Transfer efficiencies for each trophic level**A. Seegrass**

Source	I	II	III	IV	V	VI
Producers	-	8.9	12.8	14.2	3.8	0.6
Detritus	-	18.3	16.1	4.8	1.4	0.5
All flows	-	10.8	13.9	10.4	3.3	0.6
Proportion of total flow originating from detritus: 0.36						

B. Sand-gravel

Source	I	II	III	IV	V	VI
Producers	-	14.3	11.3	8.4	6.7	2.2
Detritus	-	18.6	13.8	8.5	2.9	0.8
All flows	-	15.1	11.9	8.4	5.7	2
Proportion of total flow originating from detritus: 0.37						

C. Sand

Source	I	II	III	IV	V	VI
Producers	-	24.3	4.2	1.3	0	-
Detritus	-	13.4	19.5	4.7	1.9	-
All flows	-	13.5	19.2	4.6	1.9	0.7
Proportion of total flow originating from detritus: 0.49						

D. Mud

Source	I	II	III	IV	V	VI
Producers	-	9.2	22.7	12.7	2.2	0.1
Detritus	-	21.5	14.6	3.2	0.8	0.1
All flows	-	12.8	18.8	9.1	2	0.1
Proportion of total flow originating from detritus: 0.4						

E. Total Area

Source	I	II	III	IV	V	VI
Producers	-	10.2	12.9	11.5	5	1.4
Detritus	-	17.4	13.7	6	2.3	1
All flows	-	11.5	13.1	9.9	4.5	1.4
Proportion of total flow originating from detritus: 0.35						

Table 5. A. Summary statistics after mass-balance process by ECOPATH II. B. Network flow indices. For more details and explanation see text and Christensen and Pauly (1992a).

A. Summary statistics	HABITATS				TOTAL AREA
	Seegrass	Sand-Gravel	Sand	Mud	
Sum of all consumption (g/m ² year ¹)	5344.8	8881.3	7259.5	4979.3	6091.1
Sum of all exports (g/m ² year ¹)	5046.2	9497.4	4808.7	4455	5378.1
Summ of all respiratory flows (g/m ² year ¹)	2724.8	4576.4	3760.3	2545	3163.5
Sum of all flows into detritus (g/m ² year ¹)	5631	10624.2	6010.4	5471.9	5961.2
Total system throughput (g/m ² year ¹)	18746.8	33579.3	21838.9	17451.3	20593.9
Sum of all production (g/m ² year ¹)	9117.5	16101	10245	8280.2	9976.4
Fishery's mean trophic level	3.03	2.06	3.92	3.44	2.14
Gross efficiency of fisheries (catch/net pp., %)	0.001	0.02	0.02	0.00001	0.02
Total net primary production (g/m ² year ¹)	7771	14073.8	69	7000	8541.6
Total PP/Total R	2.8519	3.0753	0.0183	2.7505	2.7
Net system production (g/m ² year ¹)	5046.155	9497.404	-3691.344	4454.975	5378.07
Total PP/Total biomass	10.5915	9.4162	0.1503	31.6656	12.22
Total biomass/total throughput	0.039	0.045	0.021	0.013	0.034
Total biomass (exc. Detritus) (g/m ² year ¹)	733.7	1494.63	458.98	221.06	699.03
Total catches (g/m ² year ¹)	7.66	122.05	1.64	0.06	131
B. Network flow indices					
Ascendency (Total) Flowbits	21557.8	43965.1	24166.1	19354.8	25092.2
Overhead (Total) Flowbits	46991	99251	62939.5	39433.4	62014.9
Capacity (Total) Flowbits	69270.4	144547	88183.5	59139	88686.8
Pathway Redundancy (of Overhead) (%)	51	53.8	52.3	49.6	52.9
A/C (%)	31.1	30.4	27.4	32.7	28
Ai/Ci (%)	21	21	19	22	19.8
Throughput cycled (g/m ² year ¹)	97.8	107	113.1	114.9	72.1
Finn's cycling index (FCI) (%)	3	2.1	4	4	2.6
Average path length (APL) (dimensionless)	2.41	2.39	2.55	2.49	2.41
Food web connectance (dimensionless)	0.227	0.238	0.231	0.322	0.195
Omnivory index (OI) (dimensionless)	0.205	0.139	0.17	0.313	0.139

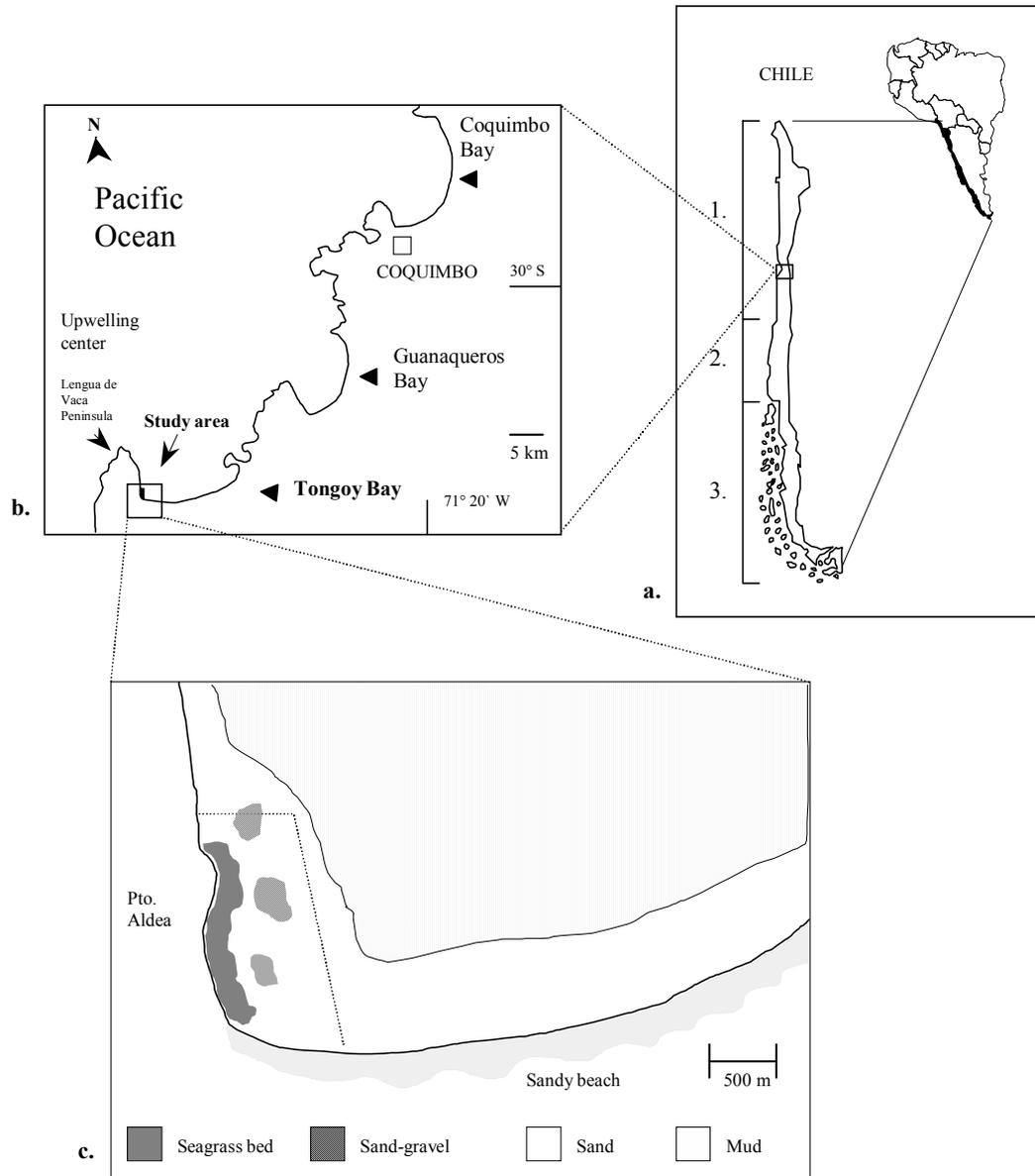


Fig. 1

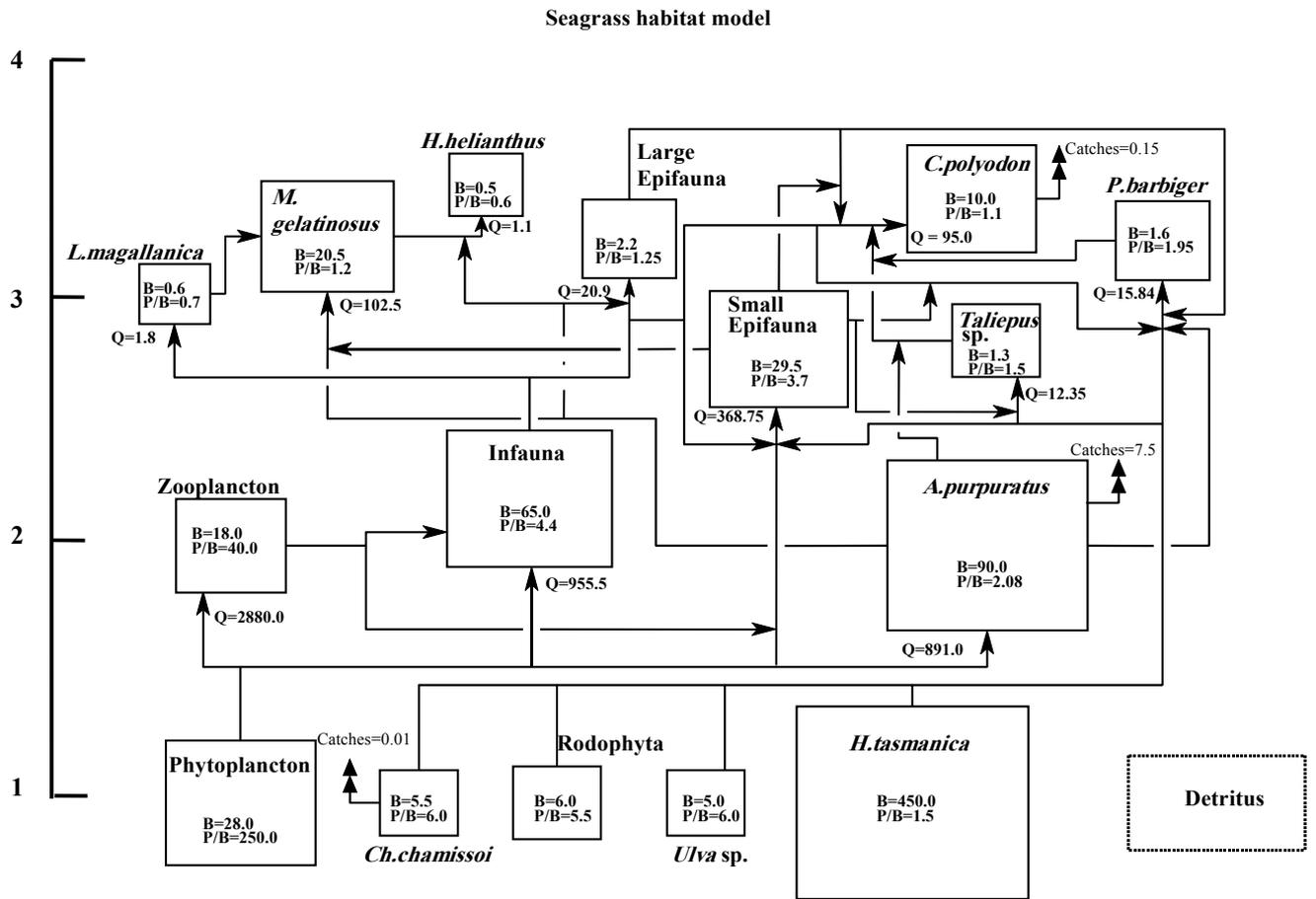


Fig. 2a

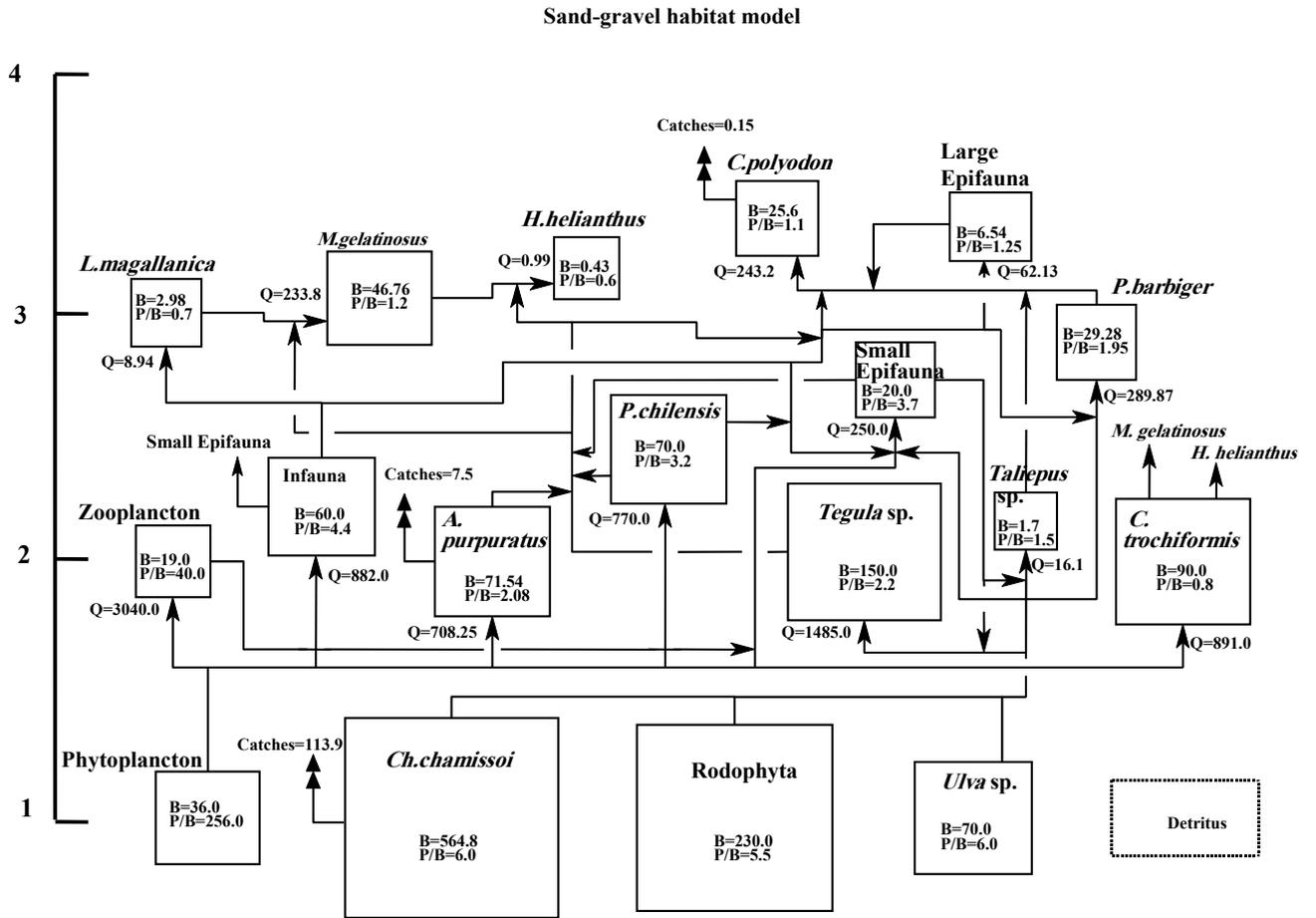


Fig. 2b

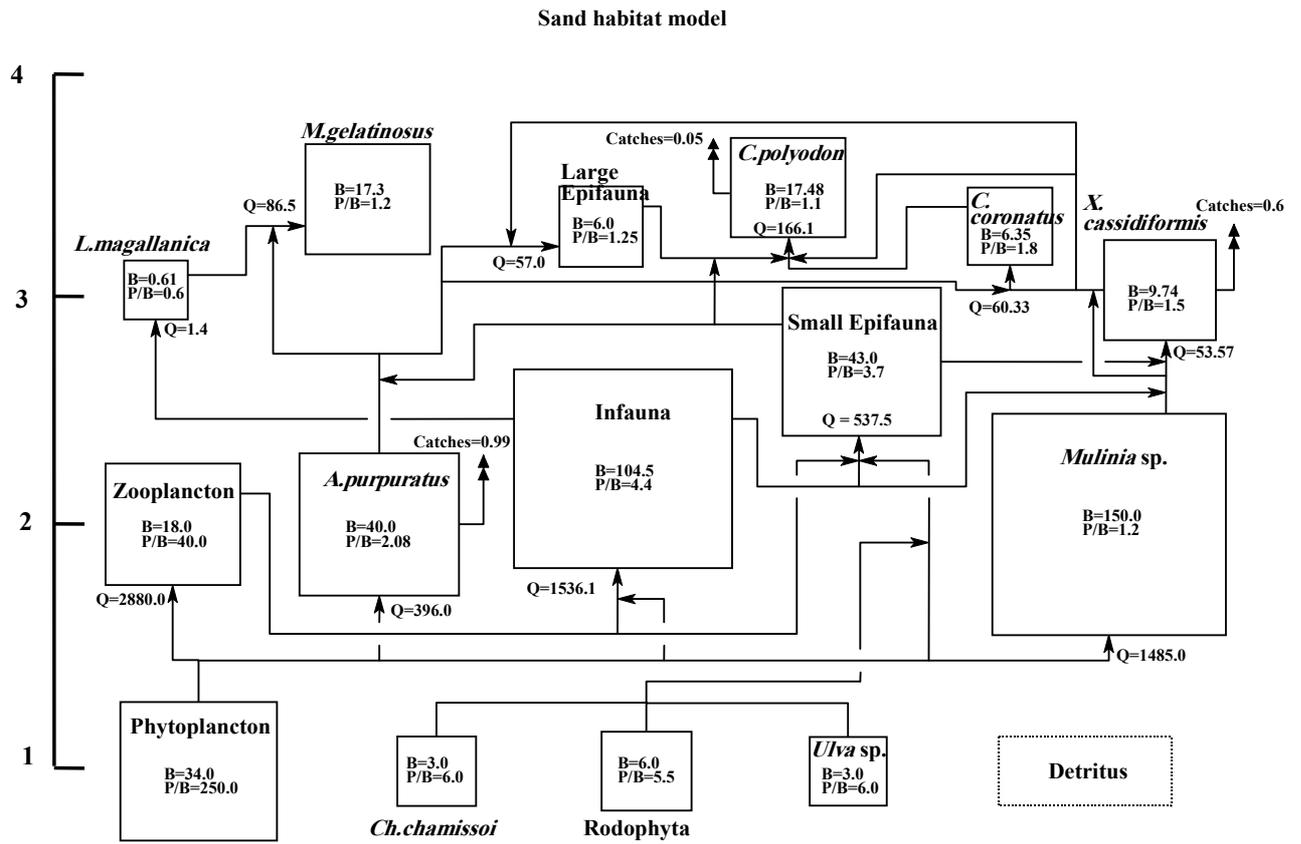


Fig. 2c

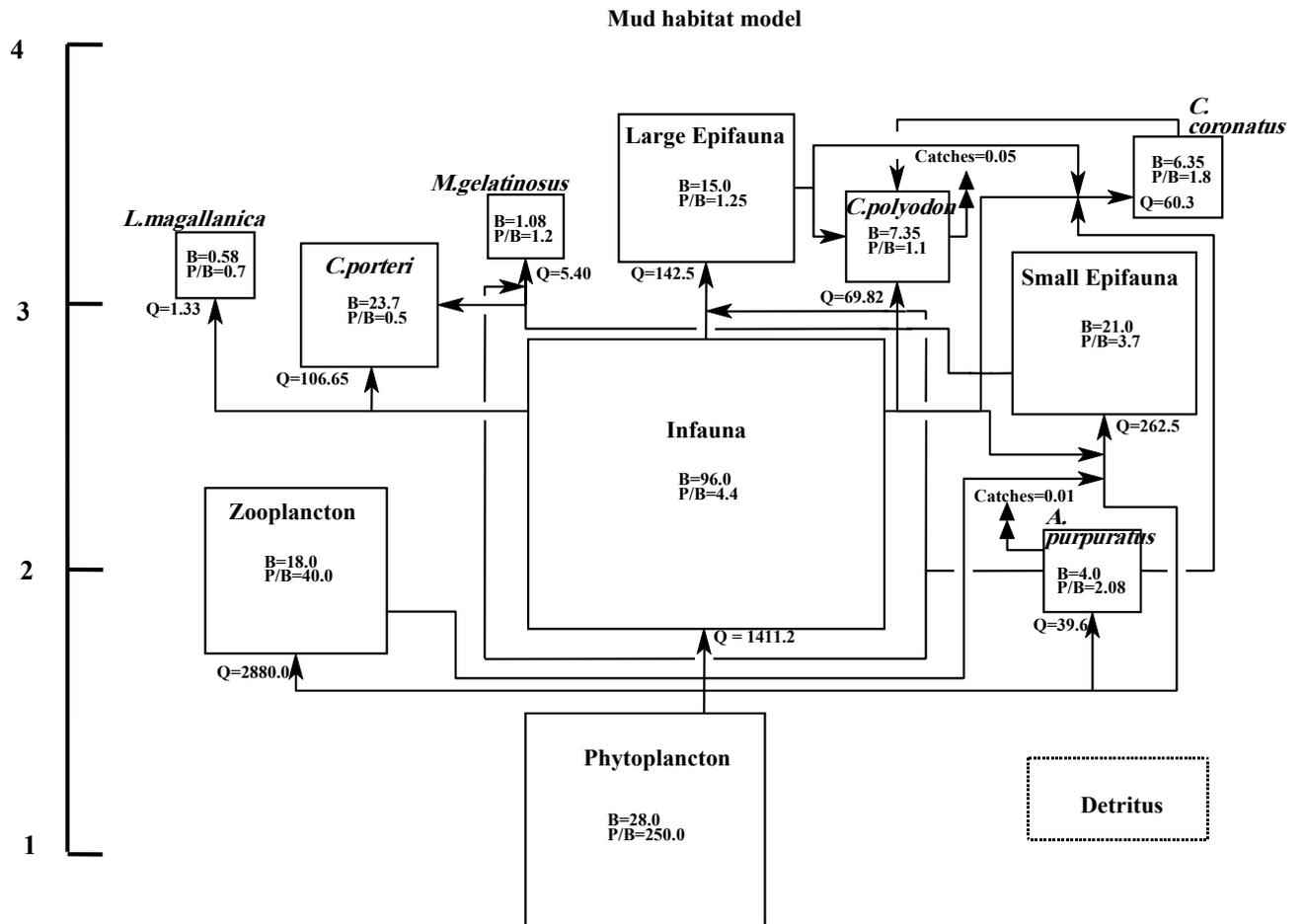


Fig. 2d

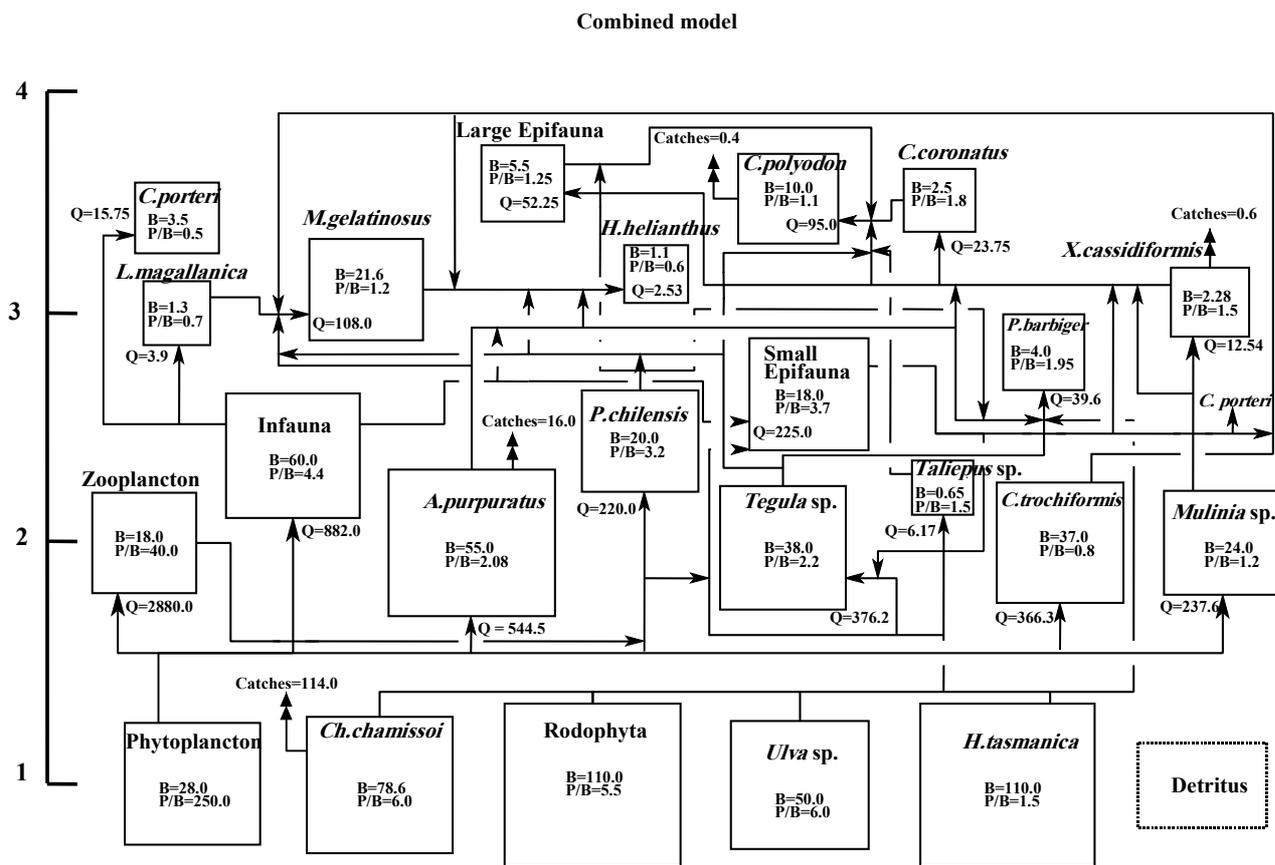


Fig. 2e

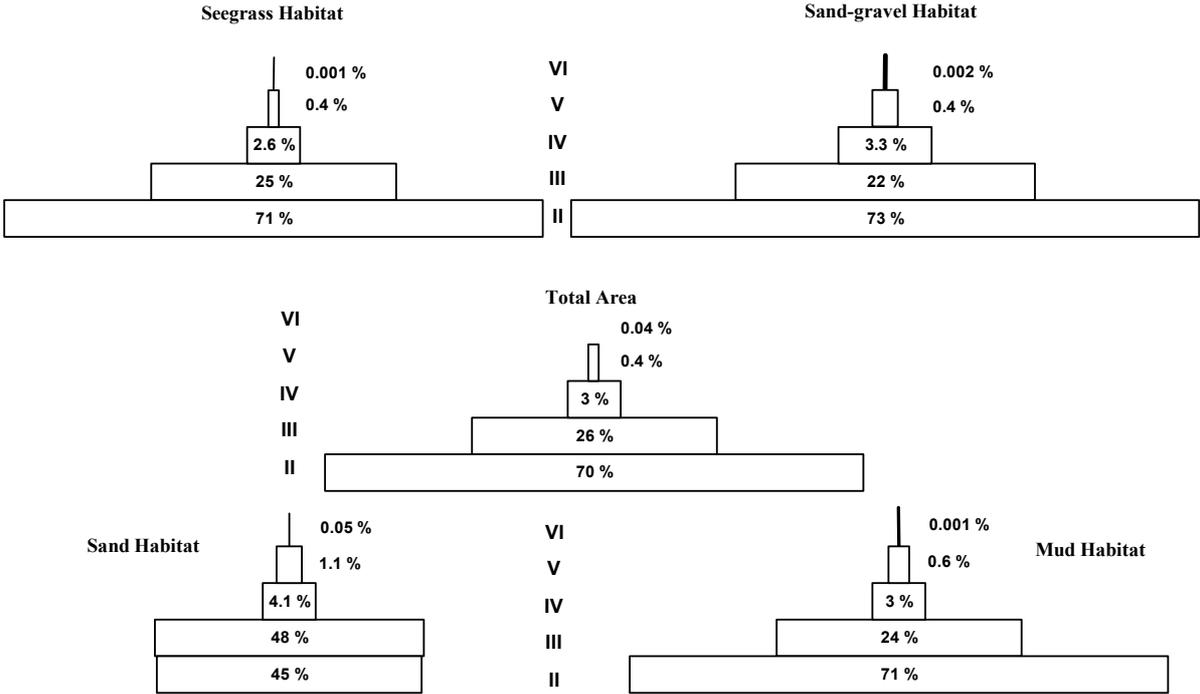
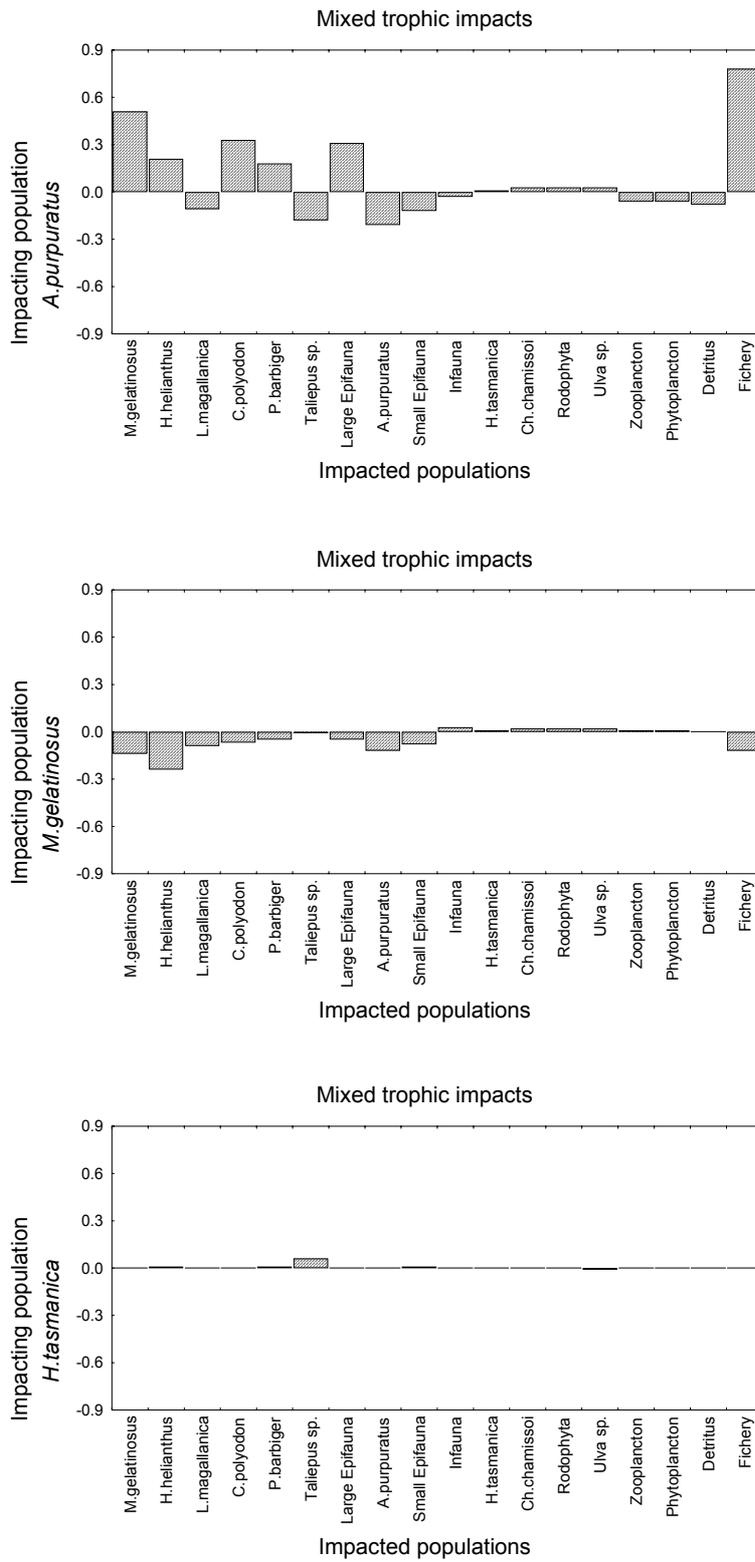
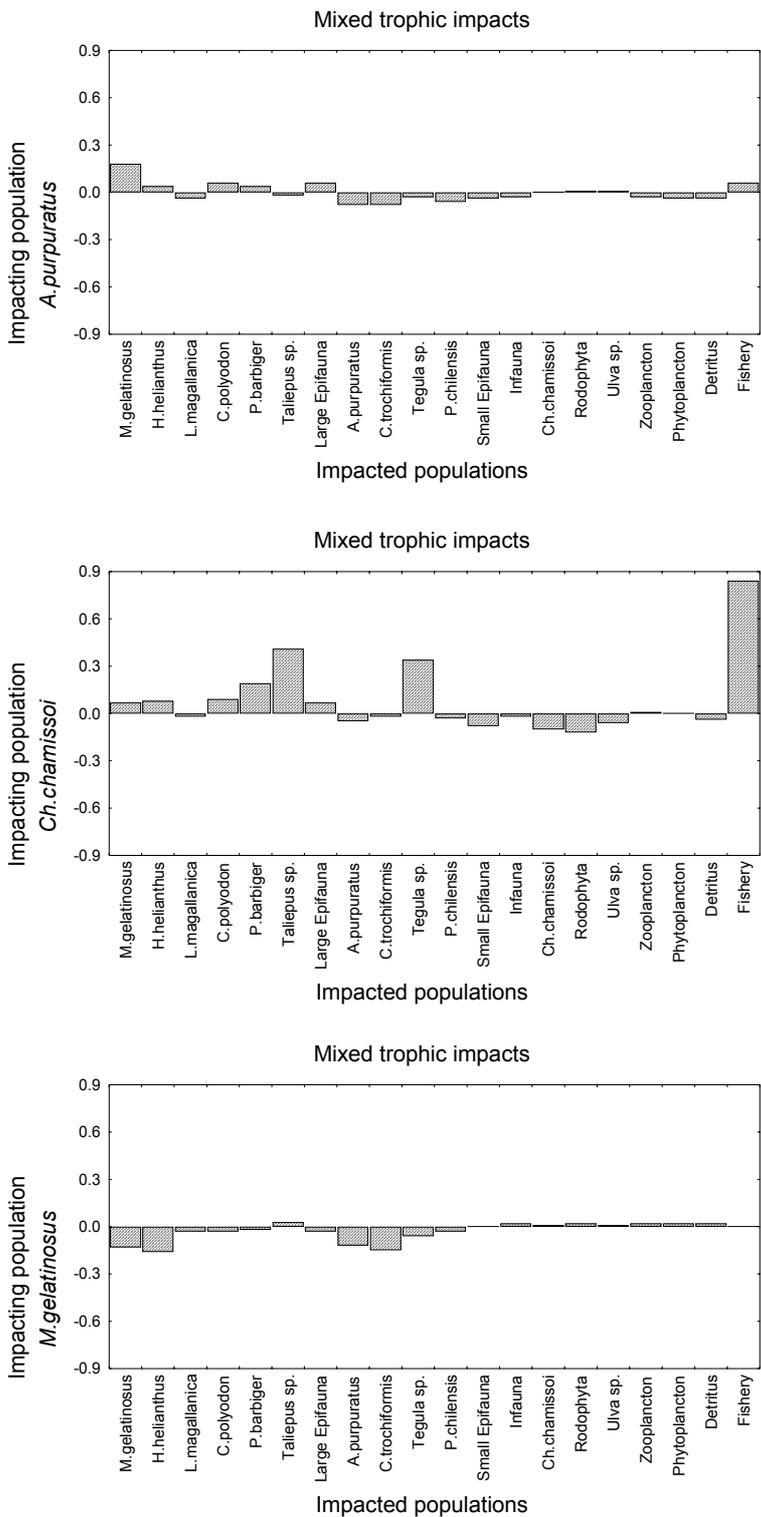


Fig. 3



a.

Fig. 4



b.

Fig. 4 continuation

7. Chapter IV

“Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios”

Marco Ortiz & Matthias Wolff

Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@zmt.uni-bremen.de & mwolff@zmt.uni-bremen.de). Fax: +49 (0) 421 238 00 30.

Key words: ECOSIM, trophic relationships, ecosystems, upwelling system, fisheries, bottom-up, mixed and top-down controls, fishing mortality.

2001

The original idea for this publication was developed by the first author. The last version of this contribution was possible after intensive intellectual discussions with the co-author.

Abstract

Within Tongoy Bay (north-central Chile), four different habitats (seagrass, sand-gravel, sand and mud) were identified and subsequently considered as subsystems for the construction of trophic mass-balance models. By using the ECOSIM software package of Walters et al. (1997) different management scenarios were simulated for these subsystems and for an overall integrated system (combining all habitats) in order to explore strategies of sustainable resource use.

Systems recovery time (*SRT*) as well as single species responses differed with the scenario simulated. The most important findings were:

- 1.- An increase in the harvest of the scallop *Argopecten purpuratus* did not drastically effect the global properties of the systems.
- 2.- A depletion of its principal predator, the sea star *Meyenaster gelatinosus*, greatly improved the availability of scallops in the subsystem seagrass, sand-gravel as well as in the integrated model.
- 3.- A biomass reduction of the snail *Xantochorus cassidiformis* produced only a small negative impact on the *SRT*, while a simulated harvest on the clam *Mulinia* sp. drastically changed the systems properties. This clam may thus be considered as a keystone species.
- 4.- Predictions of the maximum sustainable yield (*MSY*) of the scallop were lower than those obtained by single species approaches.

Our simulations allow us to conclude that:

- 1.- A strong fishery of the scallop predator, the sea star *M. gelatinosus*, would greatly increase the yield of the scallop and the other populations or resources of the systems.
- 2.- Trophic mass balance models and their simulated scenarios offer great possibilities for the planning of interventions or manipulations of natural systems.

Introduction

The intensive growth in the development of ecosystem models during the last decade has permitted us to theoretically explore our scientific understanding of natural processes and to assess alternative management policies (Jørgensen et al., 1996). The overexploitation of most aquatic resources has lead to a transformation of ecological and economical systems and has produced a situation which concerns not only the scientific community, but also environmentalist, fisheries managers, and fishermen.

While many reductionistic population models have been developed to study these complex systems, the disillusion about the predictive capability of these single species assessment strategies has increased (Walters et al., 1999). Their principal disadvantage is that they need to consider the populations under study in isolation from both biotic and abiotic surroundings (Larkin, 1977; Levins and Lewontin, 1980; Levins and Wilson, 1980; Paine, 1984; Hilborn et al., 1995; Patten, 1997; Roberts, 1997; Levins, 1998a; Walters et al., 1999; Levins and Lopez, 1999). Although some of these models seem appropriate in situations of clear stock-recruitment relationships, they only grasp proximate properties of the populations and do not make neither implicit nor explicit considerations about the "health" conditions of the ecosystems where these species inhabit. Thus, if we want to approach the global properties of these complex natural systems, the boundaries of our abstractions must be expanded towards its externalities, that is, integrating more variables, interactions and their dynamical behaviour.

Although the stability and structural properties of ecosystems have been widely analysed and discussed in the literature, especially in regard to the complexity of food webs (e.g. MacArthur, 1955; Elton, 1958; Odum, 1969; Holling, 1973; Levins, 1974, 1975; May, 1974; DeAngelis, 1975, 1980; Pimm, 1979, 1980, 1982; Briand, 1983; Briand and Cohen, 1984; Ulanowicz, 1986; Pimm and Kitching, 1987; DeAngelis et al., 1989; Lawton, 1994; Vasconcellos et al., 1997; Peterson et al., 1998; Tokeshi, 1999), few studies have been focused on the holistic dynamical modelling (multispecies) and on the prediction of alternative management policies in overexploited system around the world (Mackinson et al., 1997). So far most studies done along the Chilean coastline are based upon the population dynamics of the commercial species (Santelices, 1989; Santelices and Doty, 1989; Vásquez, 1995; Stotz, 1997; Stotz and González, 1997; Castilla, 2000) and lie essentially within the above mentioned reductionistic abstractions.

One way to integrate and to study complex natural ecosystems is through the modelling of trophic or matter/energy flow. Christensen and Pauly (1992), developed the ECOPATH II software, by which steady-state mass-balances and flows between interconnected (by depredation) compartments can be quantified. Furthermore, based on the theories of Odum (Odum, 1969) and Ulanowicz (Ulanowicz, 1986, 1997) it is possible to describe and compare systems in terms of their development (maturity) or degree of growth (size in term of flows), capacity to withstand external perturbations, stability and direct-indirect impact of the species or groups on the remainder compartments. Although ECOPATH II produces a steady state picture of the trophic flows, it represents an important baseline for further dynamical simulations.

A dynamical extension of ECOPATH II, termed ECOSIM, was developed by Walters et al. (1997). Based on this approach simulations can be made about the response of the entire system to different perturbations and to different exploitation regimes, under assumptions of bottom-up, mixed or top-down flow control mechanisms. In a recent contribution, Mackinson et al. (1997), in comparing the trophic impacts of harvesting small pelagic fish in three different upwelling ecosystems pointed out the following results: (1) after an intensive exploitation of small pelagic fishes, the standing stocks of their food and competitors increased, and their predators decreased, (2) food limitation by bottom-up control can not explain the replacement in abundance from anchovy to sardine species in the Peruvian system, and (3) estimations of fishing mortality for maximum sustainable yield (*MSY*) in small pelagics under assumptions of bottom-up control were higher than those obtained under top-down control.

The present contribution is based on trophic models previously constructed by the authors for Tongoy Bay (north-central Chile) (Wolff, 1994) and for habitat subsystems (Ortiz and Wolff, in prep). The analysis of food web into habitat or subsystems follows the recommendations suggested by May (1974), Paine (1980, 1984) and Hall and Raffaelli (1993) in regard to that the stability of the systems would be increased if the food webs are organized into subsystems. These trophic models allowed to describe the species structure and trophic flows within each subsystem and to do some preliminary impact analysis by Mixed Trophic Impact (Ulanowicz and Puccia, 1990). The main objective of this paper is to assess the resilience time of each subsystem as response to different strategies of resource exploitation and to estimate fisheries mortality corresponding to maximum sustainable yield (F_{MSY}) for the most valuable species, the scallop *Argopecten purpuratus*, under assumption of bottom up, mixed and top down flow control mechanisms. As studies of Hunter and Price (1992), Jordán et al. (1999) and Menge (2000) suggest that a control is mixed (both bottom-up and top-down) we further explore the simulations results based on this assumption. Moreover, we believe that alone bottom-up and top-down processes in communities may be

considered as another false dichotomy that dominate in ecological sciences (sensu Levins 1998a).

2. Material and Methods

2.1. Subtidal benthic system of Puerto Aldea, Tongoy Bay.

The study area of Puerto Aldea (Fig. 1) corresponds to one of 168 management areas established along the Chilean coast (Castilla 2000). These areas are assigned to fishermen organisations to maximise, within sustainable boundaries, the production and exploitation of commercial resources. In this area the following habitats can be recognised: (1) seagrass meadows, (2) sand-gravel, (3) sand, and (4) mud. A complete biotic and abiotic description of these habitats was done by Jesse (2001) and Ortiz et al. (in prep.).

Tongoy Bay and the subtidal benthic system of Puerto Aldea are protected from the prevailing south-west winds by Lengua de Vaca peninsula; all beaches are classified as of the intermediate morphodynamic state (Ortiz and Stotz, 1996). The upwelling center near Punta de Vaca (Acuña et al., 1989; Daneri et al., 2000; Montecinos and Quiroz, 2000) is among the most important one of northern Chile and supplies nutrients to the ecosystem and simultaneously prevents the establishment of a stable thermocline during summer through permanent intrusions of upwelling water to the bay. Temperature of bottom water ranges between 13°C and 17°C in winter and autumn respectively (Jesse, 2001).

2.2. ECOSIM, dynamic mass-balance approach.

The mathematical ground of ECOSIM consists of biomass dynamics described in form of coupled differential equations as:

$$\frac{dB_i}{dt} = g_i \cdot \sum_j C_{ij} - \sum_j C_{ji} + I_i - (M_i + F_i + E_i) \cdot B_i \quad (1)$$

where,

- g_i = growth efficiency of i compartment,
- C_{ji} = consumption rates of j by i compartments,
- C_{ij} = consumption rates of i by j compartments,
- I_i = immigration rate of i ,
- M_i = total mortality of i ,
- F_i = fishing mortality of i ,
- E_i = emigration rate of i ,

and additionally,

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v'_{ij} + (a_{ij} \cdot B_j)} \quad (2)$$

where,

v_{ij} and v'_{ij} = rates of behavioural exchange between invulnerable and vulnerable states, v_{ij} can be defined as the transference rate which determines if the control is top-down, bottom-up or mixed. This parameter can range from 1.0 for top-down to 0.0 for bottom-up control. A value of 0.3 represents a mixed control. For more details see ECOSIM programme.

a_{ij} = rate of effective search by predator j for prey i .

Based on previously constructed ECOPATH II models, ECOSIM permits to generate dynamical biomass predictions of each system compartment i which is affected directly by fishing, depredation, changes in food supplies, and indirectly, by fishing on other groups. Using equilibrium simulations where equilibrium biomass is plotted over a range of fishing

mortality values, it is possible to estimate –under a large scale approach- the maximum sustainable yield for the harvested compartments. For more details of the ECOSIM software package, its possibilities and weaknesses see Walters et al. (1997).

2.3. Definitions

Stability is the capacity of a system to return to a state of equilibrium after perturbations (Holling, 1973; Levins, 1974). Based on Odum's theory of ecosystems (Odum, 1969), ecological stability is considered as an exclusive property of mature systems which evolve towards an increase of size and diversity until certain limits are imposed by the available resources. On the other hand, Ulanowicz's theory (Ulanowicz, 1986, 1997) states that ecosystems organisation, in terms of Relative Ascendency (*A/C*) and Redundancy (internal flow of Overhead), may be the most important factors associated with the system stability. A *bottom-up* control means that the flow of energy between two compartments is limited by food resources or controlled by the preys; *top-down* control holds that the flow is regulated by the predators (Patten, 1997). *Resilience* is the speed at which the entire system returns to its original state after it has been stressed and displaced from that state (Pimm, 1982). *Resistance* describes the ability of the systems to withstand displacement (Begon et al., 1990). Thus stability includes both resilience and resistance. In the present study we assume that *System Recovery Time (SRT)* as obtained by our simulations is a measure of the internal stability of the systems.

2.4. The scenarios

Fig. 2 shows the scenarios that were simulated for each habitat and the whole area. All disturbances were done between the second and fourth year of the total simulation (20 years). For the scallop *A. purpuratus* and the snail *Xanthochorus cassidiformis* (harvested populations), fishing mortality was increased by 100% from the baseline. For the remainder populations a reduction by 50% of total production was simulated. For all scenarios, the dynamical simulations were done with mixed (bottom-up and top-down) regulations.

3. Results and Discussion

3.1. Dynamical simulations of biomass

Fig. 3 shows the dynamical responses of biomass in the seagrass habitat under each scenario and the combined impacts. The longest system recovery time (*SRT*) was obtained when the sea star *M. gelatinosus* was depleted (Scenario II). This, however, has a positive effect on the scallop *A. purpuratus* and also its competitors (i.e. the crab *Cancer polyodon* and the asteroid *Heliaster helianthus*). A similar pattern can be observed for the simulation with all scenarios combined. The system recovers quickly under an increase of fishing of *A. purpuratus* (Scenario I). Under a reduction of the seagrass *H. tasmanica* recovery time is intermediate with deleterious effects on the herbivorous crab *Taliepus* sp. (Scenario III). Based on these results, a management plan that implies a single reduction of *M. gelatinosus* (through collection by divers) might not be adequate because dramatic system responses (proliferation of competitors) should be expected. An alternative or additional policy may be to simultaneously exploit *C. polyodon* and *H. helianthus*. By doing so, the positive effects on both species would be counteracted and the overall top-down control by the predators on the scallops would be significantly decreased.

In the Sand-Gravel habitat observed responses are similar. An increase of fishing for *M. gelatinosus* has a large impact on the system recovery time and on the other compartments. A large positive effect could be observed for its preys, *A. purpuratus* and *Calyptrea trochiformis*, and for its competitor *H. helianthus* (Fig. 4). Contrary to the previous habitat, only a removal of *H. helianthus* seems indicated as an additional

management option. An increase of the harvest on *A. purpuratus* should only have a small impact on the system and to the other compartments (Fig. 4).

Fig. 5 illustrates the responses in the sand habitat. An increase in fishing (F) for the snail *X. cassidiformis* would produce a small effect on both the system recovery time and the other species populations. An exploitation of the clam *Mulinia* sp., however, produces large direct and indirect effects on the system properties; most of the predators would be depleted, except for the positive effect on *M. gelatinosus*. These findings point to the importance of *Mulinia* sp. within the food-web and suggest that this clam may be considered as a keystone species (Paine, 1966, 1969; 1984; Mills et al., 1993; Jordán et al., 1999). The importance of *Mulinia* sp. seems due to its high throughput of energy, its high degree of connectivity within the trophic web and its intermediate trophic position.

Fig. 6 shows the dynamical trajectory of biomass for all compartment in the combined model as a response to each scenario. A negative impact on *M. gelatinosus* produced the largest effect on the system recovery time and the other compartments if it is compared to other individual manipulations. The other extreme was observed for *X. cassidiformis* which had the smallest effect on the entire system. In this expanded model a harvest on *Mulinia* sp. did not have the large effect on the remainder populations, as was found in the Sand habitat (Fig. 5). An increased fishing of the other populations showed similar responses as for the habitat simulations.

Based on our results, an increase of fishing on the commercial scallop *A. purpuratus* should have only a small effect on the systems when compared to the other manipulations. Even though a decrease in biomass of the asteroid *M. gelatinosus* produces a proximate positive effect on the scallop in the three models, a removal of this species as a management tool must be carefully analysed because it may directly favour its competitor species. This replacement among predators under selective fishing may be explained by the dominance of direct and indirect interactions governed by competition, depredation, mutualistic and ammensalistic mechanisms (Lawlor, 1979; Higashi and Patten, 1986, 1989; Billick and Case, 1994; Wootton, 1994; Menge, 1995; Fath and Patten, 1999). This switches were described for other ecological simulations with surprisingly similar predicted and observed responses (Mackinson et al., 1997; McClanahan and Sala, 1997). However, it is important to note that Mackinson et al. (1997) obtained these similar responses only if the ecosystem was top-down controlled. Under conditions of bottom-up control, no switch between predators could be observed.

These positive responses on competitor species (or cascading effects) can also be viewed as a dominance of positive feedback which may drive the system to some other moving equilibrium (sensu Levins, 1998b). Thus, if our objective is not only to increase the production of *A. purpuratus*, but also to conserve the natural system in which it inhabits, this positive feedback must be avoided. One way to depress these positive feedback may be by fishing the other competitor species as well. The crabs *C. polyodon* must be exploited in the seagrass habitat and the asteroid *H. helianthus* must be removed both in seagrass and sand-gravel habitats. Comparable alternative management policies were suggested by McClanahan and Sala (1997) working on a Mediterranean infralittoral rocky-bottom ecosystems.

A further harvest on *Mulinia* sp. can not be recommended due to the unexpected high order effects that it produces on the remainder populations of the system. Even though the whole model, with the additional components and paths, shows a buffer effect if *Mulinia* sp. is exploited, this simulation outcome may not be realistic because this species extends on a narrow sand belt along the beach which is distant or more disconnected to the seagrass and the sand-gravel communities.

Based on our results, we think that any management policy must be supported by ecological models of the kind presented here, which represent each particular community or subsystem where the target species is inserted. It also seems imperative to consider the environmental heterogeneity of larger systems and to account for different habitats (Hunter and Price, 1992, Walters et al., 1999). This is especially important since it implies, for instance, that for each management area assigned to fishery organisations along the Chilean coast (Castilla, 2000), specific models must be developed which grasp the most relevant ecological interactions and allow the evaluation of different management options for the sustainable use of the resources.

Table 1 resumes the system recovery time obtained for both bottom-up, mixed and top-down controlling. For all scenarios, bottom-up control showed the smallest *SRT* in comparison to top-down control which under extreme condition produces oscillation behaviour for the all compartments.

3.2. Fishing mortality corresponding to the maximum sustainable yield (F_{MSY}).

Fig. 7 shows the maximum sustainable fishing for *A. purpuratus* obtained by the equilibrium simulations in seagrass, sand-gravel and whole system. The seagrass habitat may support the highest fishing pressure ($F_{MSY} = 1.06$) compared to the sand-gravel and the whole area. The values obtained in the present work are near but somewhat smaller than those proposed by Stotz and González (1997) who estimated a fishing mortality of about 1.19 for the same species in the same study area. This higher value could be the result of a bottom-up control assumption. Under mixed and top-down control mechanisms, maximum fishing for each model were small (Table 1). Based on these results, we conclude that any management strategy based on single species population models may over-estimate sustainable exploitation rates of the target species. Instead, scientist and managers should also consider simulations of multispecies models of trophic interactions for planning sustainable interventions and manipulations in natural systems.

The dynamical simulations carried out allowed to see how the effects of depletion of the biomass of some species in each subsystem propagate in time and produced relevant cascading effect in the remainder populations. Even though the responses observed were in terms of quantifiable biomass, the complex interactions among species in each community, however, make it unlikely to predict the exact amount of change. Therefore, under these circumstances a qualitative analysis, by which we can only generalise about directions of change and relative comparisons, seems to be recommended. There are, nonetheless, some sources of mistake which are directly related to the interpretation of simulations already made. Walter et al. (1997) addressed some limitations and weaknesses of ECOSIM. Firstly, the equilibrium assumptions of ECOPATH II play a important role because the data quality are directly related with the reliability of the period of time over which the simulations should be run. Secondly, ECOSIM consider only simply assumptions, such as diet relationships, absence of complex life histories and it does not take into account environmental variability. Nevertheless, if we consider only short-term dynamics (as the present work) ECOSIM can be a usefully tool in predicting the qualitative directions of biomass change and through a comparative analysis to assess the sustainability of alternative management polices (Walters et al., 1997; Mackinson et al., 1997).

References

- Acuña, E., Moraga, J. and Uribe, E., 1989. La zona de Coquimbo: un sistema nerítico de alta productividad. CPPS Rev. Pacífico Sur, N° especial, 145-157.

- Begon, M., Harper, J.L. and Townsend, C.R., 1990. Ecology: individuals, populations and communities. 2nd Ed. Blackwell Scientific Publications, Oxford.
- Billick I. and Case, T.J., 1994. Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology* 75, 1529-1543.
- Briand, F., 1983. Environmental control of food web structure. *Ecology* 64(2), 253-263.
- Briand, F. and Cohen J.E., 1984. Community food webs have scale-invariant structure. *Nature* 367, 264-267.
- Castilla, J.C., 2000. Roles of experimental marine ecology in coastal management and conservation. *J. Exp. Mar. Biol. Ecol.* 250, 3-21.
- Christensen, V. and Pauly, D., 1992. ECOPATH II. a software for balancing steady-state ecosystems models and calculating network characteristics. *Ecol. Model.* 61, 169-185.
- Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P. and Ulloa, O., 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Mar. Ecol. Prog. Ser.* 197: 41-49.
- DeAngelis, D.L., 1975. Stability and connectance in food web models. *Ecology* 56, 238-243.
- DeAngelis, D.L., 1980. Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* 61(4), 764-771.
- DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A. and Elwood, J.W., 1989. Nutrient dynamics and food-web stability. *Annu. Rev. Ecol. Syst.* 20, 71-95.
- Elton, C.S., 1958. The ecology of invasion by animals and plants. Methuen, London.
- Fath, B. and Patten, B., 1999. Review of the foundations of network analysis. *Ecosystems* 2, 167-179.
- Hall, S. and Raffaelli, D., 1993. Food Webs: theory and reality. *Advances in Ecol. Res.* 24, 187-239.
- Higashi, M. and Patten, B., 1986. Further aspects of the analysis of indirect effects in ecosystems. *Ecol. Model.* 31, 68-77.
- Higashi, M. and Patten, B., 1989. Dominance of indirect causality in ecosystems. *Am. Nat.* 133, 288-302.
- Hilborn, R., Walters, C. and Ludwig, D., 1995. Sustainable exploitation of renewable resources. *Annu. Rev. Ecol. Syst.* 26, 45-67.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1-23.
- Hunter, M.D. and Price, P.W., 1992. Playing chutes and ladders: bottom-up and top-down forces in natural communities. *Ecology* 73, 724-732.
- Jesse, S., 2001. Comparative ecology of sympatric brachyuran crab species in the shallow subtidal of the Pacific Coast of North Chile and their importance for the artisanal fishery in Puerto Aldea. PhD Dissertation, University of Bremen, Germany.
- Jordán, F., Takács-Sánta, A. and Molnár, I., 1999. A reliability theoretical quest for keystones. *Oikos* 86, 453-462.
- Jørgensen, S.E., Halling-Sørensen, B. and Nielsen, S.N., 1996. Handbook of Environmental and Ecological Modelling. CRC Lewis Publishers, Boca Raton, FL.
- Larkin, P., 1977. An epitaph for the concept of maximum sustainable yield. *Trans. Am. Fish. Soc.* 106(4), 1-11.
- Lawlor, L.R., 1979. Direct and indirect effects of n-species competition. *Oecologia (Berl)* 43, 355-364.
- Lawton, J., 1994. What do species do in ecosystems? *Oikos* 71, 367-374.
- Levins, R., 1974. The qualitative analysis of partially specified systems. *Ann. N.Y. Acad. Sci.* 231, 123-138.

- Levins, R., 1975. Evolution in Communities Near Equilibrium. In: M. Cody, J. Diamond (Editors), Ecology and evolution of communities. Harvard University Press, MA.
- Levins, R., 1998a. The internal and external explanatory theories. *Science as Culture* 7(4), 557-582.
- Levins, R., 1998b. Dialectics and systems theory. *Science & Society* 62(3), 375-399.
- Levins, R. and Lewontin, R., 1980. Dialectics and reductionism in ecology. *Synthese* 43, 47-78.
- Levins, R. and Wilson, M., 1980. Ecological theory and pest management. *Ann. Rev. Entomol.* 25, 287-308.
- Levins, R. and Lopez, C., 1999. Towards an ecosocial view of health. *Int. J. Health Services* 29(2), 261-293.
- MacArthur, R.H., 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36, 533-536.
- Mackinson, S., Vasconcellos, M., Pitcher, T. and Walters, C., 1997. Ecosystem impact of harvesting small pelagic fish in upwelling systems: using a dynamic mass-balance model. Proceedings, Forage Fishes in Marine Ecosystems Alaska Sea Grant College Program (AK-SG-97-01).
- May, R.M., 1974. Stability and complexity in model ecosystems. 2nd Edition, Princeton University Press, N.J.
- McClanahan, T.R. and Sala, E., 1997. A mediterranean rocky-bottom ecosystem fisheries model. *Ecol. Model.* 104, 145-164.
- Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Monogr.* 65, 21-74.
- Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.* 250, 257-289.
- Mills, L.S., Soulé, M.E. and Doak, D.F., 1993. The key-stone-species concept in ecology and conservation. *BioScience* 43, 219-224.
- Montecinos, V. and Quiroz, D. 2000. Specific primary production and phytoplankton cell size structure in an upwelling area off the coasts of Chile (30°). *Aquat. Sci.* 62, 364-380.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 104, 262-270.
- Ortiz, M. and Stotz, W., 1996. Distribución de juveniles recientemente asentados de *Mesodesma donacium* (Lamarck, 1818) (Mollusca: Bivalvia: Mesodesmestidae) en tres bahías de la cuarta región: variables físicas y químicas que le caracterizan. *Biol. Pesq. (Chile)* 25, 27-40.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65-75.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *Am. Nat.* 103, 91-93.
- Paine, R.T., 1980. Food webs: linkage, interaction strength and community infrastructure. The third Tansley Lecture. *J. Animal Ecol.*, 49, 667-685.
- Paine, R.T., 1984. Some approaches to modeling multispecies systems. In: R.M. May (Ed.), Exploitation of marine communities. Dahlem Konferenzen, Springer-Verlag Berlin, pp. 191-207.
- Patten, B., 1997. Synthesis of chaos and sustainability in nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. *Ecol. Model.* 100, 11-42.
- Peterson, G., Allen, C. and Holling C.S., 1998. Ecological resilience, biodiversity and scale. *Ecosystems* 1, 6-18.
- Pimm, S.L., 1979. Complexity and stability: another look at MacArthur's original hypothesis. *Oikos* 33, 351-357.

- Pimm, S.L., 1980. Food web design and the effect of species deletion. *Oikos* 35, 139-149.
- Pimm, S.L., 1982. *Food Webs*. Chapman and Hall, NY.
- Pimm, S.L. and Kitching, R.L., 1987. The determinants of food chain lengths. *Oikos* 50, 302-307.
- Roberts, C., 1997. Ecological advice for the global fisheries crisis. *Trend in Ecology and Evolution* 12, 35-38.
- Santelices, B., 1989. *Algas Marinas de Chile. Distribución, Ecología, Utilización, Diversidad*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- Santelices, B. and Doty, M., 1989. A review of *Gracilaria* farming. *Aquaculture* 78, 95-133.
- Stotz, W., 1997. Las áreas de manejo en la Ley de Pesca y Acuicultura: primeras experiencias y evaluación de la utilidad de esta herramienta para el recurso loco. *Estudios Oceanológicos (Chile)* 16, 67-86.
- Stotz, W. and González, S., 1997. Abundance, growth, and production of the sea scallop *Argopecten purpuratus* (Lamarck, 1819): bases for sustainable exploitation of natural scallop beds in north-central Chile. *Fish. Res.* 32, 173-183.
- Tokeshi, M., 1999. *Species coexistence: ecological and evolutionary perspectives*. Blackwell Science, Oxford.
- Ulanowicz, R., 1986. *Growth and development: Ecosystems phenomenology*. Springer, N.Y.
- Ulanowicz, R., 1997. *Ecology, the Ascendent Perspective. Complexity in Ecological Systems Series*, Columbia University Press, N.Y.
- Ulanowicz, R. and Puccia, Ch. 1990. Mixed trophic impacts in ecosystems. *Ceonoces* 5, 7-16.
- Vasconcellos, M., Mackinson, S., Sloman, K. and Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. *Ecol. Model.* 100, 125-134.
- Vásquez, J., 1995. Ecological effects of brown seaweed harvesting *Bot. Mar.* 38, 251-257.
- Walters, C., Christensen V., and Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish. Biol. Fish.* 7, 139-172.
- Walters, C., Pauly, D. and Christensen, V., 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539-554.
- Wootton, J.T., 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75(1), 151-165.
- Wolff, M., 1994. A trophic model for Tongoy Bay –a system exposed to suspended scallop culture (Northern Chile). *J. Exp. Mar. Biol. Ecol.* 182, 149-168.

List of Tables and Figures

Table 1. Summary the system recovery time (*SRT*) and fishing mortality (F_{MSY}) for *A. purpuratus* for each model and scenario under top-down, mixed and bottom-up controls. The flow control is determined by the parameter of vulnerability (v) of equation 2 (see text).

Fig. 1. (a) The main littoral types along the Chilean coast: 1.= dominated by exposed rocky shores; 2.= dominated by exposed sandy shores; 3.= mostly insular systems. (b) the principal bay systems of the IV Region of Coquimbo (Chile), (c) Study area of Puerto Aldea located at southern of Tongoy Bay.

Fig. 2. Simulated scenarios or management options in (a) Seagrass habitat, (b) Sand-gravel habitat, (c) Sand habitat, and (d) Whole Area. For harvested and not harvested species an increase of 100 and 50 % of fishing, respectively, was considered.

Fig. 3. Dynamical responses of biomass behaviour in Seagrass habitat subject to 2 years of increased fishing for each scenario under a mixed controlling. System recovery time (*SRT*) as a measure of system`s stability (see text).

Fig. 4. Dynamical responses of biomass behaviour in San-gravel habitat subject to 2 years of increased fishing for each scenario under a mixed controlling. System recovery time (*SRT*) as a measure of system`s stability (see text)

Fig. 5. Dynamical responses of biomass behaviour in San habitat subject to 2 years of increased fishing for each scenario under a mixed controlling. System recovery time (*SRT*) as a measure of system`s stability (see text)

Fig. 6. Dynamical responses of biomass behaviour in Whole area subject to 2 years of increased fishing for each scenario under a mixed controlling. System recovery time (*SRT*) as a measure of system`s stability (see text)

Fig. 6. Continuation.

Fig. 7. Equilibrium simulations of fishing mortality (F_{MSY}) for *Argopecten purpuratus* in seagrass, sand-gravel habitats, and whole area under mixed control.

Fig. 7. Continuation

Table 1. Summary the system recovery time (SRT) and fishing mortality (F_{MSY}) for *A. purpuratus* for each model and scenario under top-down, mixed and bottom-up flow controls.

The flow control is determined by the parameter of vulnerability (v) of equation 2 (see text).

Habitats			Control						
			Top-down			Mixed	Bottom-up		
			1	0.8	0.6	0.4	0.3	0.2	0.1
Seagrass									
Scenario I	<i>A.purpuratus</i>	SRT	Oscilations	40.8	15.2	9.4	7.5	6.5	5.5
		F_{MSY}	Multiples	0.94	1.03	1.03	1.06	1.24	1.71
Scenario II	<i>M.gelatinosus</i>	SRT	Oscilations	95.7	37.2	16.4	11.9	8.6	7.2
Scenario III	<i>H.tasmanica</i>	SRT	Oscilations	55.5	20.3	10.2	9.9	9	8.5
All (I+II+III)		SRT	Oscilations	85.6	37.8	17.4	10.4	8.5	8.4
Sand-Gravel									
Scenario I	<i>A.purpuratus</i>	SRT	Oscilations	65.7	25.9	10.1	7.7	6.2	5.5
		F_{MSY}	Multiples	0.17	0.28	0.52	0.7	1	1.5
Scenario II	<i>M.gelatinosus</i>	SRT	Oscilations	97.6	36.4	16.3	12.4	7	6.1
All (I+II)		SRT	Oscilations	>100	39.6	17.2	12.5	8.6	7.3
Sand									
Scenario I	<i>X.cassidiformis</i>	SRT	Oscilations	Oscilations	Oscilations	7.4	5.6	4.5	4.3
Scenario II	<i>Mulinia</i> sp.	SRT	Oscilations	Oscilations	Oscilations	11.2	9.5	8.4	8
All (I+II)		SRT	Oscilations	Oscilations	Oscilations	15.4	12.4	11.3	11
Whole Area									
Scenario I	<i>A.purpuratus</i>	SRT	Oscilations	>100	34.6	15.7	10.5	7.5	6.2
		F_{MSY}		0.29	0.34	0.45	0.68	0.86	1.1
Scenario II	<i>M.gelatinosus</i>	SRT	Oscilations	>100	35.6	17.7	11.7	8.3	7.1
Scenario III	<i>H.tasmanica</i>	SRT	Oscilations	>100	15.4	9.5	9.7	9.4	9.1
Scenario IV	<i>X.cassidiformis</i>	SRT	Oscilations	50.4	20.5	11	8.6	6.5	5.5
Scenario V	<i>Mulinia</i> sp.	SRT	Oscilations	>100	24.4	14.9	10.9	8.5	7
All scenarios		SRT	Oscilations	>100	37.5	17.4	11.8	9.4	9.1

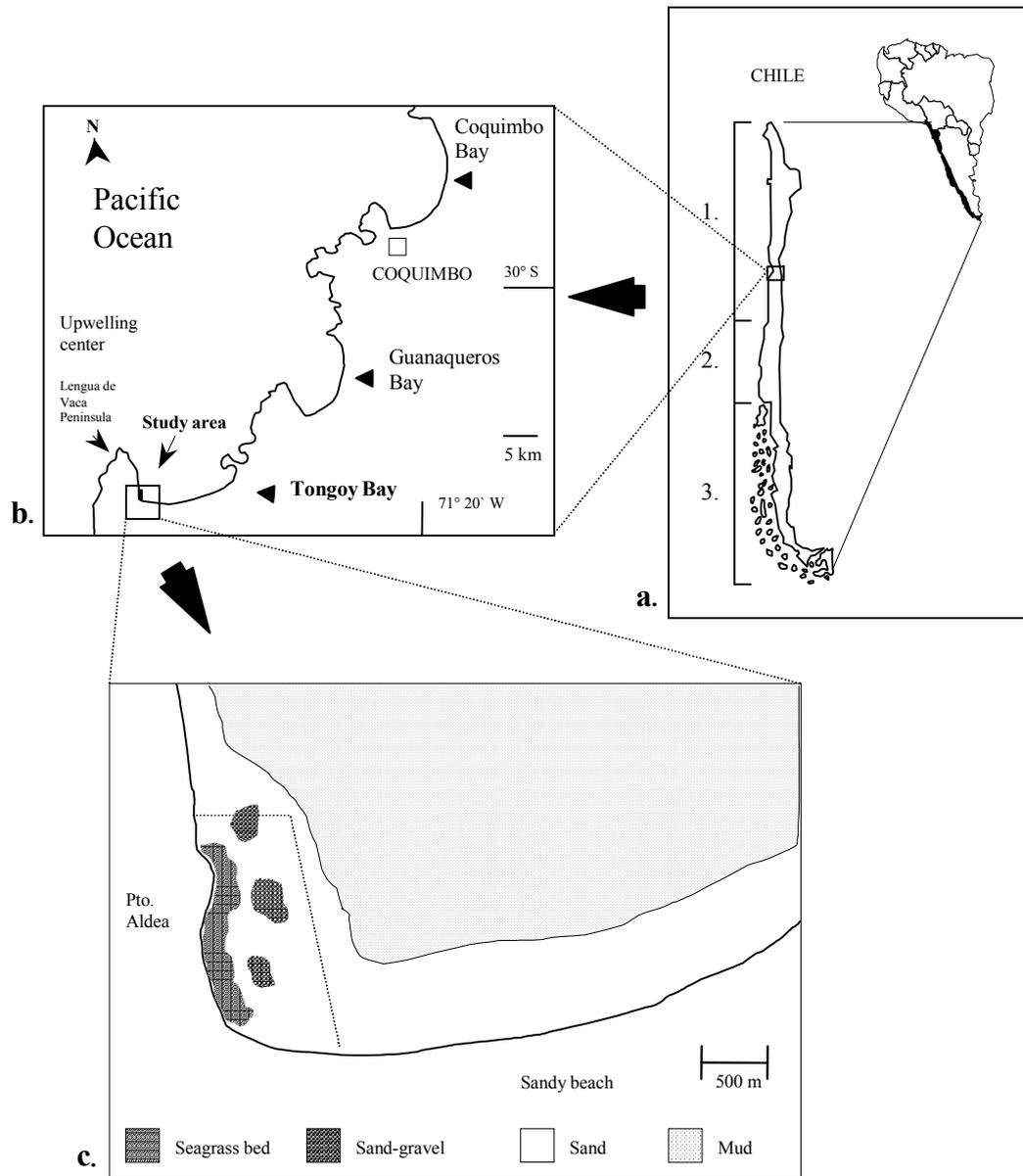


Fig. 1

FISHING MORTALITY

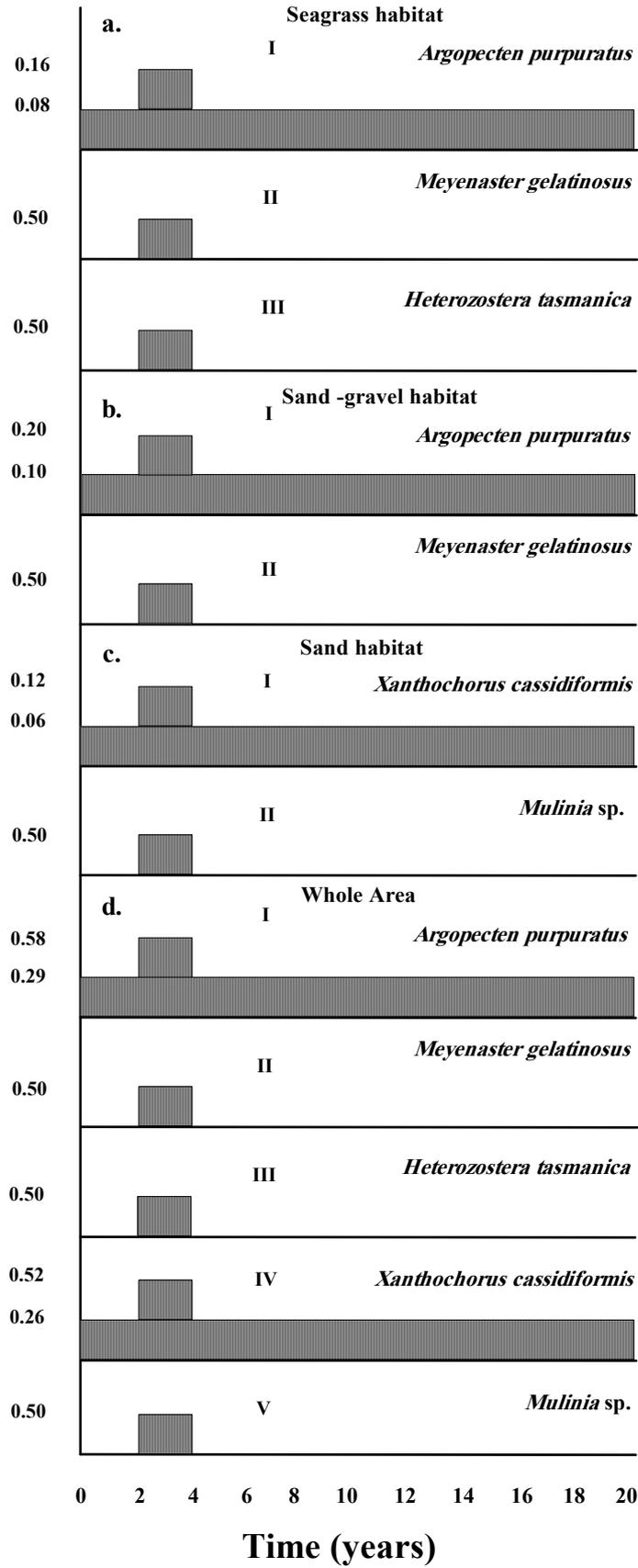


Fig. 2

Seagrass Habitat

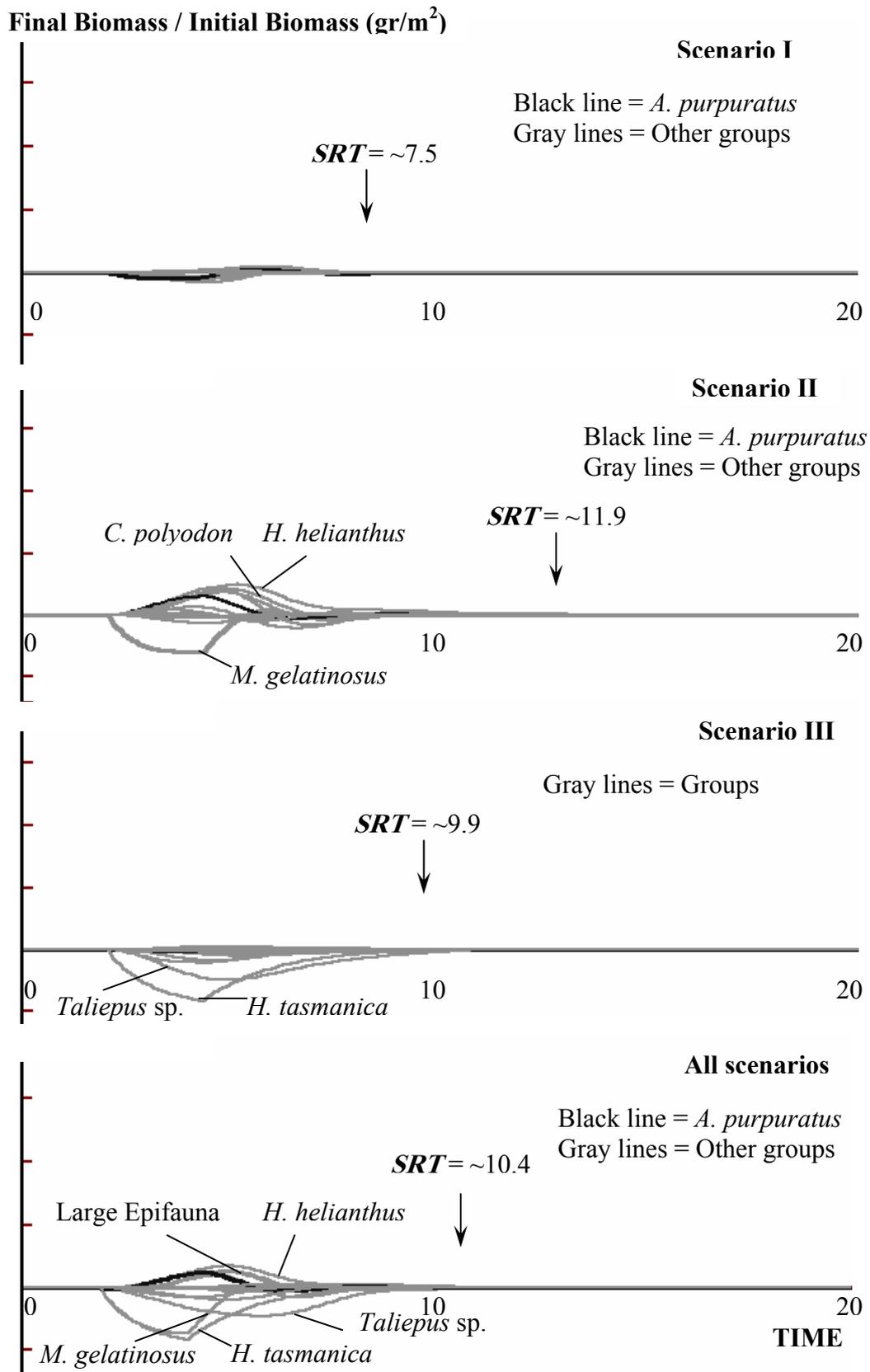


Fig. 3

Sand-Gravel Habitat

Final Biomass / Initial Biomass (gr/m²)

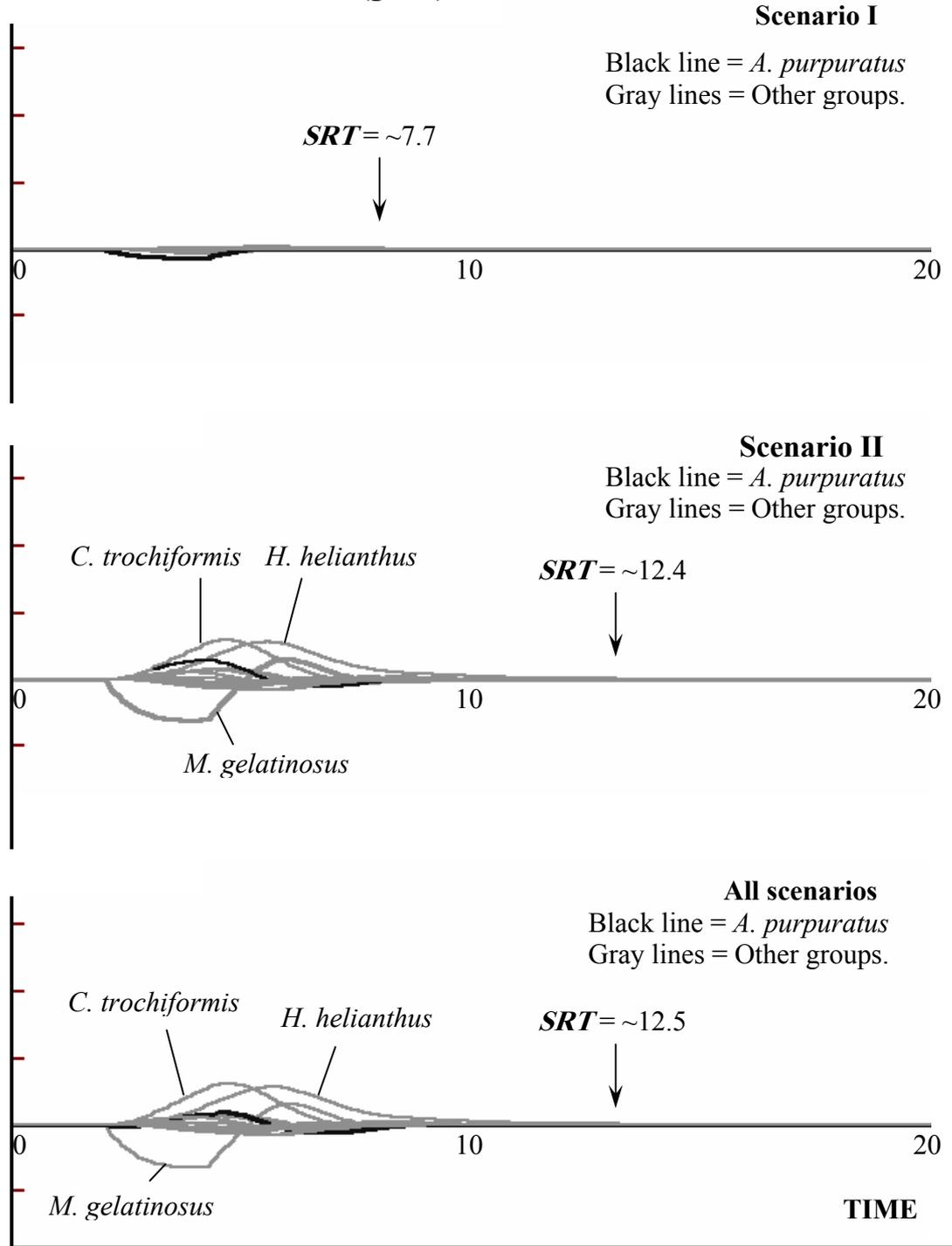


Fig. 4

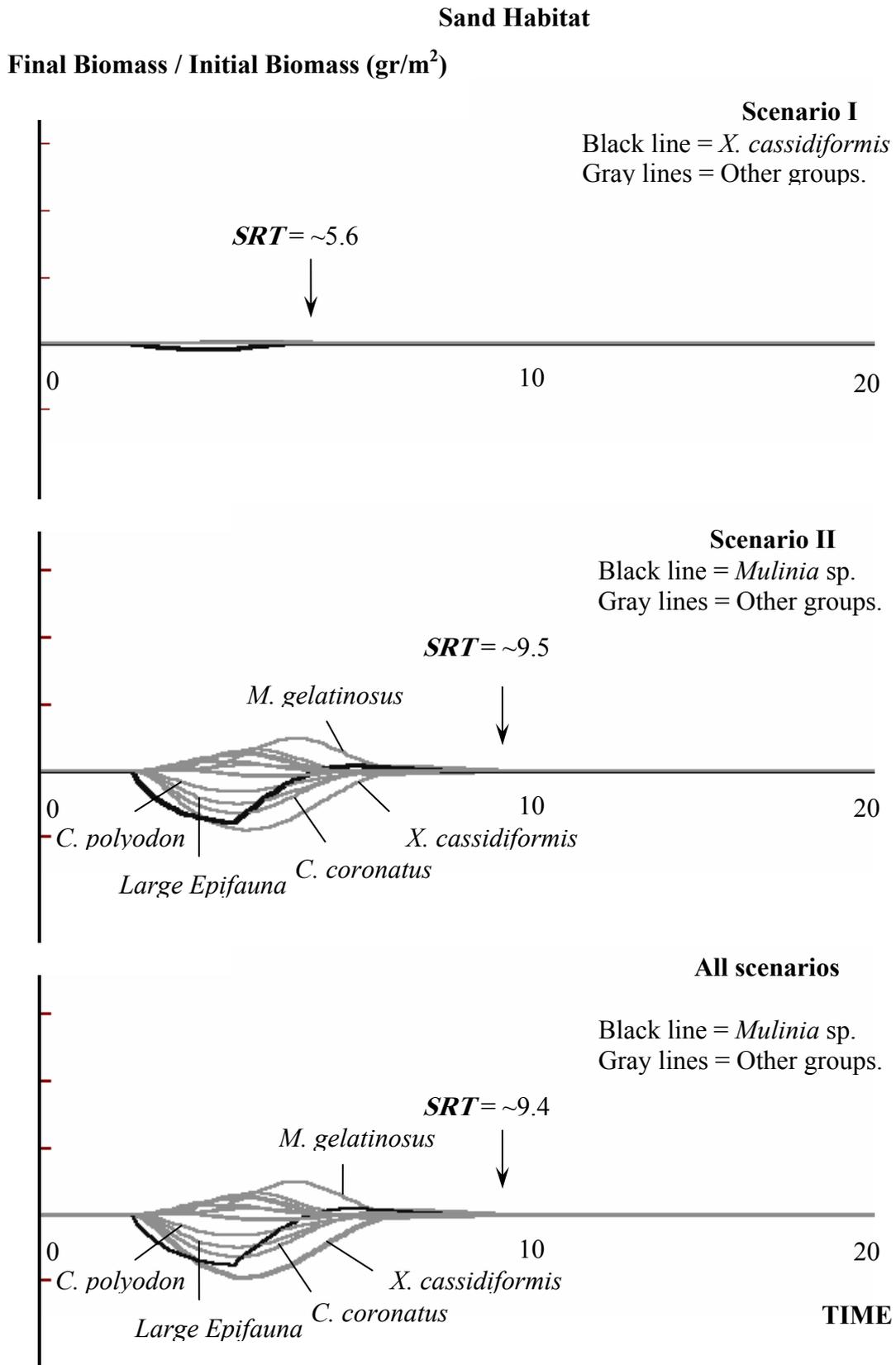


Fig. 5

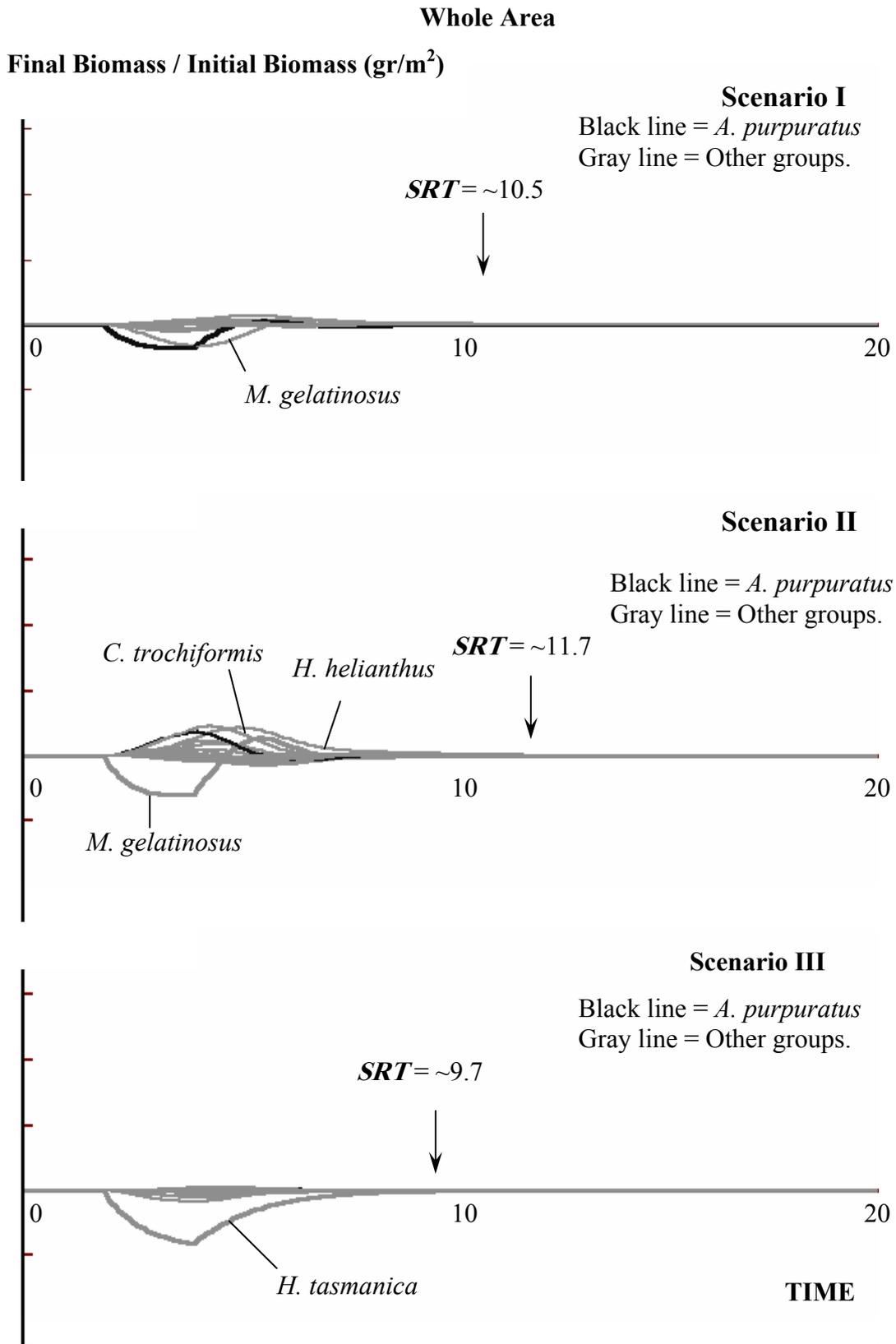


Fig. 6

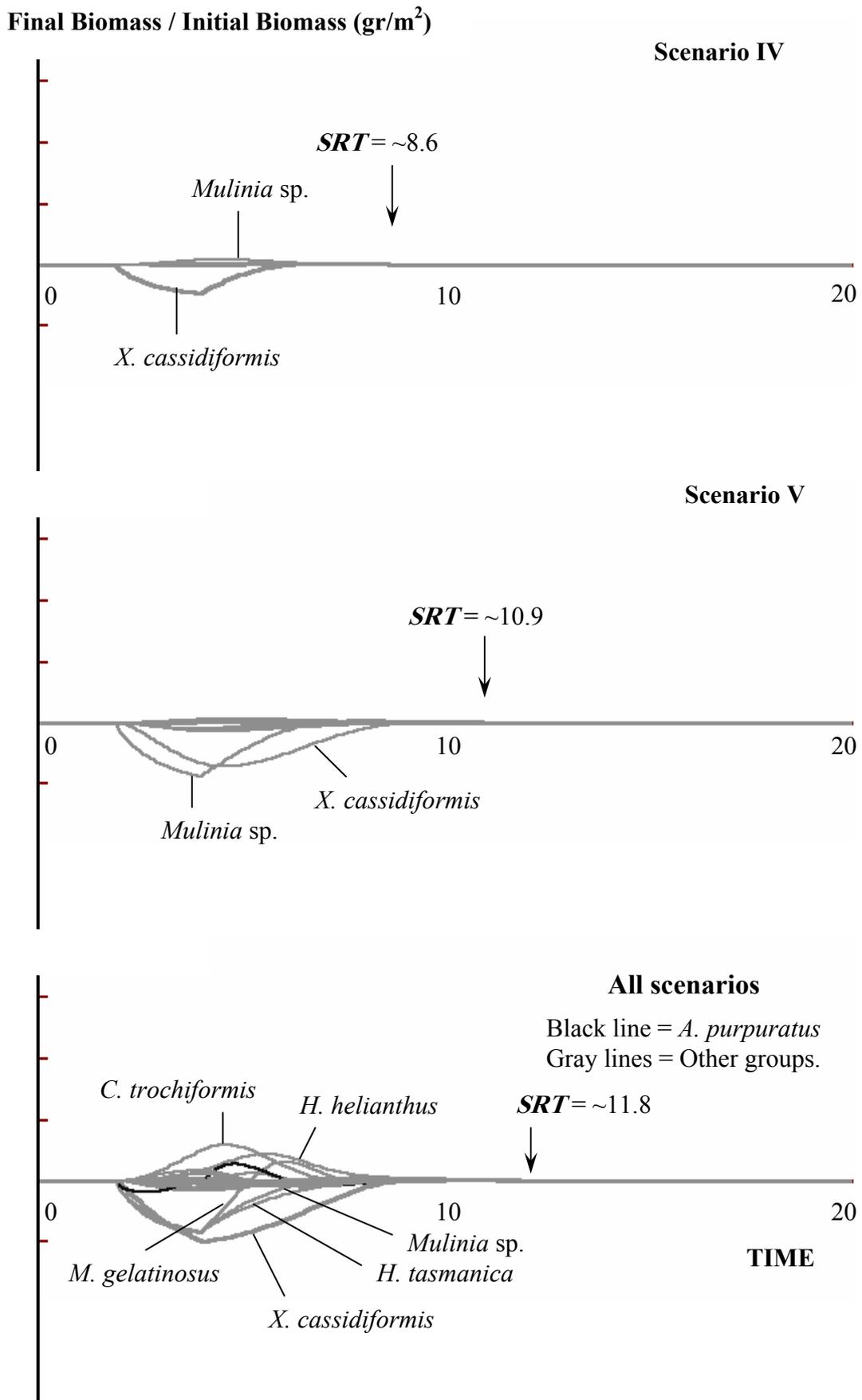


Fig. 6 continuation

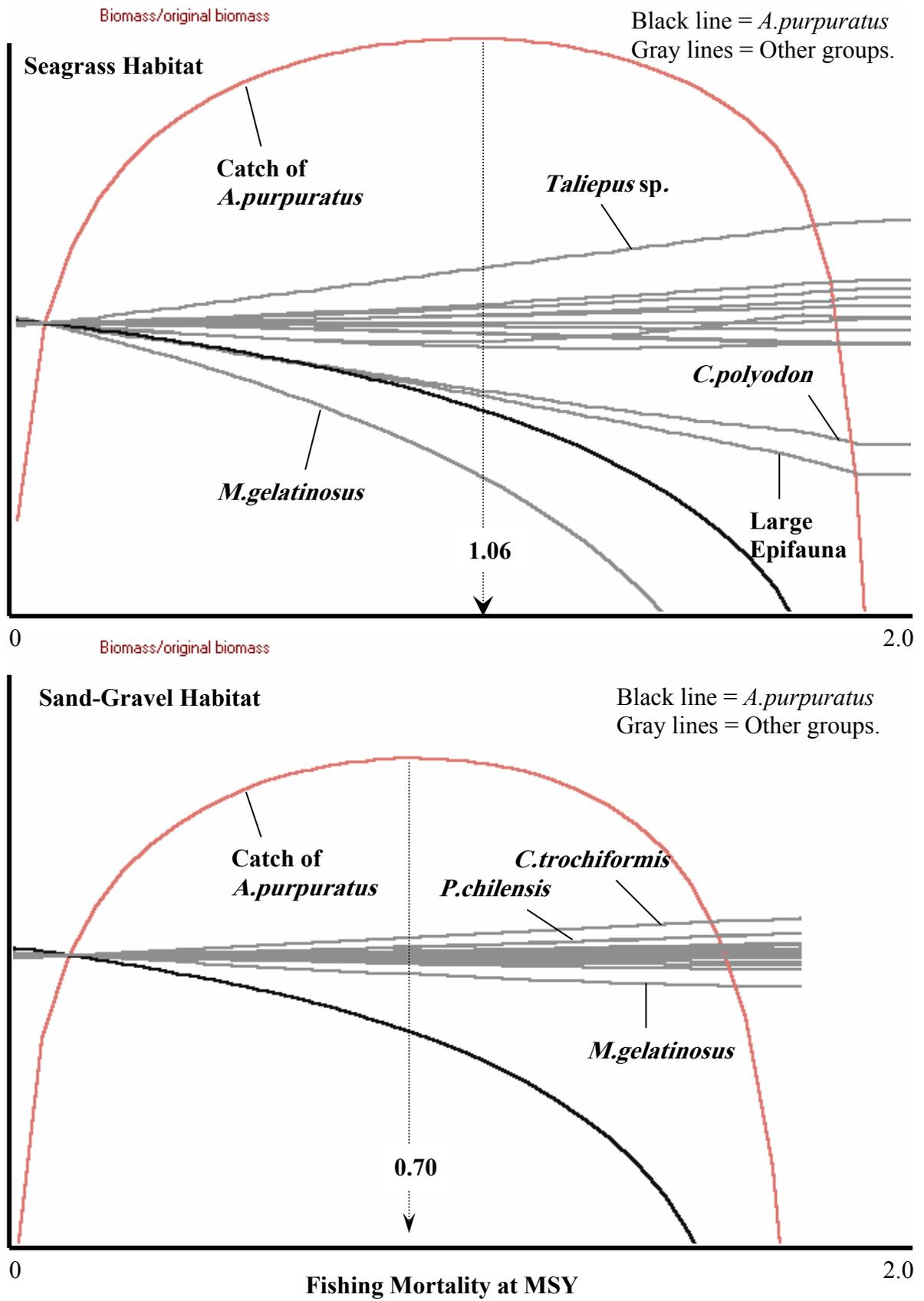


Fig. 7

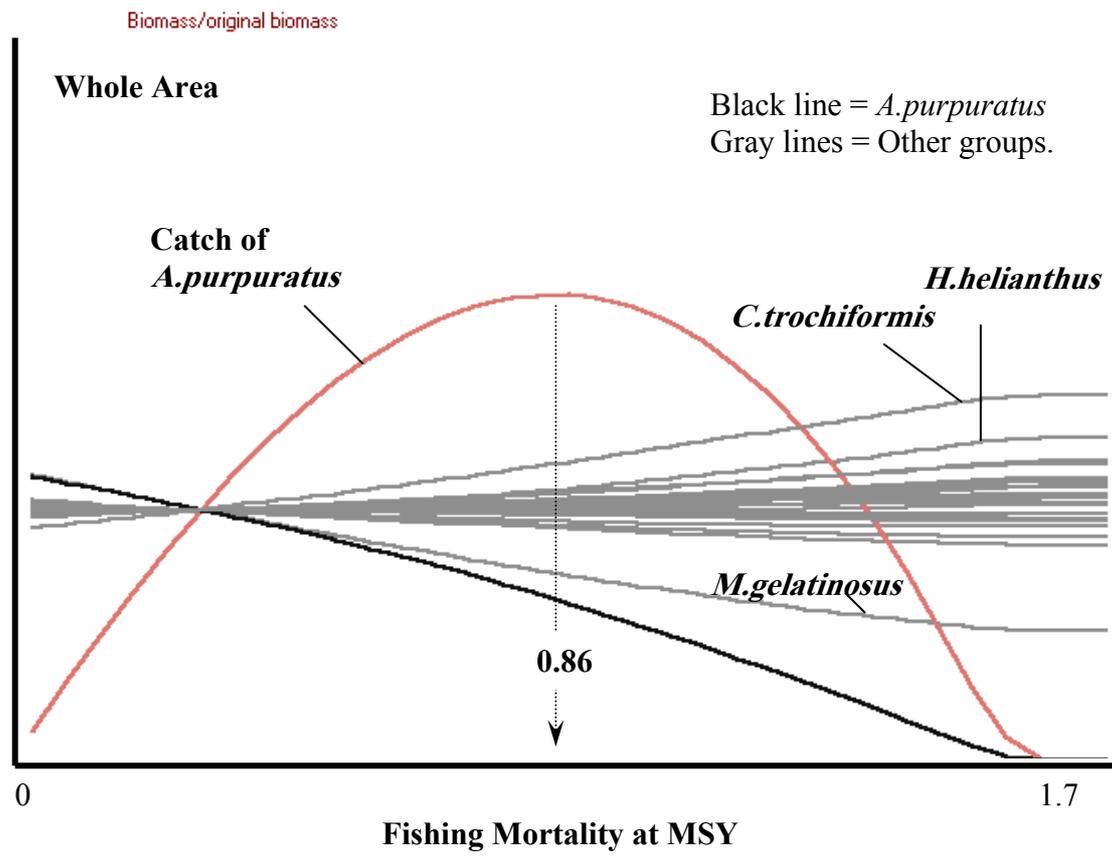


Fig. 7 continuation

8. Chapter V

“Spatially explicit trophic modelling of a harvested benthic ecosystem in Tongoy Bay (central northern Chile)“

Marco Ortiz & Matthias Wolff

Center for Tropical Marine Ecology (ZMT), Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@zmt.uni-bremen.de, mwolff@zmt.uni-bremen.de). Fax : +49 (0) 421 238 00 30.

Key words: ECOSPACE, fisheries management, subtidal communities, trophic dynamic.

2001

The original idea for this publication was developed by the first author. The last version of this contribution was possible after intensive intellectual discussions with the co-author.

ABSTRACT

A dynamical and spatial simulation model of a harvested benthic ecosystem of central northern Chile (Tongoy Bay) was constructed using the ECOSPACE software package of Walter *et al.* (1997, 1999). In this system red algae (*Chondrocanthus chamissoi*), scallops (*Argopecten purpuratus*), gastropods (*Xanthochorus cassidiformis*) and crabs (*Cancer polyodon*) are harvested intensively. The impact of harvesting these resources exclusively in the seagrass, sand-gravel, and in the sand habitats, as well as, in the seagrass and sand-gravel and in all habitats was assessed. The goal was to explore policies of sustainable exploitation of the benthic systems. The most important findings were:

- 1.) An exclusive fishing in the seagrass and sand habitats produces a population increase in the sea star *Luidia magallanica*, in the seagrass *Heterozostera tasmanica*, and in the crab *Paraxanthus barbiger*.
- 2.) Exclusive fishing in the sand-gravel habitat causes only small effects on the compartments, which suggests that this habitat is the most resistant to harvest.
- 3.) The simultaneous fishing on two or three habitats would produce the largest negative effect on the entire system. Therefore, a habitat rotation fishery is recommended.

Our study suggests that trophic-spatially explicit models offer great possibilities for the screening and planning of effective interventions or manipulations of natural systems.

INTRODUCTION

Most trophic ecosystem models assume an homogeneous distribution of the biomass of compartments in an undefined geographical space. But despite this shortcoming and the steady-state abstraction, relevant system descriptions and comparisons between ecosystems can be done by this approach (*sensu* Odum, 1969 and Ulanowicz, 1986, 1997). The dynamical version of these models offer, in addition, the possibility to make predictions of biomass changes, resilience times and maximum possible of fishing rate. These models do not grasp, however, the environmental heterogeneity which causes the patchiness of populations observed in communities (Levins, 1970; Pickett and White, 1985; Hanski, 1999). Thus, ecosystems should rather be conceptualised as constituted by different habitats, mesoscale geographical areas or subsystems (May, 1974; Paine, 1980, 1984; Hall and Raffaelli, 1993). In marine benthic systems, these distinct habitats may be defined by physical and biological factors such as substrate type, a vegetation cover, currents, depth, stochastic recruitment of certain types of organisms, ecological relationships (Lubchenco, 1983; Fairweather, 1988a; Menge, 1991; Hughes and Burrows, 1993; Underwood and Chapman, 1996), and also human-induced habitat interventions (e.g. fisheries, eutrophication, pollution, etc).

Spatially explicit models have been developed since the late 1980s, but most of these have only considered the dynamics of one or two populations linked by prey-predator, parasite-host and intra-inter competitive relationships (e.g. Wolfram, 1984; Green, 1989; Hassell *et al.*, 1991; Comins *et al.*, 1992; Lewis, 1994; Vedyushkin, 1994; Burrows and Hawkins, 1998; Ruxton and Saravia, 1998; Lett *et al.*, 1999; Akçakaya, 2000; Berger and Hildenbrandt, 2000). Few attempts have been made to explore spatial and temporal simulations of trophic relationships at community or ecosystem level. This may be partially due to the large amount of information required and the great number of differential equations needed for conventional theoretical reductionistic methods (Puccia *et al.*, 1994; Levins, 1998a,b).

Recently, Walters *et al.* (1997, 1999) developed a new technique for the modelling of complex systems termed ECOSPACE. By this approach trophic ecosystem models based on ECOPATH II (Christensen and Pauly, 1992) and ECOSIM (Walters *et al.*, 1997), can be simulated spatial and dynamically. ECOSPACE can predict spatial biomass patterns for several hundred grid cells and for a maximum of 25 ecosystem compartments. Additional inputs to the model are movement rates, trophic interactions under bottom-up, top-down or mixed control, habitat preference for each model group and the spatial distribution of fishing effort.

Previous to the here presented study, the authors constructed steady-state and dynamical trophic models for the benthic system of Tongoy Bay (northern Chile) (Wolff, 1994; Ortiz and Wolff, in prep.). By using these models the authors assessed the effect of the following alternative management strategies on the benthic system: (1) increase in the harvest rate of the scallop *Argopecten purpuratus*, and the sandy clam *Mulinia* sp., (2) removal of the undesirable predator species (e.g. asteroid *Meyenaster galatinosus*), and (3) decrease in the abundance of seagrass *Heterozostera tasmanica*. While relevant outcomes in terms of the most sustainable management strategies were obtained, these models do not consider the environmental heterogeneity of this benthic system (Jesse, 2001; Ortiz *et al.*, in prep.). Therefore, the objective of the present study was to add this environmental heterogeneity to the information of trophic interactions for the whole benthic area of Puerto Aldea (Tongoy Bay) (e.g. Wolff, 1994; Ortiz and Wolff, in prep.), and to develop a spatially explicit simulation model using ECOSPACE. Alternative management strategies (fishing effort) were assessed by the exploring and estimating the spatial changes of biomass, resulting from local colonisation and extinction processes (Levins, 1970; Hanski, 1999). When running these simulations were followed assumptions of mixed control mechanism (both top-down and bottom-up) (Hunter and Price 1992; Jordán *et al.* 1999; Menge, 2000). We also believe that mixed control is realistic and the single bottom-up or top-down processes in communities should be considered as false dichotomies, often found in ecology (*sensu* Levins 1998a).

METHODS

Description of study area

The study area of Puerto Aldea (Fig. 1) corresponds to one of 168 management areas (territorial use rights for fisheries) established along the Chilean coast (Castilla, 2000). These areas are assigned to local fishermen organisations in order to maximise, within sustainable boundaries, the production and exploitation of commercial resources. In this area, the following habitats can be distinguished: (1) seagrass meadows from 0 to 4 m depth, (2) sand and gravel between 4 and 10 m, (3) sand flats between 10 and 14 m, and (4) mud flats >14 m depth. A complete biotic and abiotic description of these habitats was done by Jesse (2001) and Ortiz *et al.* (in prep.). The bay and the benthic system of Puerto Aldea are protected from the prevailing south-west winds by Lengua de Vaca peninsula. The upwelling center near this peninsula is among the most important ones of northern Chile (Acuña *et al.*, 1989; Daneri *et al.*, 2000; Montecinos and Quiroz, 2000), supplying nutrients to the ecosystem and simultaneously preventing the establishment of a stable thermocline during summer by the permanent intrusions of upwelled water into the bay. Temperature of bottom water ranges between 13°C and 17°C from winter and autumn respectively (Jesse, 2001).

Spatially explicit dynamical trophic modelling

ECOSPACE represents biomass (B) and consumption (C) (Eqs.1 and 2) dynamics over space and temporal dimensions, that is, varying within spatial coordinates x,y and time. Therefore, the space, time and state of the variables are considered discrete by using the Eulerian

approach which considers the movement as flows of organisms among fixed spatial reference cells.

$$\frac{dB_i}{dt} = g_i \cdot \sum_j C_{ij} - \sum_j C_{ji} + I_i - (M_i + F_i + E_i) \cdot B \quad (1)$$

where,

- g_i = growth efficiency of i
- C_{ji} = consumption rates of j by i compartments
- C_{ij} = consumption rates of i by j compartments
- I_i = immigration rate of i
- M_i = total mortality of i
- F_i = fishing mortality of i
- E_i = emigration rate of i

and additionally,

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v_{ij} + (a_{ij} \cdot B_j)} \quad (2)$$

where,

v_{ij} and v_{ij} = rates of behavioural exchange between invulnerable and vulnerable states, v_{ij} can be defined as the transference rate determining if the control is top-down, bottom-up or mixed. This parameter can range from 1.0 for top-down to 0.0 for bottom-up control. A value of 0.3 represents a mixed control. For more details see ECOSIM programme (Walters *et al.*, 1997).

a_{ij} = rate of effective search by predator j for prey i .

Rectangular grids of spatial cells can be defined by ECOSPACE. For trophic relationships, fishing and movement calculations, biomass is considered as homogeneous within each cell. Additionally, it is possible to assign each cell to a given habitat type, areas with enhanced primary productivity, fishing and for restricted areas. For each cell, the immigration rate I_i (Eq.1) is assumed to consist of four emigration flows from the surrounding cells. The emigration flows are represented as instantaneous movement rates m_i times biomass B_i in each cell (Eq.3),

$$B_{i(x,y)} = m_{i(x,y)} \cdot B_{i(x,y)} \quad (3)$$

where, x,y represents cell row and column.

The instantaneous emigration (dispersal or mixing) rates m_i across cell boundaries are assumed to vary with active organism movements or passive transport by physical processes, preferred habitat, and response of organisms to depredation risk and feeding condition. The probability of movement of organisms towards suitable habitats from its surroundings can be calculated by a "habitat gradient function" for each mapped habitat type and ecosystem compartment i . To each cell a function value of 1.0 for each compartment i is assigned, which becomes 0.0 if the compartment i has been assigned to the suitable habitat and the values will increase to 1.0 if the distance from cells of suitable habitats is large.

Fishing mortality (F_i) can be spatially represented by using a gravity model included into ECOSPACE, by which the proportion of total effort (f) allocated to each cell is considered to be proportional to the sum over groups of biomass multiplied by catchability and market price of the target compartments (Eq.4),

$$G_{kc} = \frac{O_{kc} \cdot U_{kc} \left(\sum_i p_{ki} \cdot q_{ki} \cdot B_{ic} \right)}{C_{kc}} \quad (4)$$

where,

G_{kc} = the weighted attractiveness of cell c to fleet k ,

O_{kc} = is 1 if cell c is open to fleet k , and 0 is closed to harvest,

U_{kc} = is 1 if it was specified that gear k can harvest, and 0 otherwise,

p_{ki} = relative price assigned for compartment i by fleet k fishers,

q_{ki} = catchability of compartment i by fleet k ,

B_{ic} = biomass of the compartment i in cell c , and

C_{kc} = relative cost of fishing in cell c by gear k .

Finally, the spatial simulation searches for a moving equilibrium for each biomass compartment or group based on the Eq. 5,

$$B_{i(t+\Delta t)} = W_{i(t)} \cdot B_{i(t)} + (1 - W_{i(t)}) \cdot B_{i(e)} \quad (5)$$

where,

$B_{i(t+\Delta t)}$ = Biomass of compartment i moving toward the equilibrium along the time trajectory.

$B_{i(t)}$ = Biomass of compartment i at initial time of simulation.

$B_{i(e)}$ = Biomass of compartment i at equilibrium.

$W_{i(t)}$ = is the exponential weight for compartment i . Assuming it as,

$$W_{i(t)} = e^{-(Z_i + E_i) \cdot \Delta t} \quad (6)$$

where,

Z_i = Total instantaneous mortality rate.

E_i = Total instantaneous emigration rate.

For further details of the ECOSPACE model structure see Walters et al. (1999).

Basic assumptions and alternative management scenarios

Table 1 summarises the required information for ECOSPACE simulations of the benthic area of Puerto Aldea. Habitat preferences of species and species groups were based on the abundance observed by Jesse (2001) and Ortiz *et al.* (in prep.). The *dispersal rates* were set according to personal observations and based on the range given by the ECOSPACE programme. They ranged from 9 (km/year) for planktonic compartments to 1 (km/year) for species that inhabit just one habitat. *Relative dispersion in bad habitat* (not suitable) was highest (10 km/year) for mobile predators, intermediate (6 km/year) for the dominant filter-feeding species and plankton, and smallest (1 km/year) value for the species inhabiting only one habitat. The *vulnerability to predation in bad habitat* (dimensionless) was set as 1.0 for the three starfish species, plankton and infauna groups, and 100.0 for the remainder species. The *relative feeding rate in bad habitat* ranked from 1.0, 0.5 to 0.01 values. The smallest was assigned for the species that inhabit only one habitat and the highest for plankton and infauna. For the remainder species or groups an intermediate value was assigned. Through the selection of these indexes we try to consider that some species are semi-sesile or inhabitants of one habitat such as the seagrass *H. tasmanica*, the macroalgae *Ch. chamissoi*, other rodophyta, *Ulva* sp., the crab *C. porteri*, the tunicate *P. chilensis*, the sandy mussel *Mulinia* sp., the gastropods *X. cassidiformis* and *C. trochiformis*, and those inhabit all habitats or with migrations between habitats such as the crabs *C. polyodon*, *C. coronatus*, *P. barbiger*, *Taliepus* sp., large epifauna (other crabs species), the sea stars *M. gelatinosus*, *H. helianthus* and *L. magallanica*, and the snail *Tegula* sp., and small epifauna (other gastropods) (Table 1).

The combined model, which integrates the four habitats is based on the ECOPATH II model given by Ortiz and Wolff (in prep.). In this benthic area just four species are harvested: the rodophyta *Ch. chamissoi* (ca. 114 ton/year), the scallop *A. purpuratus* (ca. 16 ton/year), the snail *X. cassidiformis* (ca. 0.6 ton/year) and the crab *C. polyodon* (ca. 0.4 ton/year). Fig. 2a shows the geographical distribution of each habitat type in the study area. The different management scenarios considered in the simulations are shown in Fig. 2b. All of following scenarios were simulated over a 5 years period: I.- fishing exclusively in the seagrass habitat, II.- fishing exclusively in the sand- gravel habitat, III.- fishing exclusively in the sand habitat, IV.- fishing in both seagrass and sand-gravel habitats, and, V.- simultaneous harvest in all habitats. The simulations were done under the assumption of a mixed control (food and predator controlled) mechanism. The market prices, operational coasts and the primary production/upwelling rate were not included during the simulations.

RESULTS

Figs. 3, 4, 5, 6, 7 illustrate the spatial dynamic predictions for the most relevant species which inhabit this benthic system. The patterns represent the final configuration after 5 years of simulation. Within this period a new moving equilibrium between colonisation and extinction of grids was reached. It is important to indicate that when the simulation begins (at time=0) the species and/or compartments are homogeneously distributed in their preferred habitat with grey grids (Table 1). At the end of simulation (5 years), black and white grids represent an increase and decrease in biomass respectively.

Under a harvest pressure upon seagrass (scenario I) the starfish *L. magallanica* was positively affected, whereas the starfish *H. helianthus* experimented an opposite impact. For *L. magallanica* ECOSPACE predicted a higher 'aggregation' of biomass (in black) in the sand-gravel habitat. However, this increase promotes a subsequent colonisation of adjacent grids, reaching the seagrass and sand habitats (Fig. 3). For the exploited scallop *A. purpuratus* ECOSPACE predicts an increase in abundance basically in the seagrass habitat followed by the sand-gravel. However, the colonisation did not reach the adjacent sand habitat. The seagrass *H. tasmanica* showed also an increasing abundance slightly reaching other adjacent grids. For the crab *Taliepus* sp the programme predicted a decrease of biomass especially in the seagrass habitat. On the contrary the gastropod *Tegula* sp. increased in the sand-gravel. For the Large Epifauna a depletion of biomass in the mud habitat was observed, whereas for Infauna a slight increase in the sand-gravel was detected (Fig. 3).

The spatial responses of the compartments under scenario II are illustrated in Fig. 4. The sea star *L. magallanica* is slightly positive impacted and the species tends to colonise the adjacent grids of the seagrass and the mud habitats. For the other species selected, small changes were observed (Fig. 4), conserving their original biomass. For scenario III only the dynamical pattern of the dominant species in the sand habitat is shown here (Fig. 5). Most of the species or groups which inhabit the sand habitat showed a decrease in their biomass. The crab *C. coronatus* decreased in abundance in the sand habitat, whereas the Large Epifauna decreased in the mud habitat. For both the snail predator *X. cassidiformis* and its prey, the mussel *Mulinia* sp., ECOSPACE predicted a depletion. For the Small Epifauna and Infauna compartments a decrease, particularly in sand habitat, was also observed (Fig. 5).

Under the fishing scenario IV, ECOSPACE predicted a similar spatial dynamics for the sea star *L. magallanica* and the seagrass *H. tasmanica* compared to scenario I. Nonetheless, the colonisation of adjacent grids was reduced (Fig. 6). The principal exploited species, the rodophyta *Ch. chamissoi* and the scallop *A. purpuratus* showed a decrease in abundance. Likewise, the sea star *H. helianthus*, the tunicate *P. chilensis*, and the Large Epifauna also showed a depletion in biomass (Fig. 6). Finally, Fig. 7 shows the spatial

dynamics of the more relevant benthic species in the study area under scenario V. It is possible to observe a similar pattern for the species and groups as for scenario IV. Only for *L. magallanica* and *H. tasmanica* ECOSPACE predicts an increase of abundance with the subsequent colonisation of adjacent places (Fig. 7).

Figs 8a,b,c,d,e show the relative changes in abundance of all compartments. An interesting finding is that the scenarios I and III propagated the largest impacts on the benthic system, in comparison to the effects of the scenario II (Figs. 8a,b,c). Likewise, scenarios I and III shows a similar overall propagation of effects. On the other hand, the simultaneous harvest on the seagrass and sand-gravel (scenario IV) (Fig. 8d) and on the three habitats (scenario V) (Fig.8e) showed a similar pattern on the species and groups. Only two benthic species the sea star *L. magallanica* and the seagrass *H. tasmanica* were positively impacted (Fig. 8d,e).

DISCUSSION

Based on the ECOSPACE programme, the spatial development in abundance of the species inhabiting the four benthic systems was possible to model. Even though there is not experimental evidence to validate the spatial dynamics for all species obtained, own observations revealed similar tendencies. Recently Jesse (2001) reported for the crabs species *C. coronatus* and *C. porteri* seasonal aggregations in the sand and mud habitat. Likewise, similar clumping in the seagrass and sand-gravel has been detected for the starfish species (Ortiz, pers. obs.). Similar changes in abundance within the boundaries of the seagrass meadows with the adjacent sand-gravel habitat had been also observed (Ortiz pers. obs.). However, further studies should be conducted to estimate the migration or colonisation patterns for these species and to understand the underlying factors and processes.

It is not surprising that the spatial patterns obtained here were not very dynamic due to the low dispersal rates and the mixed flow control assumed in the simulation. For pelagic model ecosystems, with higher dispersal rates, relevant changes in the compartments have been observed (Walters *et al.* 1999). Even though ECOSPACE was not developed for detailed quantitative predictions (Walters *et al.* 1999), it may be a useful tool for the assessment of relative changes in abundance and the propagation of given effects into any system as response to different scenarios of fishing. The quality of our findings (spatial dynamics and changes in abundance) here presented is difficult to assess, especially because just few ECOSPACE models have been done and cross checked with observations and experimental results. Despite these restrictions, two clear qualitative findings seem to emerge: (1) the sand-gravel habitat seems to be the most resistant to harvest activities, and (2) the fishing on two or three habitats simultaneously would produce largest negative effects on the entire system. Therefore, a rotation harvest policy would be recommended. The follow dynamical aspects may be explained by the dominance of direct and indirect effects governed by competition, depredation, mutualistic and ammensalistic mechanism (Lawlor, 1979; Higashi and Patten, 1986, 1989; Wootton, 1992, 1994; Billick and Case, 1994; Menge, 1995; Fath and Patten, 1999; Underwood, 1999): (1) the propagation of impacts on the compartments, (2) the explosive increase of biomass in the sea star *L. magallanica* (scenarios I and III), (3) the negative correlation of abundance between both herbivorous the crab *Talipes* sp and the snail *Tegula* sp. (scenario I) and (4) the negative correlation between carnivorous crabs *C. coronatus* and the Large Epifauna (*Platymera guadichaidii* and *Hepatus chilensis*) (scenario III). Similar switches for other ecological simulations have been described (Mackinson *et al.*, 1997; McClanahan and Sala, 1997).

The propagation of severe effects upon the species and the positive responses of competitor species (*L. magallanica*) can also be interpreted as the dominance of positive

feedback which may drive the benthic system to some other dynamic equilibrium (Levins 1998b). Therefore, this positive feedback must be avoided if our goal is to harvest under sustainable boundaries. One way to depress this positive feedback may be by developing a habitat rotation fishing strategy. A simultaneous harvest on two or three habitats is not recommended, because severe impacts on the remainder populations and compartments are expected.

The dynamical spatial simulation carried out in the combined benthic model showed how the effects of the fishing activities propagate in time and space producing relevant cascading effects in the species and groups. Although detected impacts were given in terms of quantifiable biomass, the complexity of ecological interactions in these four benthic habitats make a prediction of the exact amount of change difficult. However, a qualitative analysis of the generalised direction of changes seems to be possible. There are, nonetheless, some sources of eventual bias related to simulations, such as here presented: the equilibrium assumptions of ECOPATH II plays a relevant role here as it is directly related with the problem of choosing the right period over which the simulation should be run. Another shortcoming is that ECOSPACE takes into account only trophic (diet) relationships and absence of complex life histories. Nevertheless, if only short-term dynamics are assumed (as in the present study), ECOSPACE can be a useful tool for displaying propagated changes to evaluate the sustainability of alternative management policies.

ACKNOWLEDGEMENTS

REFERENCES

- Acuña E, Moraga J, Uribe E. 1989. La zona de Coquimbo: un sistema nerítico de alta productividad. *CPPS Revista del Pacífico Sur, N° especial*: 145-157.
- Akçakaya HR. 2000. Viability analyses with habitat-based metapopulation models. *Population Ecology* 42: 45-53.
- Berger U, Hildenbrandt H. 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. *Ecological Modelling* 132: 287-302.
- Billick I, Case TJ. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology* 75: 1529-1543.
- Burrows, MT, Hawkins SJ. 1998. Modelling patch dynamics on rocky shores using deterministic cellular automata. *Marine Ecology Progress Series* 167: 1-13.
- Castilla JC. 2000. Roles of experimental marine ecology in coastal management and conservation. *Journal Experimental Marine Biology and Ecology* 250: 3-21.
- Chistensen V, Pauly D. 1992. ECOPATH II. a software for balancing steady-state ecosystems models and calculating network characteristics. *Ecological Modelling* 61: 169-185.
- Commins HN, Hassell MP, May RM. 1992. The spatial dynamic of host-parasitoid systems. *Journal of Animal Ecology* 61: 735-748.
- Daneri G, Dellarossa V, Quiñones R, Jacob B, Montero P, Ulloa O. 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Marine Ecology Progress Series* 197: 41-49.
- Fairweather PG. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Australian Journal of Ecology* 13: 401-409.
- Fath B, Patten B. 1999. Review of the foundations of network analysis. *Ecosystems* 2: 167-179.
- Green DG. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. *Vegetatio* 82: 139-153

- Hall S, Raffaelli D. 1993. Food Webs: theory and reality. *Advances in Ecological Research* 24: 187-239.
- Hanski I. 1999. Metapopulation Ecology. Oxford Series in Ecology and Evolution. Oxford.
- Hassel MP, Comins HN, May RM. 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353: 255-258.
- Higashi M, Patten B. 1986. Further aspects of the analysis of indirect effects in ecosystems. *Ecological Modelling* 31: 68-77.
- Higashi M, Patten B. 1989. Dominance of indirect causality in ecosystems. *The American Naturalist* 133: 288-302.
- Hughes RN, Burrows MT. 1993. Predatory behaviour of the intertidal snail, *Nucella lapillus*, and its effects on community structure. In *Mutualism and community organisation: behavioural, theoretical and food web approaches*, Kawanabe H, Cohen JE, Iwasaki K (Eds.), Oxford University Press, Oxford; 63-83.
- Hunter MD, Price PW. 1992. Playing chutes and ladders: bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.
- Jesse S. 2001. Comparative ecology of sympatric brachyuran crab species in the shallow subtidal of the Pacific Coast on North Chile and their importance for the artisanal fishery in Puerto Aldea. PhD Dissertation, University of Bremen, Germany.
- Jordán F, Takács-Sánta A, Molnár I. 1999. A reliability theoretical quest for keystone. *Oikos* 86: 453-462.
- Lawlor LR. 1979. Direct and indirect effects of n-species competition. *Oecologia* 43: 355-364.
- Lett C, Silver C, Barret N. 1999. Comparison of a cellular automata network and an individual-based model for the simulation of forest dynamics. *Ecological Modelling* 121: 277-293.
- Levins R. 1970. Extinction. In *Some mathematical problems in biology. Lectures on mathematics in the life sciences, N° 2*. Gerstenhaber M (Ed.); 77-107. American mathematical society, Providence, Rhode Island, USA.
- Levins R. 1998a. The internal and external explanatory theories. *Science as Culture* 7(4): 557-582.
- Levins R. 1998b. Dialectics and systems theory. *Science & Society* 62(3): 375-399.
- Lewis MA. 1994. Spatial coupling of plant and herbivore dynamics: the contribution of herbivore dispersal to transient and persistent `waves` of damage. *Theoretical Population Biology* 45: 277-312.
- Lubchenco J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity and plant escapes during succession. *Ecology* 64: 1116-1124.
- Mackinson S, Vasconcellos M, Pitcher T, Walters C. 1997. Ecosystem impact of harvesting small pelagic fish in upwelling systems: using a dynamic mass-balance model. *Proceedings, Forage Fishes in Marine Ecosystems Alaska Sea Grant College Program (AK-SG-97-01)*.
- May RM. 1974. Stability and complexity in model ecosystems. 2nd Edition, Princeton University Press, New Jersey.
- McClanahan TR, Sala E. 1997. A mediterranean rocky-bottom ecosystem fisheries model. *Ecological Modelling* 104: 145-164.
- Menge BA. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146: 69-100.
- Menge BA. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65: 21-74.

- Menge BA. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250: 257-289.
- Montecinos V, Quiroz D. 2000. Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30°). *Aquatic Sciences* 62: 364-380.
- Odum EP. 1969. The strategy of ecosystem development. *Science* 104: 262-270.
- Paine RT. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49: 667-685.
- Paine RT. 1984. Some approaches to modelling multispecies systems. In *Exploitation of marine communities*, May RM (Ed.); 191-207. Dahlem Konferenzen, Springer-Verlag, Berlin.
- Pickett ST, White PS (Eds). 1985. The ecology of natural disturbances and patch dynamics. Academic Press, London.
- Puccia Ch, Awerbuch T, Levins R. 1994. Models for new and resurgent diseases. *Annals New York Academy of Sciences* 740: 225-231.
- Ruxton GD, Saravia LA. 1998. The need for biological realism in the updating of cellular automata models. *Ecological Modelling* 107: 105-112.
- Underwood AJ. 1999. Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *Journal of Experimental Marine Biology and Ecology* 232: 125-140.
- Underwood AJ, Chapman MG. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 104: 212-224.
- Ulanowicz R. 1986. Growth and development: Ecosystems phenomenology. Springer, New York.
- Ulanowicz R. 1997. Ecology, the Ascendent Perspective. Complexity in Ecological Systems Series, Columbia University Press, New York.
- Vedyushkin MA. 1994. Fractal properties of forest spatial structure. *Vegetatio* 113: 65-70.
- Walters CJ, Christensen V, Pauly D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessment. *Reviews in Fish Biology and Fisheries* 7: 1-34.
- Walters CJ, Pauly D, Christensen V. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2: 539-554.
- Wolff M. 1994. A trophic model for Tongoy Bay –a system exposed to suspended scallop culture (Northern Chile). *Journal of Experimental Marine Biology and Ecology* 182: 149-168.
- Wolfram S. 1984. Cellular automata as models of complexity. *Nature* 311: 419-424.
- Wootton JT. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology* 73(3): 981-991.
- Wootton JT. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75(1): 151-554.

List of Tables and Figures

Table 1. Input data for ECOSPACE programme.

Fig. 1. a.) Main topographical types along the Chilean coast: 1.= dominated by exposed rocky shores, 2.= dominated by exposed sandy shores, 3.= mostly insular systems. b.) Principal bay systems of the IV Region of Coquimbo, Chile. c.) Study area of Puerto Aldea located at southern of Tongoy Bay.

- Fig. 2. a.) Spatial distribution of four habitats in the management benthic area of Puerto Aldea. (FH = fishing harbour), b.) Harvest scenarios simulated by ECOSPACE.
- Fig. 3. Biomass spatial distribution of the relevant populations and groups inhabit the seagrass habitat after 5 years of simulation under scenario I.
- Fig. 4. Biomass spatial distribution of the relevant species and groups inhabit the sand-gravel habitat after 5 years of simulation under scenario II.
- Fig. 5. Biomass spatial distribution of the relevant species and groups inhabit the sand habitat after 5 years of simulation under scenario III.
- Fig. 6. Species and groups with the largest changes in spatial biomass after 5 years of simulation under scenario IV.
- Fig. 7. Species and groups with the largest changes in spatial biomass after 5 years of simulation under scenario V.
- Fig. 8. Propagation of changes in biomass for all species and groups after 5 years of simulation under: a.) scenario I, b.) scenario II, c.) scenario III, d.) scenario IV, and e.) scenario V.

Table 1. Input data for ECOSPACE programme.

Species	Habitat Preference	Dispersal rates (km/year)	Relative dispersion in bad habitat	Vulnerability to predation in bad habitat	Relative feeding rate in bad habitat
<i>Megenaster gelatinosus</i>	Seagrass/Sand-Gravel	1.5	10	1	0.5
<i>Heliaster helianthus</i>	Seagrass/Sand-Gravel	1.5	10	1	0.5
<i>Luidia magallanica</i>	Sand Gravel	1.5	10	1	0.5
<i>Cancer polyodon</i>	Seagrass/Sand-Gravel/Sand	3	10	100	0.5
<i>Cancer porteri</i>	Mud	1	1	100	0.01
<i>Cancer coronatus</i>	Sand/Mud	3	10	100	0.5
<i>Paraxanthus barbiger</i>	Sand-Gravel	1.5	10	100	0.5
Large Epifauna	Sand/Mud	3	10	100	0.5
<i>Xanthochorus cassidiformis</i>	Sand	1	1	100	0.01
<i>Argopecten purpuratus</i>	Seagrass/Sand-Gravel	1.5	6	100	0.5
<i>Taliepus</i> sp.	Seagrass/Sand-Gravel	1.5	6	100	0.5
<i>Mulinia</i> sp.	Sand	1	1	100	0.01
<i>Calyptreaea trochiformis</i>	Sand-Gravel	1	1	100	0.01
<i>Tegula</i> sp.	Seagrass/Sand-Gravel	1.5	6	100	0.5
<i>Pyura chilensis</i>	Sand-Gravel	1	1	100	0.01
Small Epifauna	All	1.5	6	100	0.5
Infauna	All	1	1	1	1
<i>Heterozostera tasmanica</i>	Seagrass	1	1	100	0.01
<i>Chondrocanthus chamissoi</i>	Sand-Gravel	1	1	100	0.01
Rodophyta	Sand-Gravel	1	1	100	0.01
<i>Ulva</i> sp.	Sand-Gravel	1	1	100	0.01
Zooplankton	All	9	6	1	1
Phytoplankton	All	9	6	1	1
Detritus	All	1	1	1	1

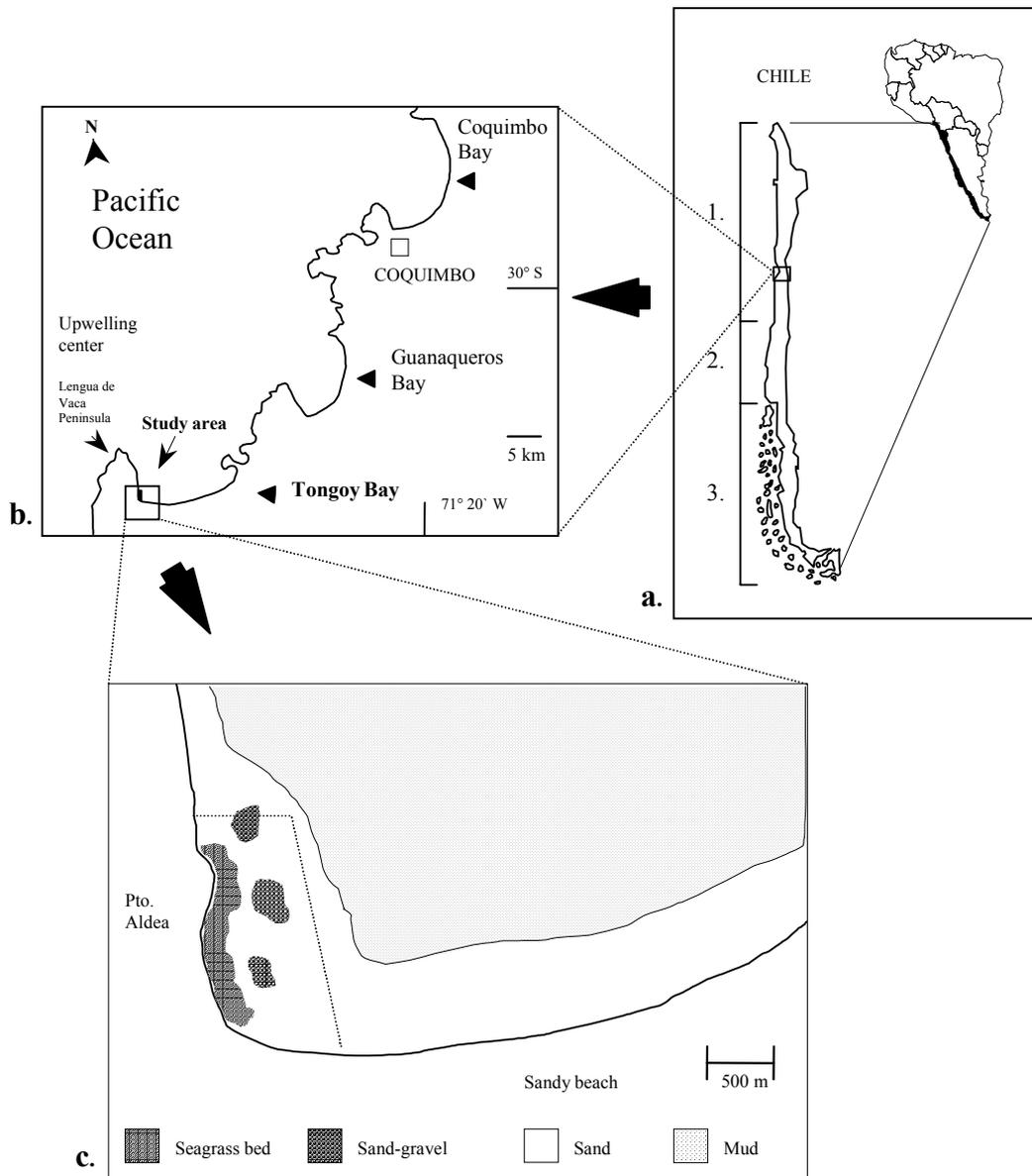


Fig. 1

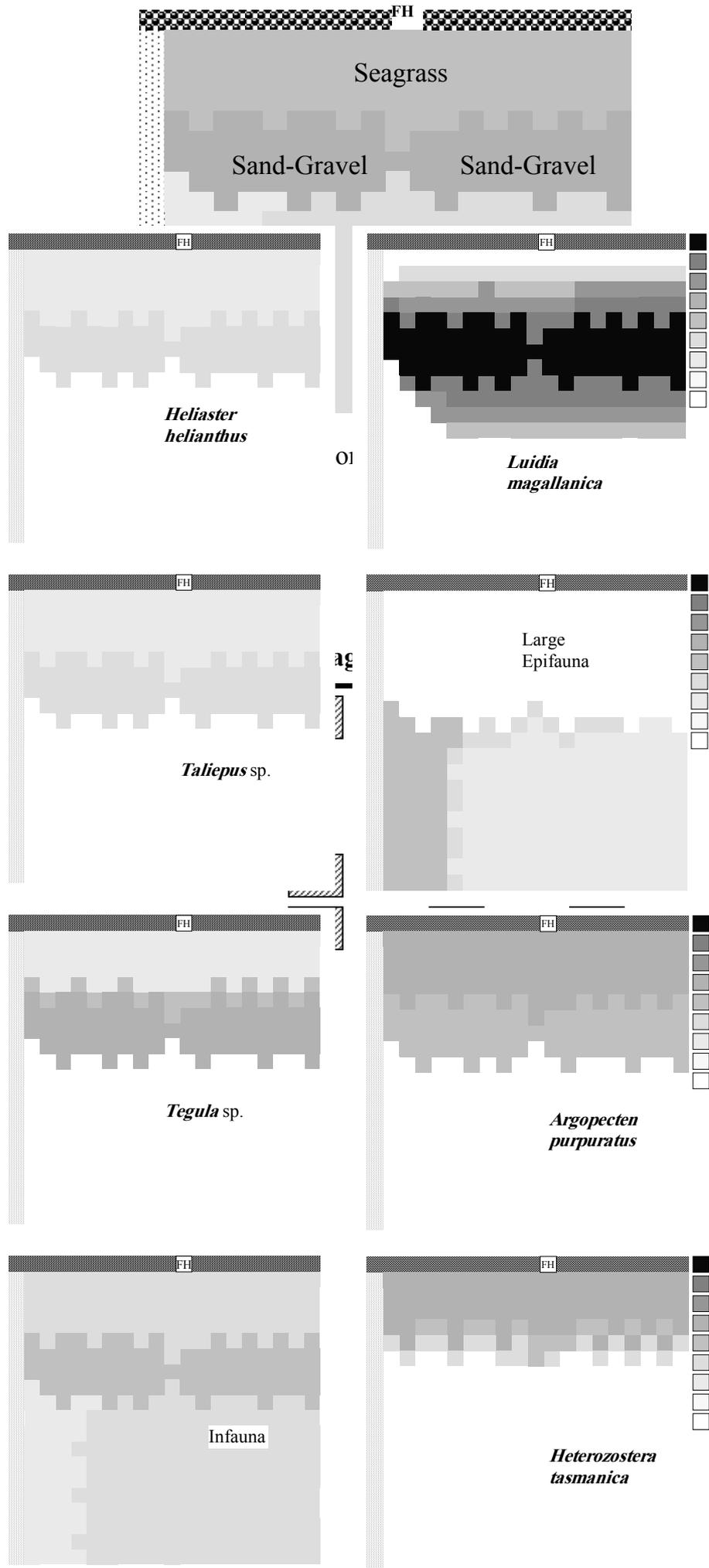


Fig. 2

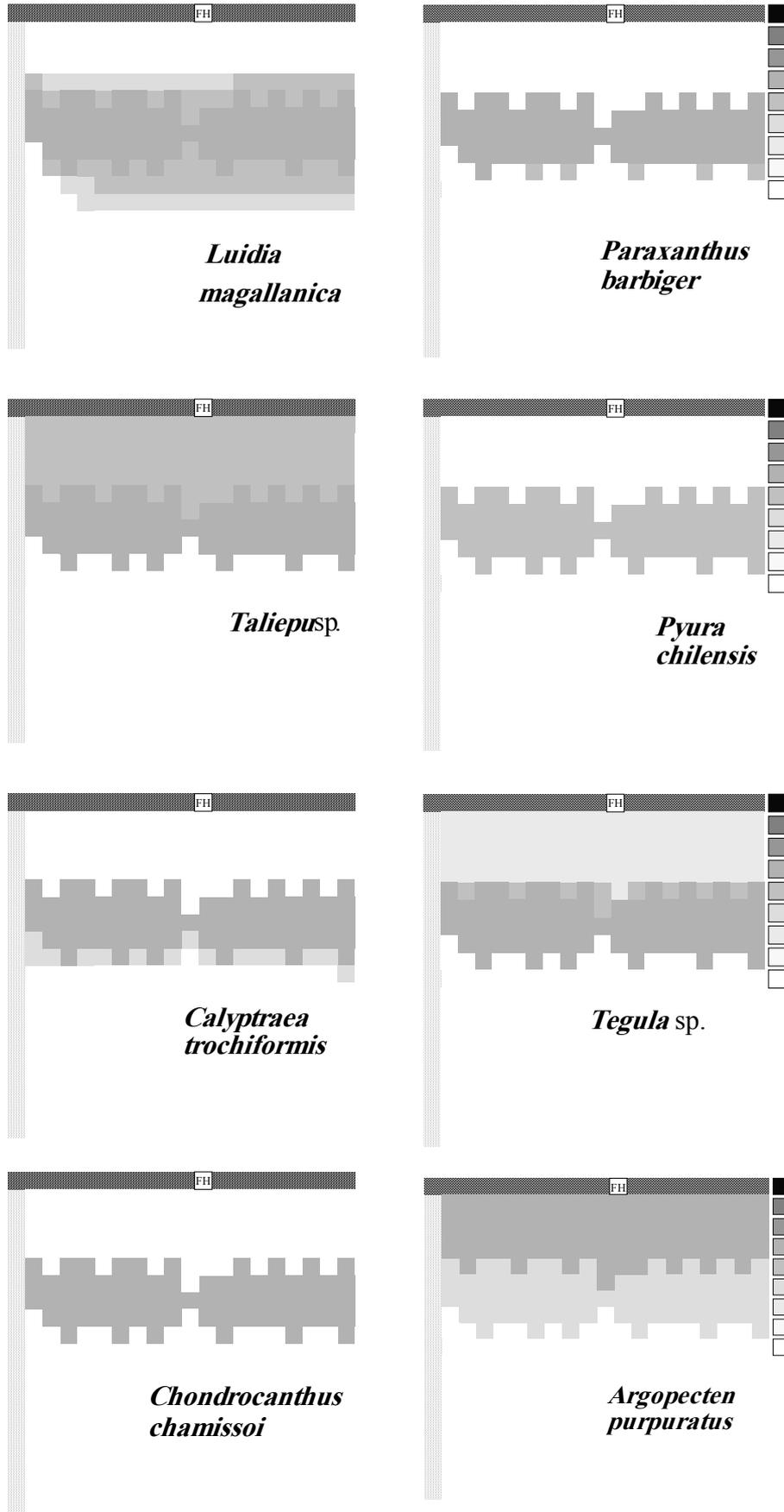


Fig. 3

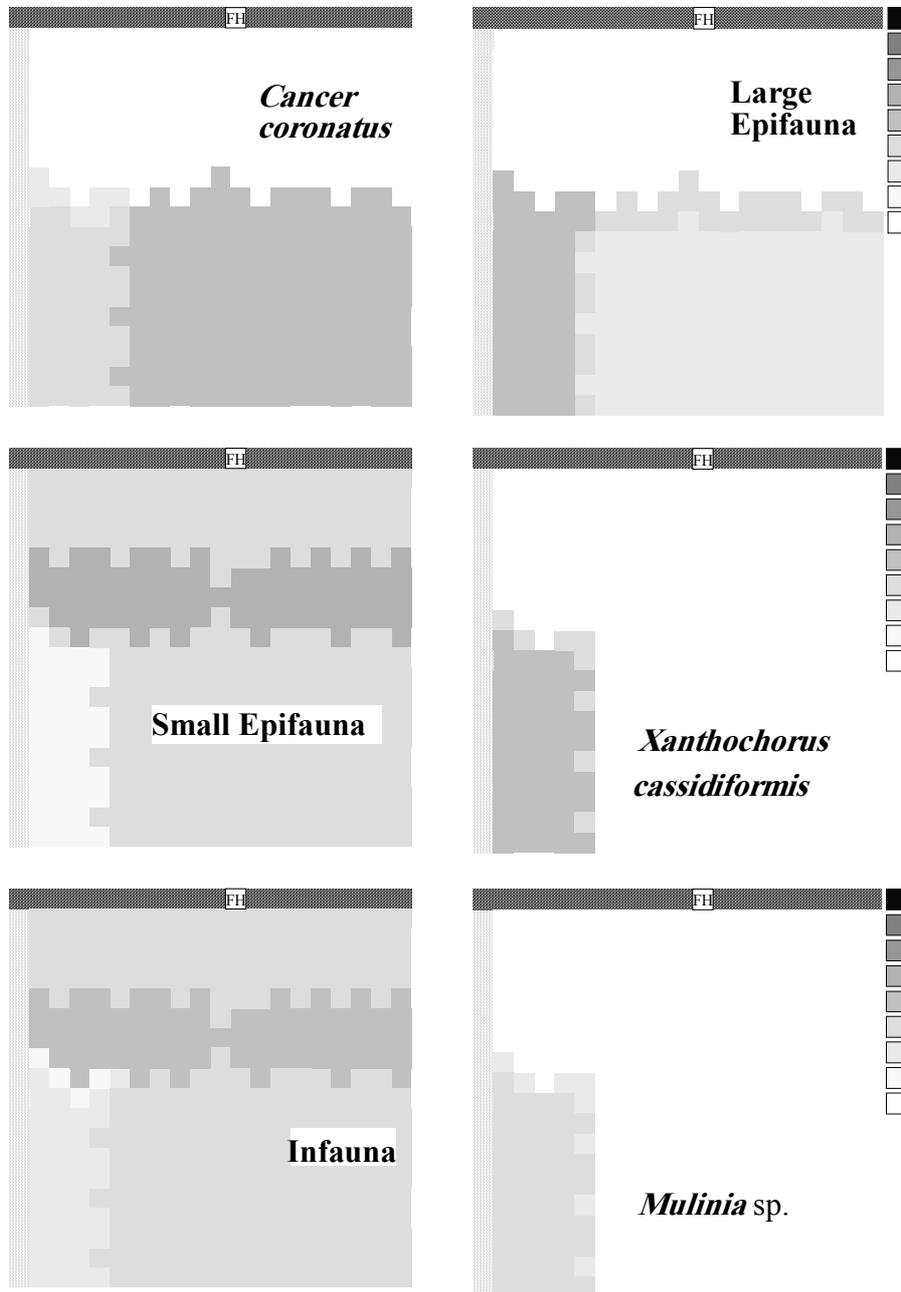


Fig. 4

This page not contain
information

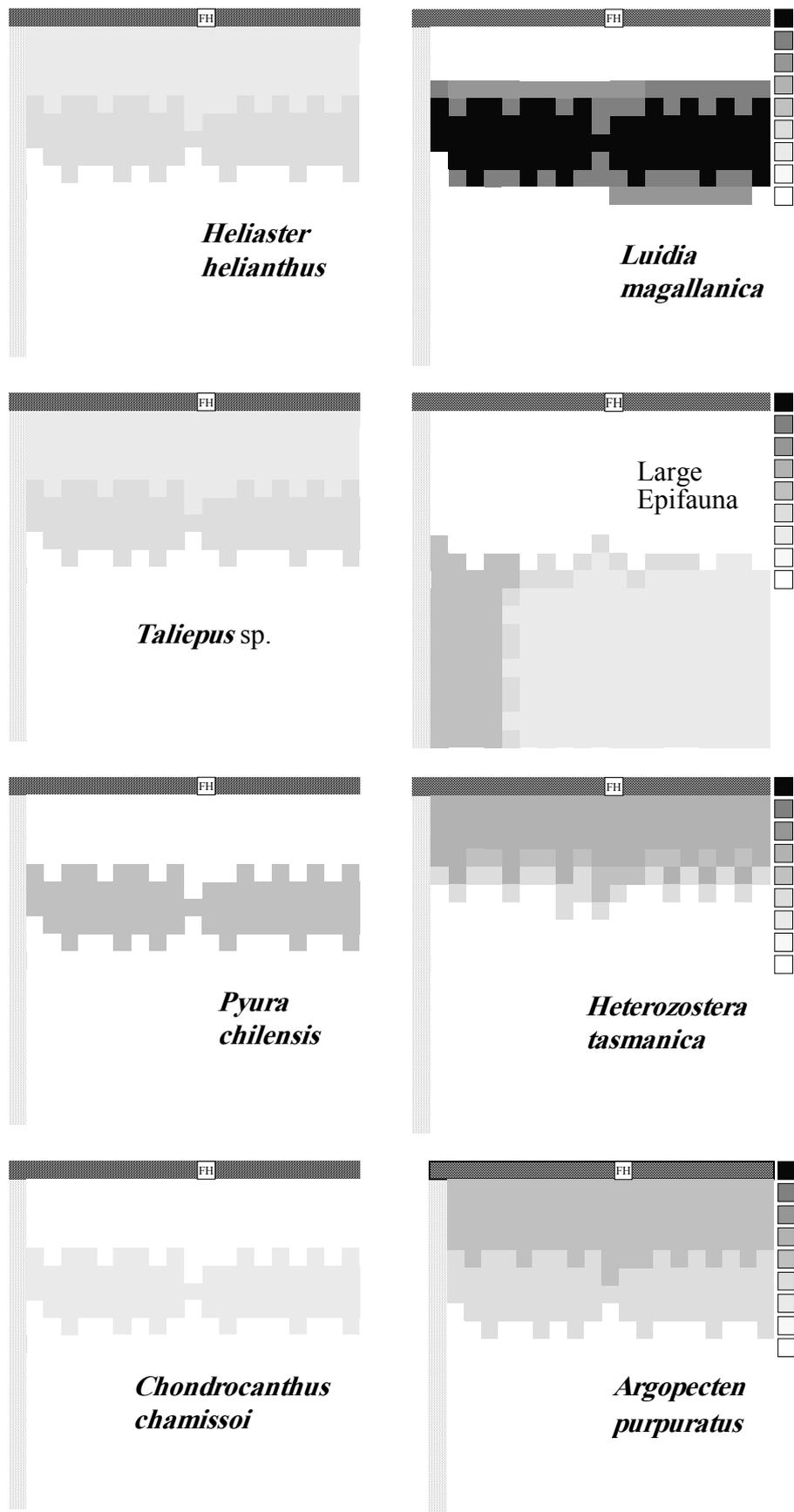


Fig. 6

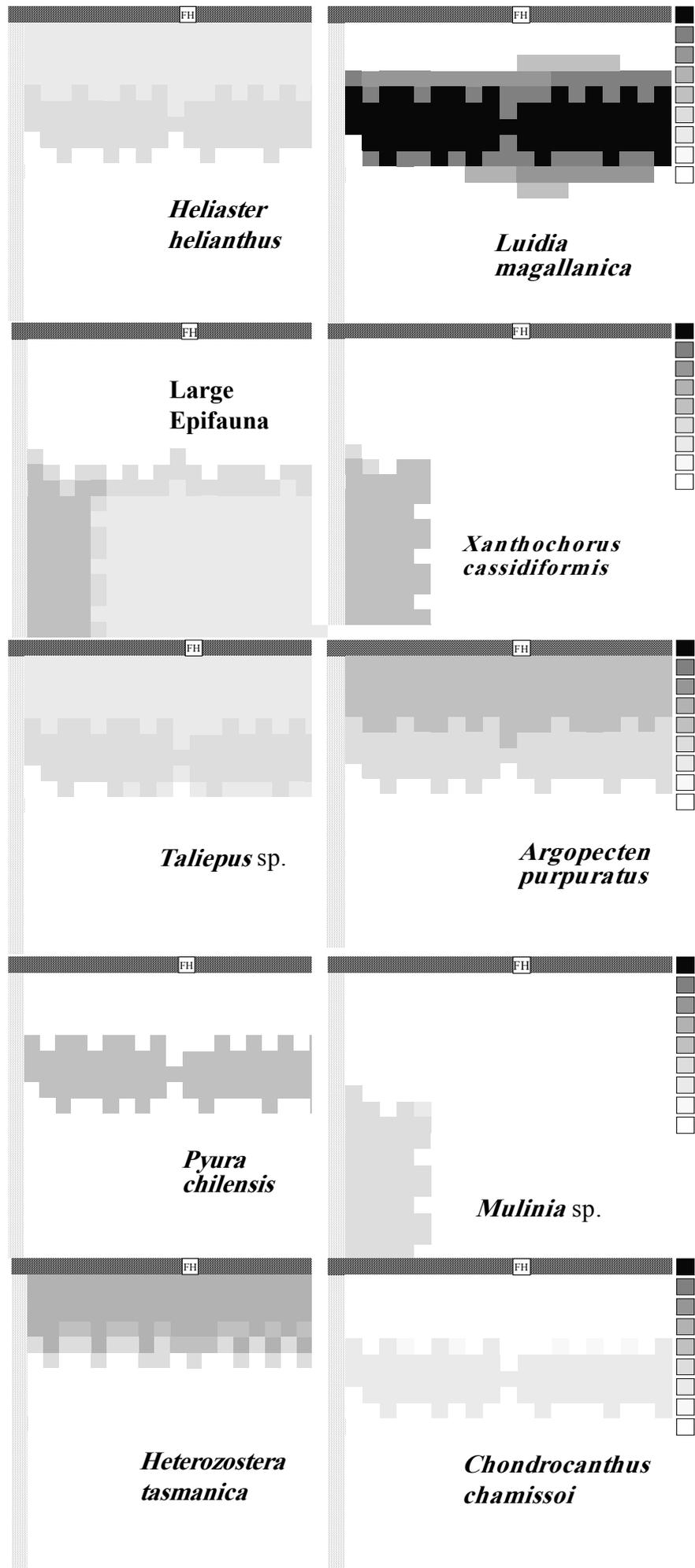


Fig. 7

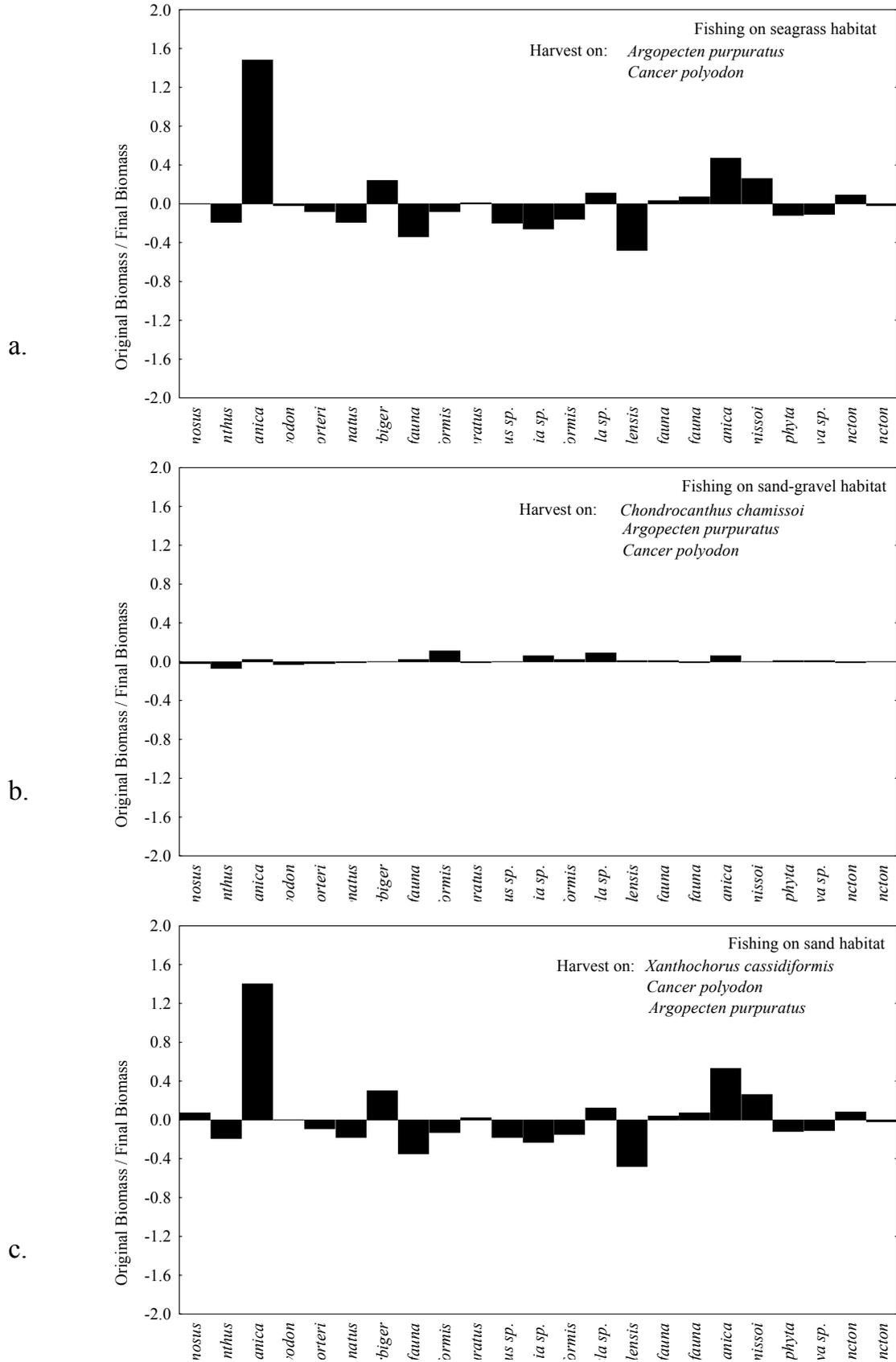
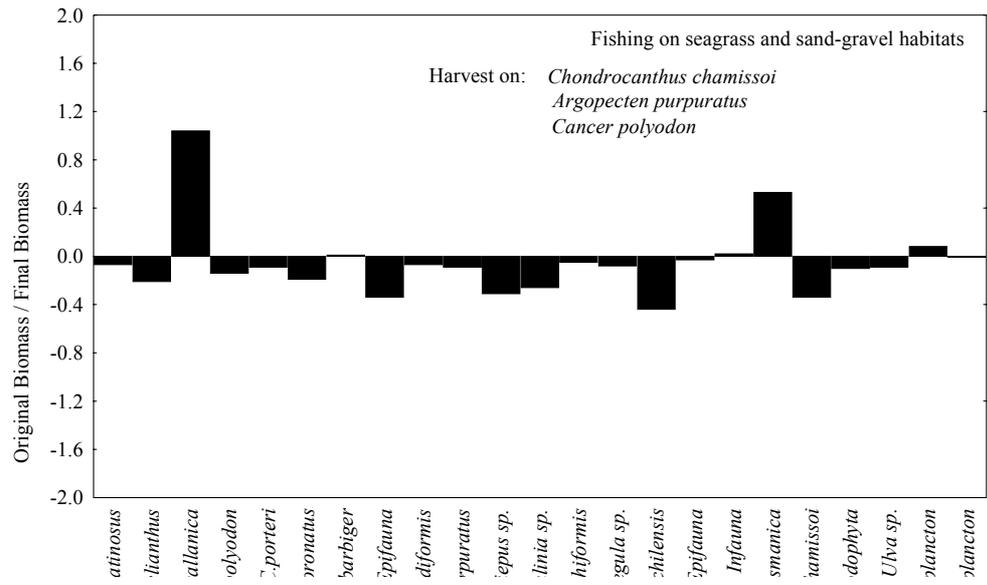


Fig. 8

d.



e.

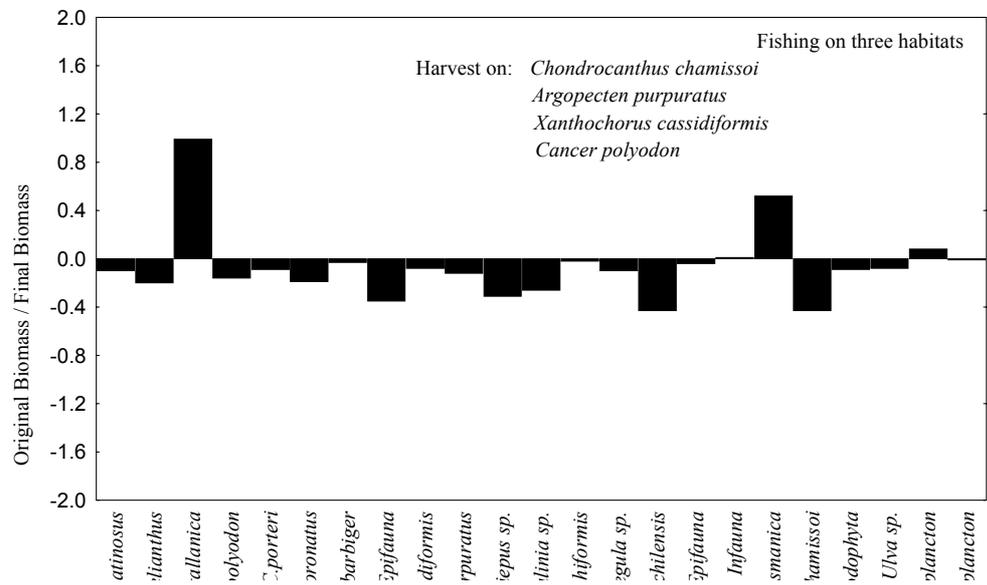


Fig. 8 continuation

9. Chapter VI

“Application of *Loop Analysis* to benthic systems in northern Chile for the elaboration of sustainable management strategies”

Marco Ortiz & Matthias Wolff

Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@uni-bremen.de; mwolff@zmt.uni-bremen.de). Fax: +49 (0) 421 238 00 30.

Key words: feedback dominance, Loop Analysis, management, scallop, starfish, sustainability, upwelling.

2001

The original idea for this publication was developed by the first author. The last version of this contribution was possible after intensive intellectual discussions with the co-author.

ABSTRACT: The present contribution is an extension of the trophic models of Wolff (1994) and Ortiz & Wolff (submitted) of benthic communities in Tongoy Bay (north-central Chile). It represents the first attempt to use the Levins's Theory (*Loop Analysis*) in a complex harvested system along the Chilean coast. Ecological and extended eco-social qualitative models were developed for seagrass, sand-gravel and sand habitats to propose sustainable management strategies for the harvest of the red algae *Chondrocanthus chamissoi*, the scallop *Argopecten purpuratus*, the snail *Xanthochorus cassidiformis* and the crab *Cancer polyodon*. The ecological models integrate the available ecological information previously described, while the second extended model also considers the fishermen and their harvest activity. Based on Levins's Theory it was possible to estimate both the local stability (sustainability) for each of these model systems and to simulate the changes in the standing stock of the main groups as response to external factors. Our results suggest that to increase the standing stock of adult scallops the following man-made interventions should be implemented: (1) Seagrass habitat: partial removal of the three predatory sea star species *L. magallanica*, *H. helianthus* and *M. gelatinosus*, (2) Sand-gravel habitat: seeding of the scallop recruits and juveniles, and removal of just the sea star *H. helianthus*. According to our results, the sand habitat would not support any harvest. The extended model for the seagrass and sand-gravel habitats were found sustainable only if the fishermen were "self-damped", that is, when the fishing effort and fish quota are restricted. Levins's Theory appears as a valuable alternative and complementary mathematical tool defining and assessing the sustainability of management options under a holistic scope. We recommend to apply this framework also in other benthic management areas along the Chilean coast.

INTRODUCTION

A conceptual model is an intellectual construction helping to integrate our knowledge and to improve our understanding of mechanisms underling a particular complex system of interest. Once the variables, factors, constants, and the relationships have been defined, it is quite easy to recognise, their internal and external domains, which correspond to the dichotomies that have dominated in the modelling of ecological complex systems: reductionism versus holism (Levins & Lewontin 1985, Levins & Wilson 1980, Pahl-Wostl 1997, Levins 1998a, Levins & Lopez, 1999). If we attempt to expand the boundaries of traditional quantitative modelling approaches, we might have to include new variables and interactions, which are not quantifiable or without known mathematical functions. Most systems modellers considering quantification of variables and processes to be the only way for understanding the complexity of natural systems would avoid this. However, both quantitative and qualitative descriptions can be legitimate ways for grasping the same phenomena (Levins 1966, May 1974, Cellier 1991) and each approach might allow to answer different and sometimes complementary questions.

In the past decades, much theoretical and experimental attention has been given to the dominance of direct and indirect interactions and causality effects in determining the structure and functioning of natural communities and ecosystems (Levins 1974, Lawlor 1979, Paine 1980, Patten 1985, Abrams 1991, Wissinger & McGrady 1993, Wootton 1994, Menge 1995, Fath & Patten 1999, Underwood 1999). A robust theoretical framework to assess the propagation of the direct and indirect effects into the complex systems is the *Loop Analysis* (Levins 1974, 1975, 1998b) which showed to have a high degree of predictability of natural phenomena (Briand & McCauley 1978, Lane & Blouin 1985, Lane & Collins 1985, Lane 1986). Therefore, it appears as an alternative modelling approach to analyse natural complex systems. Quantifiable and non quantifiable variables, the relationships between ecological and social variables, and the propagated effects in the systems as response to man-made interventions can be assessed. The *Loop Analysis* avoids both exact equations and

voluminous measurements and focuses, instead, on the nominal character of the causality interactions (positive, negative or zero), the structure of the network, and the dominance of negative and positive feedbacks. It sacrifices precision for generality and realism (sensu Levins 1966, 1993).

In previous studies, the authors developed quantitative mass-balance models (at steady-state and dynamical ones) for four different benthic habitats located at southern Tongoy Bay (Chile) (Fig. 1) (Wolff 1994, Ortiz & Wolff submitted) using the ECOPATH II (Christensen & Pauly 1992) and ECOSIM software (Walters et al. 1997). Emergent properties of these webs were described and some policies proposed such as to remove “undesired” predators that feed on commercially important species. The predicted properties and propagated effects in the systems may be biased however, due to the fact that: (1) harvest operates selectively only on the adult size groups of the valuable species, (2) other type of ecological relationships were possibly missed (i.e. mutualism, amensalism, commensalism and competence), and (3) the action of the fishermen from the outside of these quantitative abstractions were considered.

The objective of the present paper was, therefore, to expand the quantitative approaches given by Wolff (1994) and Ortiz & Wolff (submitted) using Levins’s *Loop Analysis* and including the activity of the fishermen. The steps involved in the construction of these abstractions will also be illustrated. Based on the qualitative mathematics of this theory, the sustainability (local stability) and the response to alternative management scenarios or adaptive multispecies fisheries (sensu Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999) were assessed.

MATERIAL AND METHODS

Description of the study area

The study area of Puerto Aldea (Fig. 1) corresponds to one of 168 management areas (territorial use rights for fisheries) established along the Chilean coast (Castilla 2000). These areas are assigned to local fishermen associations in order to maximise, within sustainable boundaries, the production and exploitation of commercial resources. In this area the following benthic habitats can be recognised: (1) seagrass meadows from 0 to 4 m depth, (2) sand and gravel between 4 and 10 m, (3) sand flats between 10 and 14 m, and (4) mud flats > 14 m depth. A complete biotic and abiotic description of these habitats was done by Jesse (2001) and Ortiz et al. (in prep.). The bay and the benthic system of Puerto Aldea are protected from the prevailing south-west winds by Lengua de Vaca peninsula. The upwelling center near this peninsula is among the most important ones of northern Chile (Daneri et al. 2000, Montecinos & Quiroz 2000), supplying nutrients to the ecosystem and simultaneously preventing the establishment of a stable thermocline during summer by the permanent intrusions of upwelled water into the bay. Temperature of surface water reaches 13°C and 17°C in winter and autumn respectively (Jesse 2001). In this area just four species are harvested: the red algae *Chondrocanthus chamissoi* (ca. 114 ton/year), the scallop *Argopecten purpuratus* (ca. 16 ton/year), the snail *Xanthochorus cassidiformis* (ca. 0.6 ton/year) and the crab *Cancer polyodon* (ca. 0.4 ton/year).

Loop Analysis

An useful way to analyse interconnected entities (variables) and to estimate the direct and indirect effects is with the *Loop Analysis*. Loop models offer a possibility to study and analyse complex systems of biological, ecological, physiological, social and economical fields. The models provide a framework for formulating qualitative relationships between variables within a particular system. Likewise, the estimation of local stability properties

(sustainability) and the effects of external perturbations on the variables of these models can be also assessed (Levins, 1974, 1975, 1998b, Puccia & Levins 1985, 1991).

Loop analysis is based on the equivalence between differential equations, matrix algebra and digraphs. The interactions are expressed graphically between different components of a given system. The relationships are shown as signs, indicating the type of influence each variable has upon another, namely whether it is positive, negative or neutral (zero). For instance, in ecological relationships, (+,-) denotes a predator-prey or parasite-host interaction, (-,-) represents competition between two species, while (+,+), (+,0) and (-,0) represent mutualism, commensalism and amensalism respectively. Therefore, a complex system is shown graphically as a network of vertices (circles) and edges (arrows). Each variable is represented by a circle and edges represent direction and type of interactions. Thus, if at one extreme there is an arrow, it means positive effect, while a circle means negative and zero means null effect.

A dynamical system, in particular one that can be represented by a set of differential equations as,

$$\frac{dX_i}{dt} = f_i(X_1, X_2, \dots, X_n, C_1, C_2, \dots, C_n) \quad (1)$$

where X_n represent the variables and C_n the parameters, can be drawn as a signed digraph in which the variables are the nodes or large circles, while the directed links or edges are the elements of the interaction coefficient matrix (community matrix coefficients). The link from X_j to X_i is similar to the α_{ij} in Levins (1968), where

$$\alpha_{ij} = \frac{\partial f_i(X)x^*}{\partial X_j}$$

* evaluated at equilibrium.

The element of the graph representing the link from i to j is signum (α_{ij}) where the function signum (X) is 1 when $X > 0$, 0 when $X = 0$, and -1 when $X < 0$.

A *path* is a series of links from one variable through one or more remaining variables, without crossing any variable twice. A *loop* is any closed path which returns to its starting point, not crossing any intermediate variable twice. The length of a loop is defined by the number of variables the path enters. A self-loop is a loop that starts and ends on the same variable (without passing through no other variable), hence is of length 1. A negative self-loop is called self-damping and a positive is termed self-enhancing. The value of a path or loop is the product of the signs of the interaction coefficients, the α_{ij} 's. If the value of the coefficients are known then a number can be obtained. There is usually more than one and often many loops in a signed digraph. A comparison among loops will show that some have variables in common and these are disjunct loops.

Local stability properties

Feedback at level k , where k is the number of variables, is calculated by,

$$F_k = \sum (-1)^{m+1} L(m, k) \quad (2)$$

and $L(m, k)$ is the product of m disjunct loops whose combined total length is k . Feedback has the same value as the determinant of order k in the interaction coefficient matrix. In other words, F_k is the coefficient of the $(n-k)^{\text{th}}$ term in the characteristic polynomial equation. Local stability, as determined by the Routh-Hurwitz criteria, translates into loop terms as:

Condition 1. $F_k < 0$, for all k . That is, the negative feedback at every level must exceed the positive feedback.

Condition 2. Negative feedback at the higher levels can not be too large compared with negative feedback at the lower levels in order to conserve the qualitative stability properties of the systems. This condition is a sequence of inequalities which are related to oscillation trajectory. The general expression for this condition is the following: $F_{n-2}F_{n-1} + F_{n-3}F_n > 0$.

F_n is the feedback of the entire system (n = total number of variables in the system). It is assumed that the system is locally stable when F_n is negative. The stronger the negative feedback F_n is, the greater the resistance to external changes will be (Levins 1998b). Based on this local stability criteria it is possible to estimate the sustainability of the system and simultaneously explore strategies of stabilisation.

Qualitative predictions

If the parameters (C_n in equation 1) of the system are changing, slow enough for the variables to track the movement of the equilibrium, then the equilibrium values of the variables, which are changing in magnitude, and the direction of that change can be evaluated by,

$$\frac{\partial X_i}{\partial C_h} = \frac{\sum \frac{\partial f_j}{\partial C_h} \cdot \sum_k p_{ij}^{(k)} \cdot F_{n-k}^{(comp)}}{F_n} \quad (3)$$

where,

C_h is the h^{th} parameter that is changing because of an environmental impact (“impact entering at h ”);

$\frac{\partial f_j}{\partial C_h}$ is the effect of C_h parameter change on the state of the j^{th} variable;

$p_{ij}^{(k)}$ is the path from the j^{th} to the i^{th} variable and includes k variables;

$F_{n-k}^{(comp)}$ is the feedback of the complementary subsystem. This subsystem is formed by those variables not on the path of $p_{ij}^{(k)}$; and F_n is the feedback of the whole system, which integrates all variables of the system.

When the complementary subsystem feedback and the feedback of the whole system have the same sign, the effect of a parameter change is the same as the sign of the product of the path. Feedback of opposite sign reverse the effects of the path. In other words, the disjunct and complementary feedback loops are one way to capture simultaneously the propagation of direct and indirect effects into the systems during the estimation of qualitative local stability and predictions.

Selection of boundaries and conceptual models

Seagrass habitat. Based on the available information given by Wolff (1994), León (2000), Jesse (2001), Ortiz et al. (submitted) and Ortiz & Wolff (submitted), two conceptual models integrating biological variables as well as the fishermen were enunciated. The first represents an ecological approach constituted by 15 variables (see Table 1). Even though depredation was the predominant ecological interaction, other relevant relationships as mutualism, commensalism, amensalism and competence were also captured by the model. The positive effect (refuge and structure) of seagrass on recruits, juveniles and adults of *A. purpuratus* (ApR , ApJ and ApA), I and SE was considered, which has previously been described for other comparable systems and species (e.g. Pohle et al. 1991, Connolly 1997, Reusch 1998, Bell et

al. 1999, Bologna & Heck 1999, Edgar 1999, Rose et al. 1999, Lee et al. 2001). Furthermore, a negative influence or resistance that exerts seagrass (*Ht*) on the mobility of three seastar species (*Mg*, *Hh*, and *Lm*) was postulated. Microbial film (*MF*) was considered to be positively influenced by faeces of all organism and to exert a positive effect as food source on filter feeders (*ApR*, *ApJ* and *ApA*) (sensu Prieur et al. 1990), infauna (Kemp 1986, Plante et al. 1989, Grossmann & Reichardt 1991, Plante & Mayer 1994, Plante & Shriver 1998), and equinodermata (Findlay & White 1983). The increase of seagrass productivity due to bio-deposition of faecal material of filter feeders (Bertness 1984, Reusch et al 1994, Peterson & Heck 1999, 2001) is also grasped by a mutualistic relationships between scallops, *MF* and *Ht*. Interrelations within the scallop are conceptualised as follow: *ApR* exerts a positive effect on *ApJ* and this also on *ApA*, whereas *ApR* and *ApA* are connected by a mutualistic interaction. These relationships are similar to those described in population models (Caswell 1989). *ApA* was considered self-enhanced as it supports an intensive harvest. Contrary, for the crab *C. polyodon* both classes are represented by a prey-predator interaction due to the known cannibalism (Wolff & Cerda 1992). *ApR* and *CpJ* are self-damped due to the environmental constraints to their survival. The seagrass (*Ht*), infauna (*I*) and microbial film (*MF*) are considered self-damped due to substrate limitations. Primary production (*PP*) is self-enhanced because it is assumed that under upwelling regimes there is no nutrient limitation. Two negative interactions (aggressive competence) between *CpJ* and *LE* (Jesse 2001) and mutual feeding of *Mg* and *Hh* were also considered (Ortiz pers. obs.). External (man-made) positive impacts on *ApJ* and *ApR*, and negative on *Lm*, *Hh* and *Mg* were assumed (Fig. 2). These external disturbances represent alternative management scenarios to increase the standing stock of *ApA*.

The second model was expanded by integrating the fishermen (*F*) as a variable which act upon *ApA* and *CpA* through harvest. However, only the *ApA* suffers an intensive fishery. It is important to note that *ApA* was not self-enhanced in this model, as fishermen (*F*) were included. The sustainability of the following five management scenarios was estimated: [A] increasing the standing stock of juvenile scallops (*ApJ*), [B] increasing the standing stock of recruits (*ApR*), and [C], [D] and [E] partial removal of the starfish predators *Lm*, *Hh* and *Mg* respectively. The changes in the variables under an external positive impact on *F* were estimated (Fig. 3).

Sand-gravel habitat. The ecological model contains 20 variables (Table 2). The same three size-classes for scallops and the crab *C. polyodon* were considered (*ApR*, *ApJ*, *ApA*, *CpJ* and *CpA*). The self-dynamics for *ApR*, *CpR*, *I*, *PP* and *MF* were as described in the seagrass model and are based on the same explanations. The mollusc *Calyptraea trochiformis* (*Ct*) and the sea squirt *Pyura chilensis* (*Pch*) were considered self-damped due to their sessile life and substrate constraints. Small and large epifauna (*SE* and *LE*) with the dynamics as described in the seagrass model were also considered. The crab *P. barbiger* (*Pb*) was considered self-enhanced because significant seasonal changes in abundance for this species were detected (Ortiz et al. submitted). The interactions among the age-classes for *Ap* and *Cp* were as described for the seagrass habitat. *ApA* and *CpA* were assumed self-enhanced due to harvest. The red algae *Chondrocanthus chamissoi* (*Chch*), other macroalgae (*OM*) (other rodophytas and *Ulva* sp.), and the herbivorous snail *Tegula* sp. (*T* sp) were also integrated. *Chch* and *OM* were considered self-enhanced due to significant seasonal changes in biomass. *Chch* is also intensively harvested. Besides depredation other interactions were also postulated. The substrate (*S*) was assumed to exert a positive effect on *Ct*, *Pch*, *Chch* and *OM* as available substrate. Moreover, a positive effect as available refuge for *CpJ* was considered. *Pch* exerts a negative effect on *Ct* because it overgrows *Ct*. Both *Pch* and *Ct* offer available substrate for *Chch* and *OM*. The changes in equilibrium levels of all variables in this community under

external positive impacts on ApJ , ApR , S , and negative on Lm , Hh , Mg were estimated (Fig. 4). These external disturbances represent alternative management options to increase the standing stock of ApA and $Chch$.

An expanded model integrating the fishermen (F) which harvest ApA and CpA was enunciated and the sustainability of the following management scenarios was assessed: [A] increasing the standing stock of juveniles scallops (ApJ), [B] increasing the standing stock of recruits (ApR), [C], [D] and [E] partial removal of the predatory starfish species Lm , Hh and Mg respectively, and [F] increase of the available substrate (artificial) for increasing algae settlement. The changes in the variables under an external positive impact on F were estimated (Fig. 5).

Sand habitat. The ecological model was constructed with 13 variables (Table 3). Juveniles and adults size classes for the crab *Cancer coronatus* (CcJ and CcA) and for the sand mussel *Mulinia* sp. (MJ and MA) were considered. Both classes of *C. coronatus* were connected as prey-predator pair due to cannibalism (Jesse 2001) and the classes of *Mulinia* sp. were connected by a mutualistic relationships. The crab *Cancer polyodon* (Cp), the snail *Xanthochorus cassidiformis* (Xc) and the starfishes *M. gelatinosus* (Mg) and *L. magallanica* (Lm), the small and large epifauna, infauna, primary productivity and microbial film (SE , LE , I , PP and MF) were also integrated. MF , I and PP were assumed self-enhanced based on the same explanation given in the other models as were Cp and Xc due to harvest pressure, and CcA because this group present relevant seasonal migration between sand habitat and deeper systems (Jesse 2001). CcJ were considered self-damped due to the environmental constraints to their survival, and MJ and MA due to their semi-sessile behaviour and substrate limitations. Depredation predominated in this ecological model. The changes in the equilibrium standing stocks of the variables as response to negative external perturbations on Lm , Mg and MA were assessed (Fig. 6). Both represent alternative management strategies.

The extended model includes the fishermen (F) which harvest on Cp and Xc . The sustainability of the following three management scenarios was evaluated: [A] and [B] represent the partial removal of the starfish species Mg and Lm respectively, and [C] represent the eventual harvest on MA . Therefore, the strategies [A] and [B] represent attempts to increase the standing stocks of *X. cassidiformis* and *Mulinia* sp. respectively (Fig. 7). The qualitative change in the variables under an external negative impact on F was estimated.

RESULTS

Seagrass habitat. Fig. 2 shows the conceptual ecological model for the seagrass habitat. According to the calculations of the *Loop Analysis* the system is not entirely stable because just the first criterion of stability was reached. ($F_n = -1.0$; 2° criterion < 0). This means that although the system is locally stable, it will oscillate around an equilibrium after disturbance. In regard to the qualitative predictions, positive impacts on the juvenile (ApJ) and recruit (ApR) scallops, which would correspond to an eventual seeding programme, would produce an unexpected negative effect on the standing stock of the scallop adults ApA (Table 4A). Likewise, a positive impact on ApJ would promote the increase of equilibrium values of the three starfish species. On the other hand, a removal of the three seastar species would increase the standing stock of the adult scallops, the crab *C. polyodon* (CpA) and the small epifauna (SE) (Table 4A).

The expanded model is illustrated in Fig. 3. In this integrative abstraction the sustainability of the system strongly depends on the dynamical behaviour of fishermen (F). The sustainability of the system (both criteria) under just fishery activity on ApA and CpA is reached only if the fishermen are a self-damped (Fig. 3). Likewise, all other management

scenarios explored would only be sustainable in time if F is self-damped. The highest sustainability is obtained when all scenarios are simultaneously applied. On the contrary, the scenario [B] presented the smallest local stability (Table 5). Regarding the qualitative changes in the variables as response to a positive external impact on fishermen (F) (for instance a stimuli from the market), an expected decrease in the standings stock of ApA is only avoided if F is self-damped (Table 4B).

Sand-gravel habitat. The ecological model for this habitat was found also only partially sustainable, because only the first criterion of stability was reached ($F_n = -96.0$, 2° criterion < 0) (Fig. 4). An eventual positive external impact on both ApR and ApJ would increase the standing stock of adult scallops ApA (Table 6A), while an increase of the available substrate (S) would not produce the expected positive effect on the abundance of the commercial red algae *Ch. chamissoi* (*Chch*). A removal of the starfish *Lm* and *Hh* would have a positive direct effect on the ApA and a positive indirect effect on the *Chch*. On the other hand, a removal of *M. gelatinosus* (*Mg*) would decrease the standing stock of ApA . Only a depletion of *Hh* would increase the standing stock of the exploited crab CpA (Table 6A).

Fig. 5 illustrates the expanded model for the sand-gravel habitat. The harvest on *Chch*, ApA and CpA reached the local stability (both criteria) only when the fishermen are self-damped. However, sustainability for all management scenarios was not obtained. In decreasing order the scenarios [E], [D]+[E], [B]+[E] and [A]+[E] would be the most sustainable man-made interventions. Contrary, the scenario [A]+[B]+[C]+[D]+[F] would transform the system into a highly unsustainable one (Table 7). The self-damped dynamic of F in this model is not a sufficient condition to buffer the external positive perturbation on itself (Table 6B).

Sand habitat. Unfortunately the ecological model of this habitat was not found locally stable ($F_n = +56.0$, 2° criterion < 0) (Fig. 7). In regard to the qualitative changes in the variables as response to external impacts on the starfish species, a negative perturbation on *Mg* produces a negative direct effect on the snail *Xc* and negative indirect on the crab *Cp*, whereas both classes of sand mussel are increased. On the other hand, a negative impact on *L. magallanica* (*Lm*) produces opposite effects on the same species (Table 8A). A negative impact on *MA* would decrease its standing stock (Table 8A).

The expanded model is shown in Fig. 7. No sustainability was found for any of the management scenarios explored (Table 9). However, if a positive external perturbation impacts on the F , they would not show a qualitative change and the exploited species would be positively effected (Table 8B).

DISCUSSION

Models for three exploited complex benthic systems of Tongoy Bay (northern Chile) were analysed using Levins's Loop Analysis. Despite the fact that some interactions were assumed without complete evidence for their existence, we feel that the conceptual models here presented can be considered as realistic descriptions of the processes and relationships underlying each community.

The relative constancy in abundance of the seagrass *H. tasmanica* (Ortiz per. obs.), and the structural function that it offers to most of the invertebrates species (Connolly 1997, Reusch 1998, Rose et al. 1999, Lee et al. 2001) seem to be insufficient to organise and structure a stable system. A similar result was obtained for the sand-gravel ecological model. These findings may be a consequence of the significant seasonal changes (biomass) of the scallops in both habitats and of the macroalgae species in the sand-gravel (by harvest) (Ortiz et al. submitted). The sand model was estimated to be locally unstable which implies that it

would not support harvest activities nor management policies. One explanation for this finding may be the seasonal migration between sand and deep systems of the predatory crab *C. coronatus* which feeds intensively in the sand habitat (Jesse 2001). Likewise, the intensive fishery on the snail *X. cassidiformis* and on the predatory crab *C. polyodon* may have some influence. These processes (perturbations) suggest that the sand system is constantly being driven between alternative or transitional assemblages, preventing the development of a stable community. However, we estimate that more studies should be conducted to justify our conclusion.

Although the analysis of the ecological models would support some adaptive management interventions (*sensu* Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999) to increase the standing stock of the commercial species, these models do not include the dynamics of fishery activities. Our extended models revealed that the seagrass and sand-gravel systems can only be sustainably used if the fishermen are self-damped, implying that fishing effort and catch quota must be constrained. Therefore, both management practices would be recommended. Non-linear quantitative theoretical studies that have analysed the fishery effects on multispecies systems described similar conclusions to the ones here presented (May et al. 1979, Beddington & May 1980, Beddington & Cooke 1982, Azar et al. 1995).

Based on the direct and indirect effects propagated in the seagrass habitat, any man-made intervention for increasing the biomass of recruits and juveniles of the scallop *A. purpuratus* (larvae collectors, introductions) can not be recommended as they do not produce the expected positive impact on the adult exploited scallops. On the other hand, the partial removal of the three starfish *L. magallanica*, *H. helianthus* and *M. gelatinosus* would have a positive effect on the scallop adults. However, at the same time an unexpected positive effect would be propagated on standing stock of the crab *C. polyodon*. This positive response on the competitor species or cascading effect can be interpreted as the dominance of a positive feedback at lower level which may have a negative impact on the holistic stability. The ecosystems are open to several types of natural perturbations which may eventually maximise the deleterious influence of this positive feedback on the stability of the entire community, which might be driven to some other moving equilibrium (*sensu* Levins 1998c). Hence, if our objective is not only to increase the standing stock of the commercial species, but also to conserve the natural system in which they inhabit, this positive feedback must be avoided. One way to depress it may be by fishing the crab *C. polyodon* as well.

In the sand-gravel habitat a more complex propagation of effects was observed. In this habitat we recommend to implement management strategies that favour the abundance of recruits and juveniles of *A. purpuratus*. The artificial introduction (surplus) of available substrate would not increase the abundance of the commercial red algae *Ch. chamissoi*. Some experimental field studies (unpublished) confirm our finding. This response might be explained by the parallel increase of the mollusc *C. trochiformis* and the sea squirt *P. chilensis* (both sessile species) which eventually would compete with the macroalgae for the substrate. However, the above three interventions would have a positive indirect effect on the sea star *L. magallanica* and *H. helianthus*. In this particular situation, we would suggest to remove *L. magallanica* only to historical levels of ca. 2.0 g wet weight/m² (*sensu* Ortiz et al. submitted) because its further removal would be highly unsustainable for the system. Based on our analysis, just the removal of the sea star *H. helianthus* should be implemented as positive effects would be expected on the standing stock of the three commercial species, the red algae *Ch. chamissoi*, the adult of *A. purpuratus* and adult of *C. polyodon*.

Finally, we have shown that the *Loop Analysis* is useful theoretical framework and an alternative to the reductionistic abstractions if the holistic sustainability of different man-made interventions is assessed, representing a way to integrate quantifiable and non-quantifiable variables and relationships in the models. This seems particularly important as the widespread crash of exploited populations, reported in the global fishery crisis, appears to be at least in part rooted in the reductionistic models and methods (Larkin 1977, Hilborn et al. 1995, Patten 1997, Roberts 1997, Walters et al. 1999). Similar conclusion have been drawn for pest management in agricultural systems (Levins & Wilson 1980, Levins & Vandermeer 1990, Andow & Rosset 1990, Levins 1998a).

CONCLUSIONS

The present work was the first attempt to assess the sustainability of different management options in one of the 168 territorial management areas established along the Chilean coast using the Levins's Theory. Despite the fact that the models represent three different systems and some of the ecological relationships were only postulated, similar tendencies were found. For instance, when the fishermen (F) are considered self-damped, the sustainability (local stability) strongly increases in the seagrass and sand-gravel systems. In other words, the fishing effort and catch quota should be restricted. Based on our results, the following management options in the seagrass and sand-gravel habitats would be recommended: (1) any activity focused towards the increase of juveniles and recruits of the scallop *A. purpuratus* (collector of larvae, man-assisted introductions) should be exclusively carried out in the sand-gravel habitat, (2) the three starfish species should be partially removed in the seagrass habitat, and only *H. helianthus* in the sand-gravel. Further studies would have to be focused towards the assessment of the structural function of the seagrass *H. tasmanica* and the macroalgae species, and the contribution of bacteria or organic matter as food source of filter-feeders, starfish and crab species. Even though Levins's Theory does not allow far explicit quantitative reasoning, "what if" questions can be answered with sufficient understanding and realism. Based on its mathematics and the dominance of negative and positive feedbacks, we conclude that this theoretical framework should be used in other benthic management areas along the Chilean coast, especially, if our aim is to assess the sustainability of different adaptive management options for multispecies fisheries (Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999, Castilla 2000). This theory arises as an alternative to the pure reductionistic measures of sustainability (see Bell & Morse 1999).

Acknowledgements.

MO is deeply grateful to Prof. Richard Levins for earlier suggestions on here presented models.

LITERATURE CITED

- Abrams P (1991) Strengths of indirect effects generated by optimal foraging. *Oikos* 62: 167-176
- Andow D, Rosset P (1990) Integrated Pest Management. In: Carroll R, Vandermeer J, Rosset P (eds) *Agroecology*. McGraw-Hill, NY, 413-439
- Azar C, Holmberg J, Lindgren K (1995) Stability analysis of harvesting in a predator-prey model. *J theor Biol* 174: 13-19
- Beddington J, May R (1980) Maximum sustainable yields in systems subject to harvesting at more than one trophic level. *Math Biosci* 51: 261-281
- Beddington J, Cooke J (1982) Harvesting from a prey-predator complex. *Ecol. Model.* 14: 155-177

- Bell S, Morse S (1999) Sustainability Indicators. Measuring the immeasurable? 1st Edition, Earthscan Publications, London, 175 pp
- Bell S, Robbins B, Jensen S (1999) Gap dynamics in a seagrass landscape. *Ecosystems* 2: 493-504
- Bertness M (1984) Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* 65: 1794-1807
- Bologna P, Heck K (1999) Macrofaunal associations with seagrass epiphytes relative importance of trophic and structural characteristics. *J Exp Mar Biol Ecol* 242: 21-39
- Briand F, McCauley E (1978) Cybernetic mechanisms in lake plankton systems: how to control undesirable algae. *Nature* 273: 228-230
- Castilla JC (2000) Roles of experimental marine ecology in coastal management and conservation. *J Exp Mar Biol Ecol* 250: 3-21
- Caswell H (1989) Matrix population models. Sinauer, MA, USA, 328 pp
- Cellier F (1991) General System Problem Solving Paradigm for Qualitative Modeling. In: Fishwick P, Luker P (eds) Qualitative Simulation Modeling and Analysis. Springer-Verlag, NY, pp. 51-71.
- Christensen V, Pauly D (1992) ECOPATH II a software for balancing steady-state ecosystems models and calculating network characteristics. *Ecol Model* 61: 169-185
- Connolly R (1997) Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. *Hydrobiologia* 346: 137-148
- Daneri G, Dellarossa V, Quiñones R, Jacob B, Montero P, Ulloa O (2000) Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Mar Ecol Prog Ser* 197: 41-49
- Edgar G (1999) Experimental analysis of structural versus trophic importance of seagrass beds. I. Effects on macrofaunal and meiofaunal invertebrates. *Vie et Milieu* 49(4): 239-348.
- Fath B, Patten B (1999) Review of the foundations of network analysis. *Ecosystems* 2: 167-179
- Findlay R, White D (1983) The effects of feeding by the sand dollar *Mellita quinquesperforata* (Leske) on the benthic microbial community. *J Exp Mar Biol Ecol* 72: 25-41
- Grossmann S, Reichardt W (1991) Impact of *Arenicola marina* on bacteria in intertidal sediments. *Mar Ecol Prog Ser* 77: 85-93
- Hilborn R, Walters C, Ludwig C (1995) Sustainable exploitation of renewable resources. *Ann Rev Ecol Syst* 26: 45-67
- Jesse S (2001) Comparative ecology of sympatric brachyran crab species in the shallow subtidal of the Pacific Coast of North Chile and their importance for the artisanal fishery in Puerto Aldea. PhD Dissertation, University of Bremen, Germany.
- Kemp P (1986) Direct uptake of detrital carbon by the deposit-feeding polychaeta *Euzonus mucronata* (Treadwell). *J Exp Mar Biol Ecol* 99: 49-61
- Lane P (1986) Symmetry, change, perturbation, and observing mode in natural communities. *Ecology* 67(1): 223-239.
- Lane P, Blouin A (1985) Qualitative analysis of the pelagic foodwebs of three acid-impacted lakes in Nova Scotia, Canada. *Int. Revue ges. Hydrobiol* 70(2): 203-220
- Lane P, Collins T (1985) Food web models of a marine plankton community network: an experimental mesocosm approach. *J Exp Mar Biol Ecol* 94: 41-70.
- Larkin P (1977) An epitaph for the concept of maximum sustained yield. *Trans Amer Fish Soc* 106(1): 1-11

- Lawlor LR (1979) Direct and indirect effects on n-species competition. *Oecologia* 43: 355-364
- Lee S, Fong C, Wu R (2001) The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling natural beds. *J Exp Mar Biol Ecol* 259: 23-50
- León R (2000) Relaciones tróficas del Cancar polyodon (Poepping 1836). Tesis para obtener el título de Biólogo Marino, Universidad Católica del Norte, Sede Coquimbo, Chile.
- Levins R (1966) The strategy of model building in population biology *Am Sci* 54: 421-431
- Levins R (1968) Evolution in changing environments. Princeton Monograph Series, Princeton, NJ, 120 pp
- Levins R (1974) The qualitative analysis of partially specified systems. *Annals NY Acad Sci* 231: 123-138
- Levins R (1975) Evolution in Communities near Equilibrium. In: Cody M, Diamond J (eds) Ecology and evolution of communities. Harvard University Press, MA. pp. 16-50.
- Levins R (1993) A response to Orzack and Sober: formal analysis and the fluidity of science. *The Quart Rev of Biol* 68(4): 547-555
- Levins R (1998a) The internal and external in explanatory theories. *Science as Culture* 7(4): 557-582
- Levins R (1998b) Qualitative Mathematics for Understanding, Prediction, and Intervention in Complex Ecosystems. In: Rapport D, Costanza R, Epstein P, Gaudet C, Levins R (eds) Ecosystem Health. Blackwell, Inc, MA. pp. 178-204.
- Levins R (1998c) Dialectics and systems theory. *Science & Society* 62(3): 375-399.
- Levins R, Wilson M (1980) Ecological theory and pest management *Ann Rev Entomol* 25: 287-308
- Levins R, Lewontin R (1985) The dialectical biologist. Harvard University Press, Cambridge, MA, 303 pp.
- Levins R, Vandermeer J (1990) The Agroecosystem Embedded in a Complex Ecological Community. In : Carroll R, Vandermeer J, Rosset P (eds) Agroecology. McGraw-Hill, NY. pp. 341-362
- Levins R, Lopez C (1997) Toward an ecosocial view of health. *Inter J Health Services* 29(2): 261-293.
- May R (1974) Stability and complexity in model ecosystems 2nd Edition. Monographs in Population Biology N°6, Princeton University Press, NJ. 265 pp.
- May R, Beddington J, Clark C, Holt S, Laws R (1979) Management of multispecies fisheries. *Science* 205: 267-276
- Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol Monogr* 65: 21-74
- Montecinos V, Quiroz D (2000) Specific primary production and phytoplankton cell size structure in an upwelling area off the coast of Chile (30°). *Aquat Sci* 62: 364-380
- Pahl-Wostl (1997) Dynamic structure of a food web model: comparison with a food chain model. *Ecol Model* 100: 103-123
- Patten B (1985) Energy cycling in the ecosystem. *Ecol Model* 28: 1-71
- Patten B (1997) Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. *Ecol Model* 100: 11-42
- Peterson B, Heck K (1999) The potential of suspension bivalves to increase seagrass productivity. *J Exp Mar Biol Ecol* 240: 37-52
- Peterson B, Heck K (2001) Positive interactions between suspension-feeding bivalves and seagrass –a facultative mutualism. *Mar Ecol Prog Ser* 213: 143-155

- Plante C, Mayer L (1994) Distribution and efficiency of bacteriolysis in the gut of *Arenicola marina* and three additional deposit feeders. *Mar Ecol Prog Ser* 109: 183-194
- Plante C, Shriver A (1998) Patterns of differential digestion of bacteria in deposit feeders: a test of resource partitioning. *Mar Ecol Prog Ser* 163: 253-258
- Plante C, Jumars P, Baross J (1989) Rapid bacterial growth in the hindgut of a marine deposit feeder. *Microb Ecol* 18: 29-44
- Pohle D, Bricelj V, Garcia-Esquivel Z (1991) The eelgrass canopy: an above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten irradians*. *Mar Ecol Prog Ser* 74: 47-59
- Prieur D, Mével G, Nicolas J, Plusquellec A, Vigneulle M (1990) Interactions between bivalve molluscs and bacteria in the marine environment. *Oceanogr Mar Biol Annu Rev* 28: 277-352
- Puccia Ch, Levins R (1985) *Qualitative Modeling of Complex Systems: an introduction to Loop Analysis and Time Averaging*. Harvard University Press, MA, 259 pp.
- Puccia Ch, Levins R (1991) *Qualitative Modeling in Ecology: Loop Analysis, signed digraphs, and Time Averaging*. In : Fishwick P, Luker P (eds) *Qualitative Simulation Modeling and Analysis*. Springer-Verlag, NY. pp. 119-143
- Reusch T (1998) Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. *Mar Ecol Prog Ser* 167: 149-153
- Reusch T, Chapman A, Gröger J (1994) Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Mar Ecol Prog Ser* 108: 265-282
- Robert C (1997) Ecological advice for the global fisheries crisis. *TREE* 12: 35-38
- Rose C, Sharp W, Kenworthy W, Hunt J, Lyons W, Prager E, Valentine J, Hall M, Whitfield P, Fourqurean J (1999) Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. *Mar Ecol Prog Ser* 190: 211-222
- Ulanowicz R (1986) *Growth and development: Ecosystems phenomenology*. Springer, NY, 203 pp.
- Underwood AJ (1999) Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *J Exp Mar Biol Ecol* 232: 125-140
- Walters C, Hilborn R (1978) Ecological optimization and adaptive management. *Ann Rev Ecol Syst* 9: 157-188
- Walters C, Korman J (1999) Cross-scale modelling of Ripirian ecosystem responses to hydrologic management. *Ecosystems* 2: 411-421
- Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessment. *Rev Fish Biol Fish* 7: 139-172
- Walters C, Pauly D, Christensen V (1999) Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2: 539-554
- Wissinger S, McGrady J (1993) Intraguild predation and competition between dragonfly larvae: direct and indirect effects on shared prey. *Ecology* 74: 207-218
- Wootton JT (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75(1): 151-165
- Wolff M (1994) A trophic model for Tongoy Bay –a system exposed to suspended scallop culture (Northern Chile). *J Exp Mar Biol Ecol* 182: 149-168.
- Wolff M, Cerda G (1992) Feeding ecology of the crab *Cancer polyodon* in La Herradura Bay, northern Chile: II Food spectrum and prey consumption. *Mar Ecol Prog Ser* 100: 119-125.

List of Tables and Figures

Table 1. Community matrix for the seagrass habitat. The nominal effect of j -species on i -species is showed. This model is constituted by the following 16 variables: Three age-classes for the scallops *Argopecten purpuratus*, adults (ApA), juveniles (ApJ) and the recruits (ApR), and two classes for the crab *Cancer polyodon*, adults (CpA) and juveniles (CpJ), the seagrass *Heterozostera tasmanica* (Ht), microbial film (MF), primary productivity (PP), infauna (I), small and large epifauna (SE and LE), the crab *Paraxanthus barbiger* (Pb), the seastars *Meyenaster gelatinosus* (Mg), *Heliaster helianthus* (Hh), *Luidia magallanica* (Lm), and the fishermen (F). Th infauna (I) includes polychaeta and buried bivalves, SE comprises other molluscs such as *Turritella cingulata*, *Nasarius gayi*, *Mitrella unifasciata*, *Nucula pisum* and *Chiton* spp., and LE includes other crabs species such as *Hepatus chilense*, *Platymera gaudichaudi* and *Gaudichaudia gaudichaudia*. [A], [B], [C], [D], [E] represent alternative management scenarios, and [h] is harvest. For more details see text. Soft lines indicates the postulated relationships based on incomplete evidence.

Table 2. Community matrix for the sand-gravel habitat. The nominal effect of j -species on i -species is showed. This model includes the following 21 variables: Three size-classes for the scallops and the crab *C. polyodon* (ApA , ApJ , ApR , CpA and CpJ), the mollusc *Calyptraea trochiformis* (Ct), the sea squirt *Pyura chilensis* (Pch), small and large epifauna (SE and LE), infauna (I), primary productivity (PP), microbial film (MF) the crab *P. barbiger* (Pb), the sea stars *M. gelatinosus* (Mg), *L. magallanica* (Lm) and *H. helianthus* (Hh), the red algae *Chondrocanthus chamissoi* ($Chch$), other macroalgae (OM) (other rodophytas and *Ulva* sp.), the herbivorous snail *Tegula* sp. (Tsp), artificial substrate (S) and the fishermen (F). [A], [B], [C], [D], [E], [F] represent alternative management scenarios, and [h] is harvest. For more details see text. Soft lines indicates the postulated relationships based on incomplete evidence.

Table 3. Community matrix for the sand habitat. The nominal effect of j -species on i -species is showed. This model comprises the following 14 variables: two age-classes for the crab *Cancer coronatus*, adults (CcA) and juveniles (CcJ), and also two classes for the sand mussel *Mulinia* sp, adults (MA) and juveniles (MJ), the crab *C. polyodon* (Cp), the predator snail *Xantochorus cassidiformis* (Xc), the sea stasfishes *M. gelatinosus* (Mg) and *L. magallanica* (Lm), small and large epifauna, infauna, primary productivity and microbial film (SE , LE , I , PP and MF), and the fishermen (F). [A], [B], [C] represent alternative management scenarios, and [h] is harvest. For more details see text. Soft lines indicates the postulated relationships based on incomplete evidence.

Table 4. A. Qualitative predictions in the equilibrium values (standing stocks) of all variables in the ecological model of seagrass habitat as response to positive external impact on the recruits (ApR) and juveniles (ApJ) of the scallop *Argopecten purpuratus*, and negative impact on the sea star species *Luidia magallanica* (Lm), *Heliaster helianthus* (Hh) and *Meyenaster gelatinosus* (Mg). B. Qualitative predictions in the eco-social model of seagrass habitat as response to positive impact on fishermen (F).

Table 5. Holistic sustainability measures (F_n and 2° criteria) in the eco-social model of seagrass habitat under two fishermen self-dynamics. Management scenarios: [A] increasing the standing stock of juveniles scallops (ApJ), [B] increasing the standing stock of recruit scallops (ApR), [C], [D] and [E] partial removal of the starfish *L. magallanica* (Lm), *H. helianthus* (Hh) and *M. gelatinosus* (Mg) respectively.

Table 6. A. Qualitative predictions in the equilibrium values (standing stocks) of all variables in the ecological model of sand-gravel habitat as response to positive external on the recruit

(*ApR*), juveniles (*ApJ*) scallops and substrate (*S*), and negative on the sea star species *Lm*, *Hh* and *Mg*. B. Qualitative predictions in the eco-social model of sand-gravel model as response to positive impact on *F*.

Table 7. Holistic sustainability measures (*F_n* and *2° criteria*) in the eco-social model of sand-gravel habitat under two fishermen self-dynamics. Management scenarios: [A] increasing the standing stock of *ApJ*, [B] increasing the standing stock of *ApR*, [C], [D] and [E] partial removal of the predatory sea star *Lm*, *Hh* and *Mg* respectively, and [F] increase of the available substrate (*S*).

Table 8. A. Qualitative changes in the equilibrium values (standing stocks) of all variables in the ecological model of sand habitat as response to negative external impact on the three sea star species *M. gelatinosus* (*Mg*), *L. magallanica* (*Lm*) and the adults of sand mussel *Mulinia* sp. (*MA*). B. Qualitative predictions in the eco-social model of sand-habitat as response to positive impact on the fishermen.

Table 9. Holistic sustainability measures (*F_n* and *2° criteria*) in the eco-social model of sand habitat under two fishermen self-dynamics. Management scenarios: [A] and [B] partial removal of the starfish *Mg* and *Lm* respectively, and [C] represents an eventual harvest on the mussel adults *MA*.

Fig. 1. A.- The main littoral types along of the Chilean coast: 1.= Dominated by exposed compact rocky shores; 2.= dominated by exposed sandy shores; 3.= mostly insular systems. B.- The principal bay systems of the IV Region of Coquimbo (Chile). C.- Study area of Puerto Aldea located at southern of Tongoy Bay.

Fig. 2. Ecological model of seagrass community. Holistic sustainability measures (*F_n* and *2° criterion*). See text for more details. To note that only ecological variables are connected. The soft lines (interactions) indicate postulated relationships.

Fig. 3. Eco-social expanded model of seagrass habitat. Holistic sustainability measures (*F_n* and *2° criterion*) under two fishermen self-dynamics. [A], [B], [C], [D] and [E] management scenarios, [*h*] is harvest. The soft connections indicate postulated relationships.

Fig. 4. Ecological model of sand-gravel habitat. Holistic sustainability measures (*F_n* and *2° criterion*). See text for more details. Only the ecological variables are connected. The soft connections indicate postulated relationships.

Fig. 5. Eco-social model of sand-gravel habitat. Holistic sustainability measures (*F_n* and *2° criterion*) under two fishermen self-dynamics. [A], [B], [C], [D], [E] and [F] management scenarios, [*h*] is harvest. The soft connections indicate postulated relationships.

Fig. 6 Ecological model of sand habitat. Holistic sustainability measures (*F_n* and *2° criterion*). Only the ecological variables are connected. See text for more details. The soft connections indicate postulated relationships.

Fig. 7 Eco-social model of sand habitat. Holistic sustainability measures (*F_n* and *2° criterion*) under two fishermen self-dynamics. [A], [B] and [C] management scenarios and [*h*] is harvest. The soft connections indicate postulated relationships.

Table 3

		<i>j</i>													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>aij</i>		<i>CcA</i>	<i>CcJ</i>	<i>Cp</i>	<i>Mg</i>	<i>Lm</i>	<i>MF</i>	<i>SE</i>	<i>LE</i>	<i>PP</i>	<i>I</i>	<i>MJ</i>	<i>MA</i>	<i>Xc</i>	<i>F</i>
	<i>CcA</i>	+	+	-	0	0	+	+	+	0	+	+	+	+	0
	<i>CcJ</i>	-	-	-	0	0	+	+	-	0	+	+	0	0	0
	<i>Cp</i>	+	+	0	0	0	0	+	+	0	0	0	+	+	-
	<i>Mg</i>	0	0	0	0	+	+	+	0	0	0	0	0	+	0
	<i>Lm</i>	0	0	0	0	0	+	0	0	0	+	+	+	0	0
	<i>MF</i>	+	+	+	+	+	-	+	+	+	+	+	+	+	0
i.	<i>SE</i>	-	-	-	-	0	0	0	-	0	+	0	0	-	0
	<i>LE</i>	-	+	-	0	0	0	+	0	0	+	+	+	+	0
	<i>PP</i>	0	0	0	0	0	0	0	0	+	-	-	-	0	0
	<i>I</i>	-	-	0	0	-	+	-	-	+	-	0	0	-	0
	<i>MJ</i>	0	-	0	0	0	+	-	-	+	0	-	+	-	0
	<i>MA</i>	-	0	-	0	-	+	-	-	+	0	+	-	-	0
	<i>Xc</i>	-	0	-	-	0	+	+	-	0	+	+	+	0	-
	<i>F</i>	0	0	+	0	0	0	0	0	0	0	0	0	+	(-)(+)

Table 4

A. **Responses**

Input to	<i>ApA</i>	<i>ApJ</i>	<i>ApR</i>	PP	MF	I	<i>CpJ</i>	<i>CpA</i>	SE	<i>Ht</i>	<i>Lm</i>	<i>Hh</i>	<i>Mg</i>	LE	<i>Pb</i>
+ <i>ApJ</i>	-	+	-	-	+	+	+	-	-	+	+	+	+	-	+
+ <i>ApR</i>	-	+	0	0	+	0	0	0	0	0	0	0	0	0	0
- <i>Lm</i>	+	-	+	+	-	-	+	+	+	-	-	-	-	-	-
- <i>Hh</i>	+	-	+	+	-	-	0	+	+	-	-	0	-	0	-
- <i>Mg</i>	+	-	+	+	-	-	0	+	+	-	-	-	0	0	-

B. **Responses**

Input to	<i>ApA</i>	<i>ApJ</i>	<i>ApR</i>	PP	MF	I	<i>CpJ</i>	<i>CpA</i>	SE	<i>Ht</i>	<i>Lm</i>	<i>Hh</i>	<i>Mg</i>	LE	<i>Pb</i>	F
+ F(-)	+	-	-	+	-	+	+	-	-	-	-	+	+	-	+	-
+ F(+)	-	+	+	-	+	-	-	+	+	+	+	-	-	+	-	+

Table 5

Sustainability assessment in the seagrass habitat		
Management	Fishermen dynamic	
	<i>Self-damped</i>	<i>Self-enhanced</i>
[A]	$F_n = -94.0; 2^\circ \text{criterion} > 0$	$F_n = -40.0; 2^\circ \text{criterion} > 0$
[B]	$F_n = -8.0; 2^\circ \text{criterion} > 0$	$F_n = +46.0; 2^\circ \text{criterion} < 0$
[C]	$F_n = -30.0; 2^\circ \text{criterion} > 0$	$F_n = +24.0; 2^\circ \text{criterion} < 0$
[D]	$F_n = -17.0; 2^\circ \text{criterion} > 0$	$F_n = +37.0; 2^\circ \text{criterion} < 0$
[E]	$F_n = -17.0; 2^\circ \text{criterion} > 0$	$F_n = +37.0; 2^\circ \text{criterion} < 0$
[A]+[B]	$F_n = -90.0; 2^\circ \text{criterion} > 0$	$F_n = -36.0; 2^\circ \text{criterion} > 0$
[A]+[C]	$F_n = -112.0; 2^\circ \text{criterion} > 0$	$F_n = -58.0; 2^\circ \text{criterion} < 0$
[A]+[D]	$F_n = -99.0; 2^\circ \text{criterion} > 0$	$F_n = -45.0; 2^\circ \text{criterion} > 0$
[A]+[E]	$F_n = -99.0; 2^\circ \text{criterion} > 0$	$F_n = -45.0; 2^\circ \text{criterion} > 0$
[B]+[C]	$F_n = -26.0; 2^\circ \text{criterion} > 0$	$F_n = +28.0; 2^\circ \text{criterion} < 0$
[B]+[D]	$F_n = -13.0; 2^\circ \text{criterion} > 0$	$F_n = +41.0; 2^\circ \text{criterion} < 0$
[B]+[E]	$F_n = -13.0; 2^\circ \text{criterion} > 0$	$F_n = +41.0; 2^\circ \text{criterion} < 0$
[C]+[D]	$F_n = -35.0; 2^\circ \text{criterion} > 0$	$F_n = +19.0; 2^\circ \text{criterion} > 0$
[C]+[E]	$F_n = -35.0; 2^\circ \text{criterion} > 0$	$F_n = +19.0; 2^\circ \text{criterion} > 0$
[D]+[E]	$F_n = -22.0; 2^\circ \text{criterion} > 0$	$F_n = +32.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[C]	$F_n = -108.0; 2^\circ \text{criterion} > 0$	$F_n = -54.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[D]	$F_n = -95.0; 2^\circ \text{criterion} > 0$	$F_n = -41.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[E]	$F_n = -95.0; 2^\circ \text{criterion} > 0$	$F_n = -41.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]+[D]	$F_n = -113.0; 2^\circ \text{criterion} > 0$	$F_n = -59.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[C]+[E]	$F_n = -113.0; 2^\circ \text{criterion} > 0$	$F_n = -59.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[C]+[D]+[E]	$F_n = -118.0; 2^\circ \text{criterion} > 0$	$F_n = -64.0; 2^\circ \text{criterion} < 0$

Table 6

A.																					
Responses																					
Input to	<i>ApA</i>	<i>ApJ</i>	<i>ApR</i>	PP	S	<i>Ct</i>	<i>CpJ</i>	<i>CpA</i>	<i>Pch</i>	OM	<i>Ch ch</i>	I	SE	LE	MF	<i>Tsp</i>	<i>Pb</i>	<i>Lm</i>	<i>Hh</i>	<i>Mg</i>	
+ <i>ApJ</i>	+	-	+	+	+	+	+	-	+	-	-	+	+	+	-	-	-	-	+	-	
+ <i>ApR</i>	+	-	0	0	0	0	0	0	0	0	0	0	0	+	0	0	-	0	0	0	
+S	+	-	-	+	+	-	-	+	+	-	-	+	+	+	-	-	-	-	+	-	
- <i>Lm</i>	+	-	+	+	+	+	+	-	-	+	+	-	+	+	-	-	+	-	+	-	
- <i>Hh</i>	+	-	+	+	+	-	+	+	-	+	+	+	+	+	-	-	-	-	+	-	
- <i>Mg</i>	-	+	-	-	-	+	-	-	+	-	-	-	-	-	+	+	+	+	-	+	

B.																					
Responses																					
Input to	<i>ApA</i>	<i>ApJ</i>	<i>ApR</i>	PP	S	<i>Ct</i>	<i>CpJ</i>	<i>CpA</i>	<i>Pch</i>	OM	<i>Ch ch</i>	I	SE	LE	MF	<i>Tsp</i>	<i>Pb</i>	<i>Lm</i>	<i>Hh</i>	<i>Mg</i>	F
+F(-)	+	+	-	+	-	-	-	+	+	-	+	+	+	-	-	-	+	-	-	+	+
+F(+)	-	-	+	-	+	+	+	-	-	+	-	-	-	+	+	+	-	+	+	-	-

Table 7

Sustainability assessment in the sand-gravel habitat		
Management	Fishermen dynamic	
	<i>Self-damped</i>	<i>Self-enhanced</i>
[A]	$F_n = + 48.0; 2^\circ \text{criterion} > 0$	$F_n = + 240.0; 2^\circ \text{criterion} > 0$
[B]	$F_n = + 12.0; 2^\circ \text{criterion} > 0$	$F_n = + 204.0; 2^\circ \text{criterion} > 0$
[C]	$F_n = + 96.0; 2^\circ \text{criterion} > 0$	$F_n = + 288.0; 2^\circ \text{criterion} > 0$
[D]	$F_n = 0.0; 2^\circ \text{criterion} > 0$	$F_n = + 192.0; 2^\circ \text{criterion} > 0$
[E]	$F_n = - 252.0; 2^\circ \text{criterion} > 0$	$F_n = - 60.0; 2^\circ \text{criterion} > 0$
[F]	$F_n = +204.0; 2^\circ \text{criterion} > 0$	$F_n = + 396.0; 2^\circ \text{criterion} > 0$
[A]+[B]	$F_n = + 84.0; 2^\circ \text{criterion} > 0$	$F_n = + 276.0; 2^\circ \text{criterion} < 0$
[A]+[C]	$F_n = +168.0; 2^\circ \text{criterion} > 0$	$F_n = + 360.0; 2^\circ \text{criterion} > 0$
[A]+[D]	$F_n = + 72.0; 2^\circ \text{criterion} > 0$	$F_n = + 264.0; 2^\circ \text{criterion} < 0$
[A]+[E]	$F_n = - 180.0; 2^\circ \text{criterion} > 0$	$F_n = + 12.0; 2^\circ \text{criterion} > 0$
[A]+[F]	$F_n = +276.0; 2^\circ \text{criterion} > 0$	$F_n = + 468.0; 2^\circ \text{criterion} < 0$
[B]+[C]	$F_n = +132.0; 2^\circ \text{criterion} > 0$	$F_n = + 324.0; 2^\circ \text{criterion} > 0$
[B]+[D]	$F_n = + 36.0; 2^\circ \text{criterion} > 0$	$F_n = + 228.0; 2^\circ \text{criterion} < 0$
[B]+[E]	$F_n = - 216.0; 2^\circ \text{criterion} > 0$	$F_n = - 24.0; 2^\circ \text{criterion} > 0$
[B]+[F]	$F_n = +240.0; 2^\circ \text{criterion} > 0$	$F_n = + 432.0; 2^\circ \text{criterion} < 0$
[C]+[D]	$F_n = +120.0; 2^\circ \text{criterion} < 0$	$F_n = + 312.0; 2^\circ \text{criterion} > 0$
[C]+[E]	$F_n = - 132.0; 2^\circ \text{criterion} > 0$	$F_n = + 60.0; 2^\circ \text{criterion} > 0$
[C]+[F]	$F_n = +324.0; 2^\circ \text{criterion} > 0$	$F_n = + 516.0; 2^\circ \text{criterion} > 0$
[D]+[E]	$F_n = - 228.0; 2^\circ \text{criterion} > 0$	$F_n = - 36.0; 2^\circ \text{criterion} > 0$
[D]+[F]	$F_n = +228.0; 2^\circ \text{criterion} > 0$	$F_n = + 420.0; 2^\circ \text{criterion} > 0$
[E]+[F]	$F_n = - 24.0; 2^\circ \text{criterion} > 0$	$F_n = + 168.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]	$F_n = +204.0; 2^\circ \text{criterion} > 0$	$F_n = + 396.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[D]	$F_n = +108.0; 2^\circ \text{criterion} > 0$	$F_n = + 300.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[E]	$F_n = - 144.0; 2^\circ \text{criterion} > 0$	$F_n = + 48.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[F]	$F_n = +312.0; 2^\circ \text{criterion} > 0$	$F_n = + 504.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[C]+[D]	$F_n = +228.0; 2^\circ \text{criterion} > 0$	$F_n = + 420.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]+[E]	$F_n = - 24.0; 2^\circ \text{criterion} > 0$	$F_n = + 168.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]+[F]	$F_n = +432.0; 2^\circ \text{criterion} > 0$	$F_n = + 624.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]+[D]+[E]	$F_n = 0.0; 2^\circ \text{criterion} > 0$	$F_n = + 192.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]+[D]+[F]	$F_n = +456.0; 2^\circ \text{criterion} > 0$	$F_n = + 648.0; 2^\circ \text{criterion} < 0$
[A]+[B]+[C]+[D]+[E]+[F]	$F_n = +228.0; 2^\circ \text{criterion} > 0$	$F_n = + 420.0; 2^\circ \text{criterion} < 0$

Table 8

A.		Responses												
Input to	<i>CcA</i>	<i>CcJ</i>	<i>Cp</i>	<i>Mg</i>	<i>Lm</i>	MF	SE	LE	PP	I	<i>MJ</i>	<i>MA</i>	<i>Xc</i>	
- <i>Mg</i>	+	+	-	-	+	+	+	-	-	-	+	+	-	
- <i>Lm</i>	-	-	+	-	-	+	-	+	+	+	-	-	+	
- <i>MA</i>	+	+	+	+	+	+	+	-	-	-	+	-	-	

B.		Responses													
Input tp	<i>CcA</i>	<i>CcJ</i>	<i>Cp</i>	<i>Mg</i>	<i>Lm</i>	MF	SE	LE	PP	I	<i>MJ</i>	<i>MA</i>	<i>Xc</i>	F	
+ F(-)	+	-	+	-	-	-	-	-	+	+	+	-	+	0	
+ F(+)	+	-	+	-	-	-	-	-	+	+	+	-	+	0	

Table 9

Sustainability assessment in the sand habitat		
Management	Fishermen dynamic	
	<i>Self-damped</i>	<i>Self-enhanced</i>
[A]	$F_n = + 72.0; 2^\circ \text{criterion} > 0$	$F_n = + 72.0; 2^\circ \text{criterion} > 0$
[B]	$F_n = + 36.0; 2^\circ \text{criterion} > 0$	$F_n = + 36.0; 2^\circ \text{criterion} > 0$
[C]	$F_n = + 64.0; 2^\circ \text{criterion} > 0$	$F_n = + 64.0; 2^\circ \text{criterion} > 0$
[A]+[B]	$F_n = + 72.0; 2^\circ \text{criterion} > 0$	$F_n = + 72.0; 2^\circ \text{criterion} > 0$
[A]+[C]	$F_n = + 96.0; 2^\circ \text{criterion} > 0$	$F_n = + 96.0; 2^\circ \text{criterion} > 0$
[B]+[C]	$F_n = + 64.0; 2^\circ \text{criterion} > 0$	$F_n = + 64.0; 2^\circ \text{criterion} > 0$
[A]+[B]+[C]	$F_n = + 96.0; 2^\circ \text{criterion} > 0$	$F_n = + 96.0; 2^\circ \text{criterion} > 0$

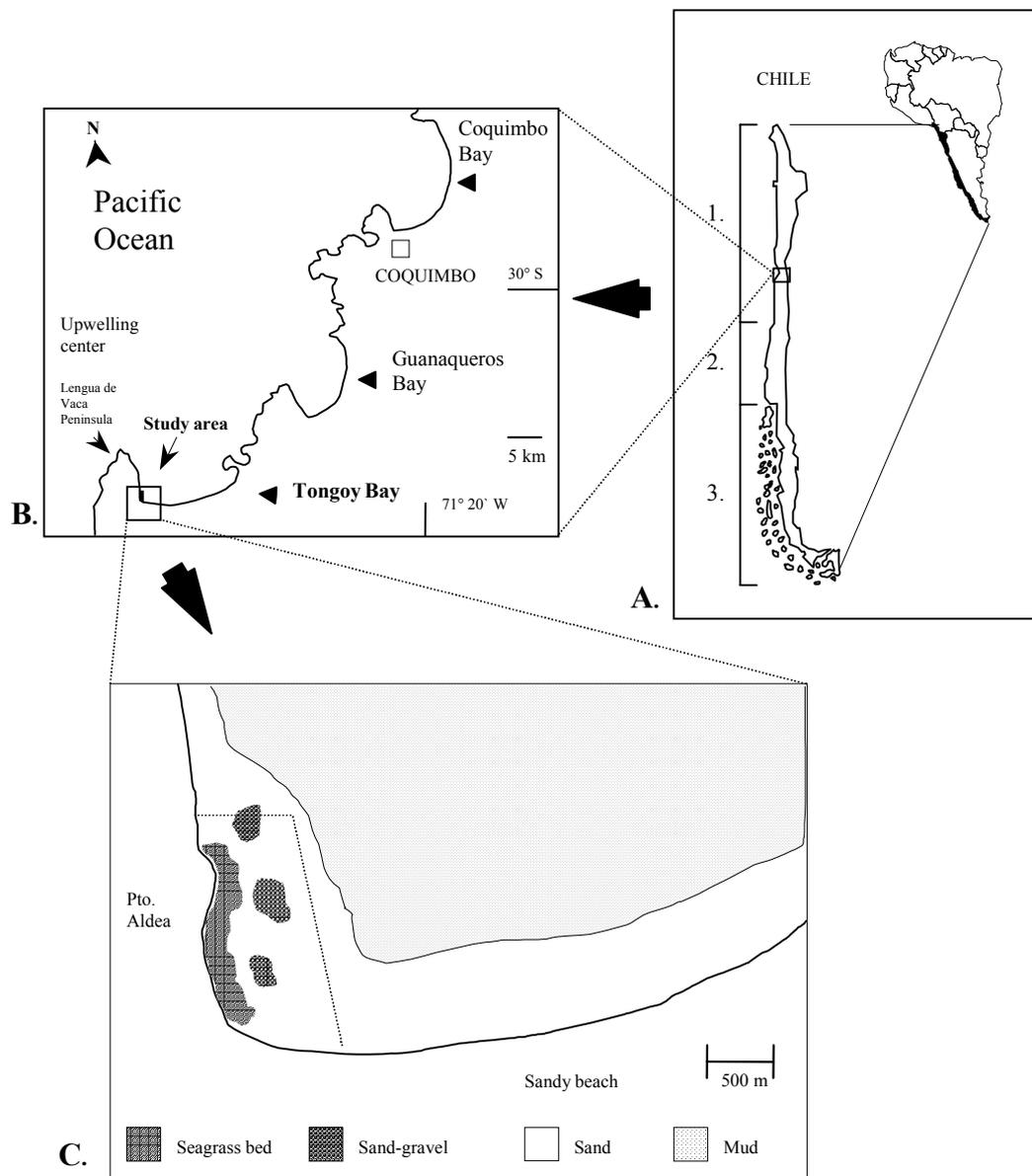


Fig. 1

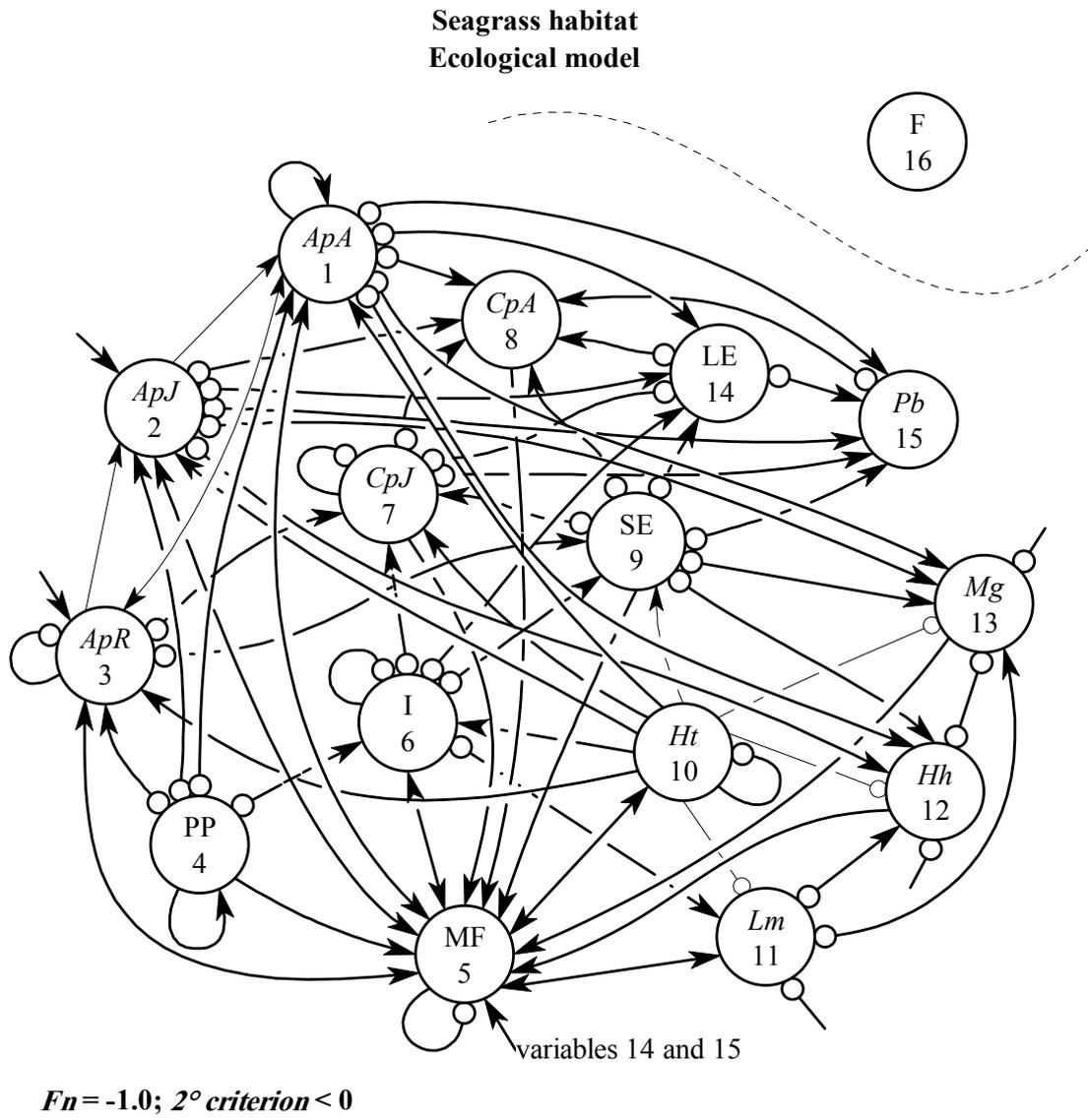


Fig. 2

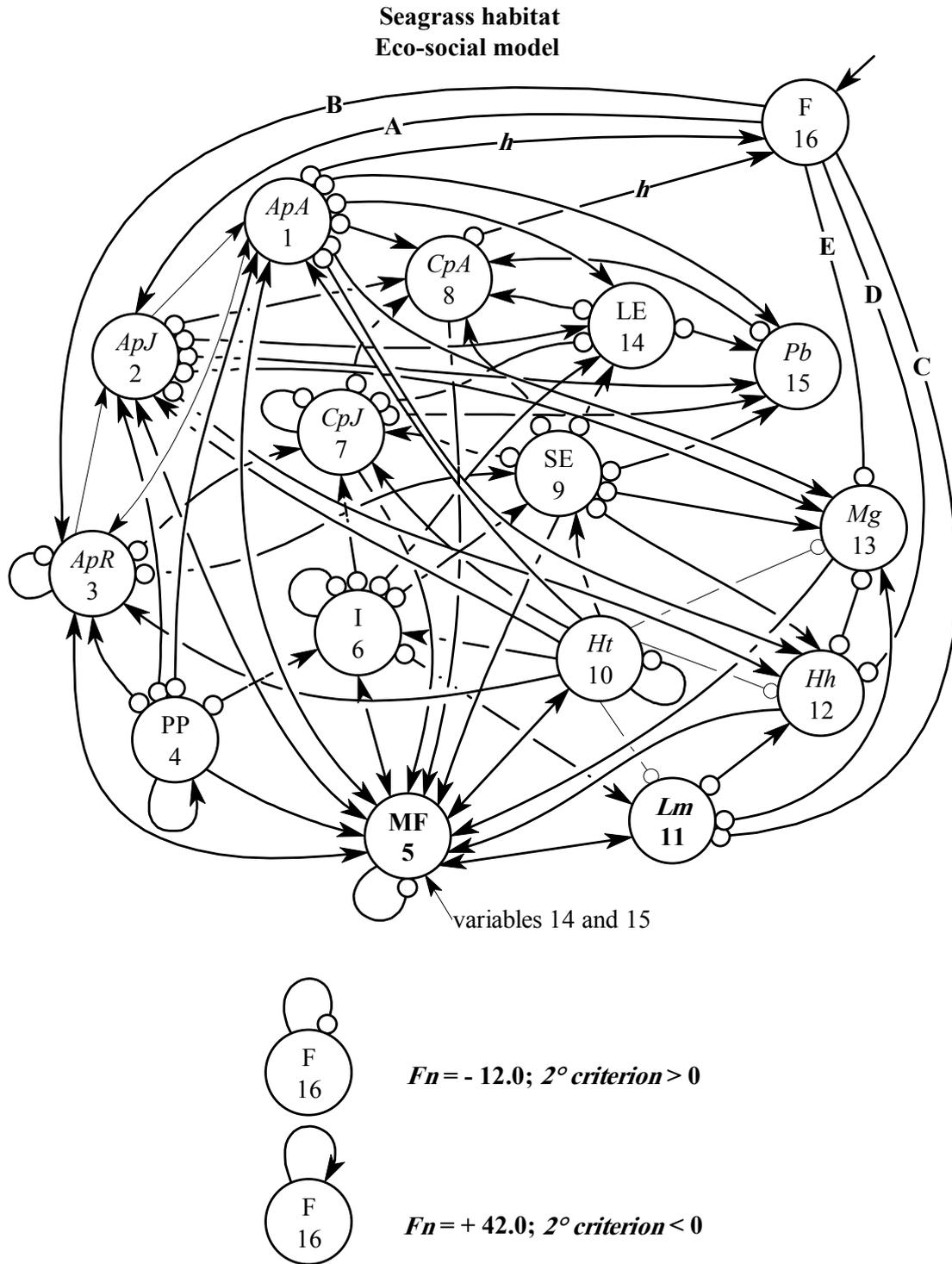


Fig. 3

**Sand-Gravel habitat
Ecological model**

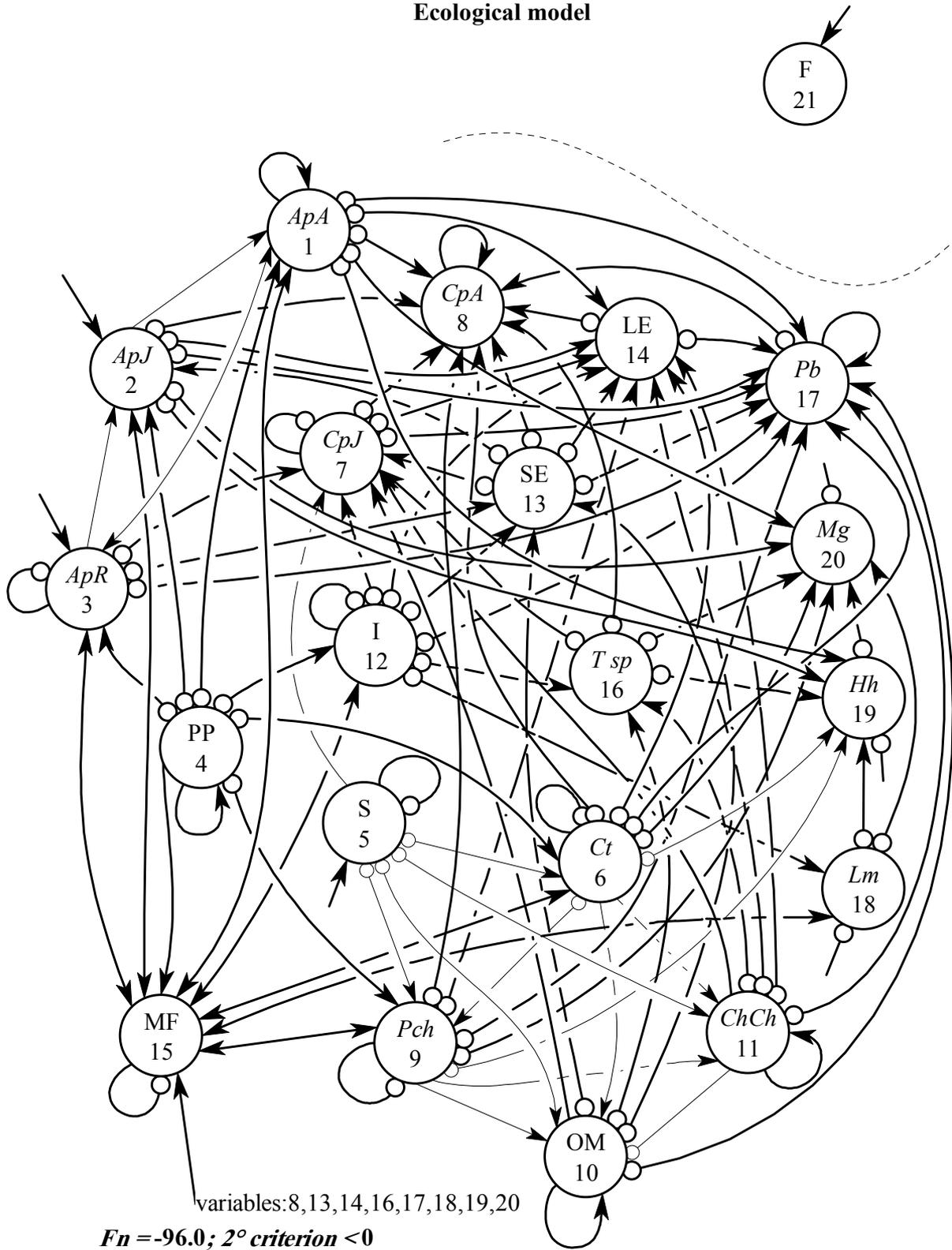


Fig. 4

Sand-Gravel habitat
Eco-social model

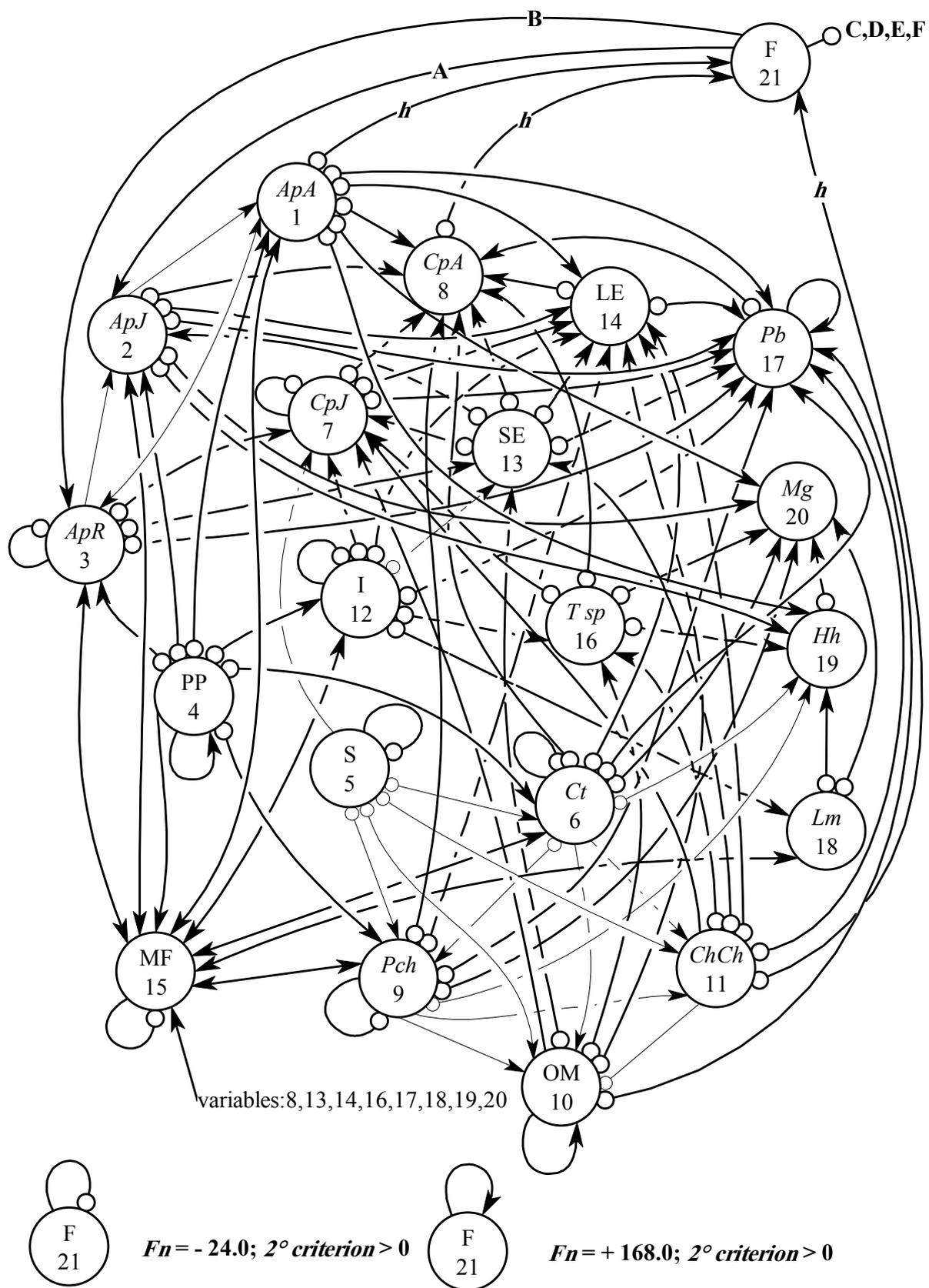


Fig. 5

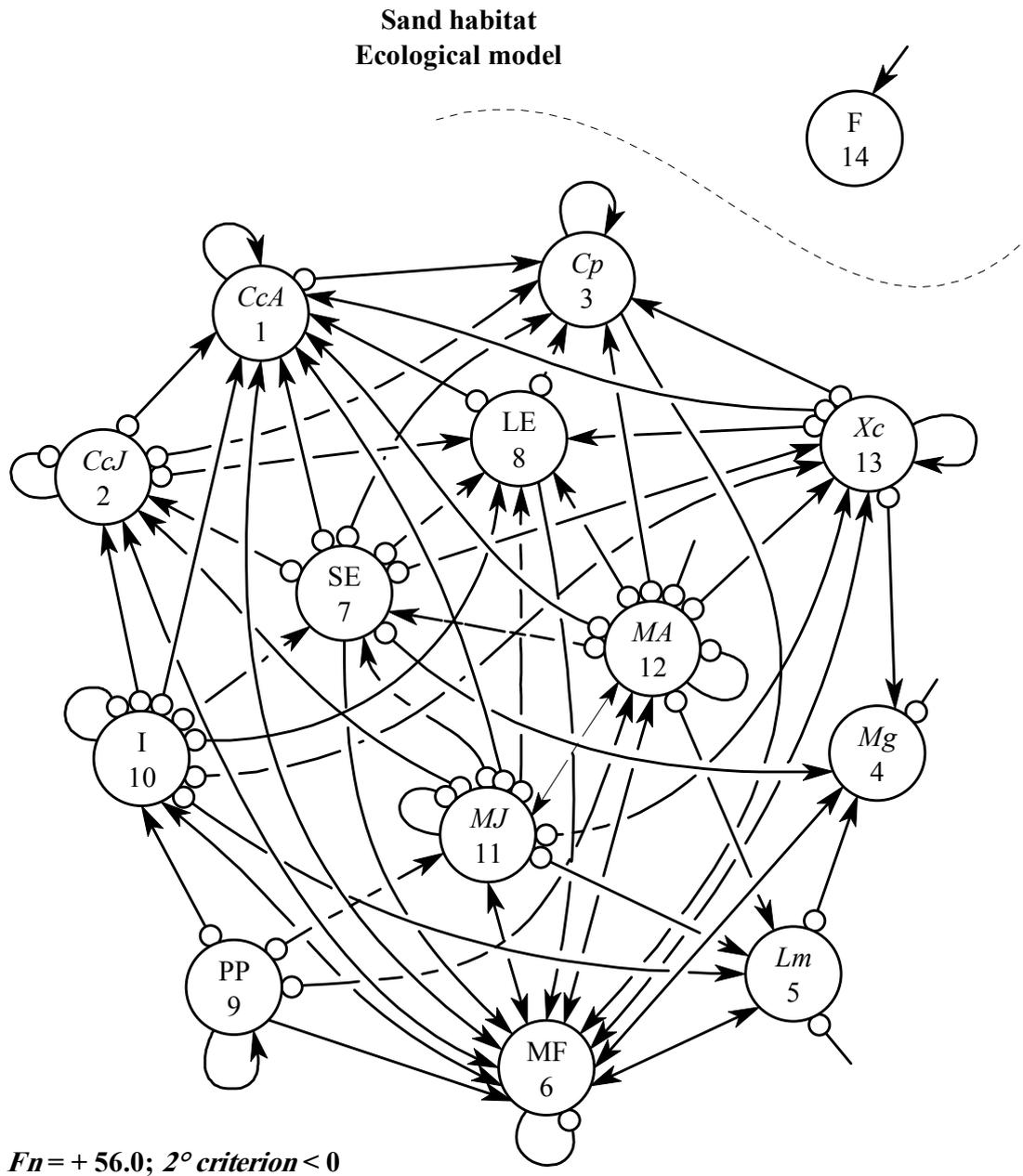


Fig. 6

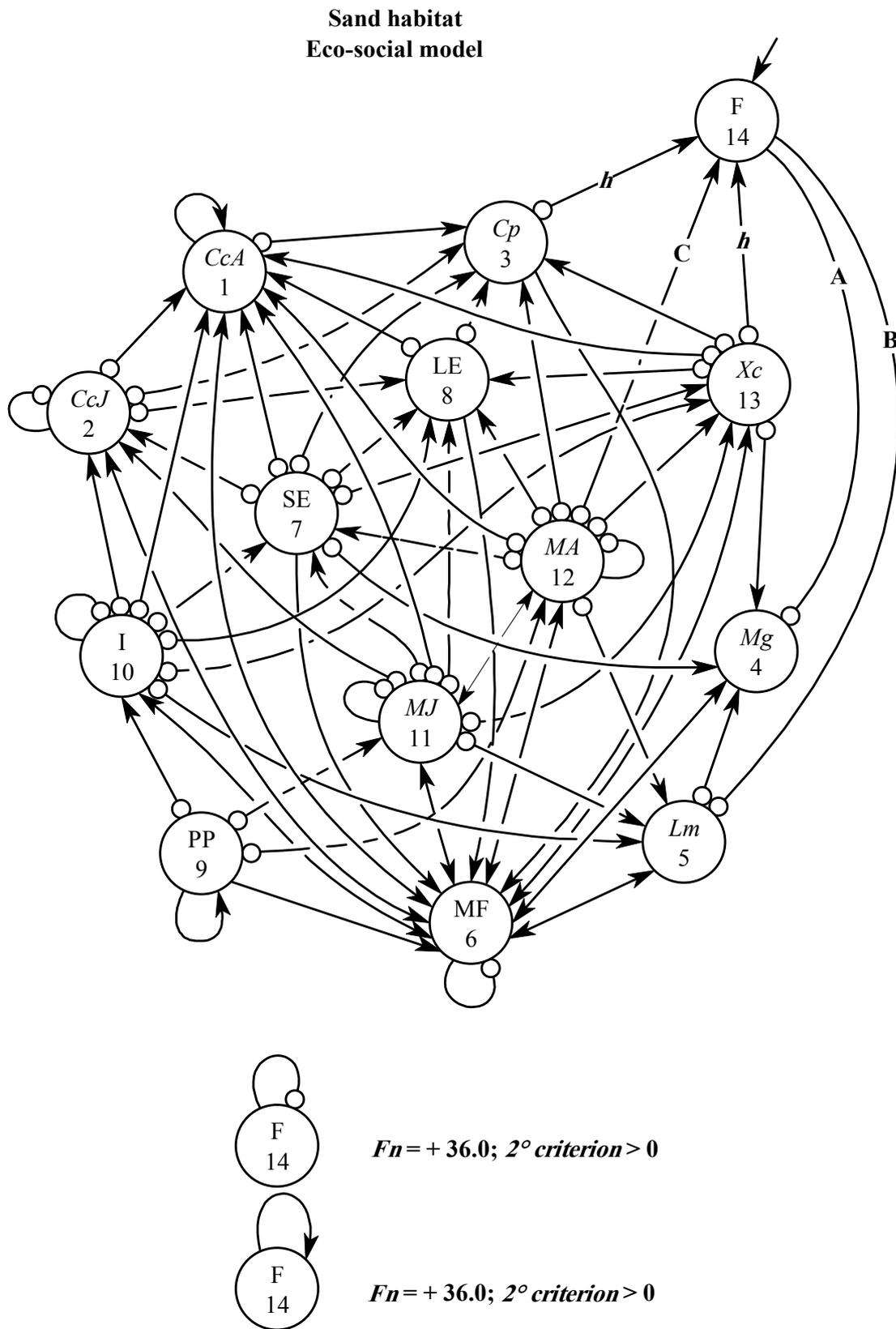


Fig. 7

10. Chapter VII Discussion & Conclusions

“Quantitative and qualitative holistic modelling of complex benthic systems to improve sustainable interventions: a comparative analysis”

Marco Ortiz & Matthias Wolff

Zentrum für Marine Tropenökologie (ZMT), Fahrenheitstrasse 6, D-28359 Bremen, Germany (eMail: mortiz@zmt.uni-bremen.de; mwolff@zmt.uni-bremen.de)

2001

The original idea for this publication was developed by the first author. The last version of this contribution was possible after intensive intellectual discussions with the co-author.

Abstract

The stability or capacity to withstand perturbations (used as a measure of sustainability) and the propagation of direct and indirect effects of human interventions were estimated in subtidal benthic habitats (seagrass, sand-gravel, sand and mud) of northern Chile by the use of the following modelling approaches: ECOPATH II (Christensen & Pauly 1992), ECOSIM (Walters et al. 1997), ECOSPACE (Walters et al. 1999) and LOOP ANALYSIS (Levins 1974, 1998b). The LOOP ANALYSIS has compared to the trophic modelling approaches the great advantage that: (1) other interactions beside trophic flows can be considered such as competence, amensalism, commensalism and mutualism, and (2) the local stability of the system can be estimated by the analysis of negative and positive feedbacks.

According to the relative *Ascendancy* (*Ascendancy/Capacity*) and *Redundancy* stability measures given by Ulanowicz (1986, 1997) and the holistic sustainability measure (F_n) of Levins (1998b) the sand-gravel habitat seems to be the most resistant or sustainable ecological system. Extended models integrating the fishermen were found locally stable only when the fishermen are self-damped, implying that the fishing effort and catch quota should be constrained. The trophic models revealed that the removal of the “undesirable” sea star predator *Meyenaster gelatinosus* would increase the standing stock of the commercial scallop *Argopecten purpuratus* in the seagrass habitat, whereas in the sand-gravel habitat the same intervention may have adverse effects. The fishing effort for a maximum sustainable yield *A. purpuratus* in the seagrass, sand-gravel and combined habitat models would be relatively lower under top-down and mixed control assumptions than if pure bottom-up (food limited) control was assumed for the same species and the same study area. Even though the debate of what mechanism controls the dynamic of the natural communities (top, mixed or bottom-up) is still controversial, we suggest that the estimation of maximum sustainable yield (F_{MSY}) exclusively based on population models may lead to erroneous predictions of F_{MSY} and might therefore have deleterious consequences for the dynamics of the commercial species. Therefore, we recommend to use holistic explorations (as those used in this study) as alternative strategies to establish a plan for man-made interventions and the estimation of maximum possible fishing effort.

Analysis

Since population models have not been sufficiently successful to help and protect ecological systems from deleterious man-made interventions, such as fisheries, pest management, diseases and immunisation practices, etc., scientists started to look for alternative large scale and more holistic abstractions (Larkin 1977, Levins & Vandermeer 1990, Levins 1994, 1998a, Hilborn et al. 1995, Patten 1997, Roberts 1997, Levins & Lopez 1999, Walters et al. 1999). The dominance of the *Cartesian* or *Newtonian* philosophy in the natural sciences, that aim to study the objects in isolation from their surroundings, may be explained by the easy and simple recognition of the object-boundaries and the quantification of their properties with high precision. On the other hand, the holistic or *Hegelian* philosophy, which approaches the same problem by the integration of the remainder objects was often considered as irrational and intractable.

Over the last two decades, at least two different theoretical frameworks have been widely applied to analyse and understand the underlying processes in complex natural systems. The first considers the flow of energy or matter between interconnected parts (variables, populations, functional groups) and the second just grasps the qualitative nature of the interactions. Within the first, the steady-state ECOPATH II (Christensen & Pauly 1994), the dynamical ECOSIM (Walters et al. 1997), and the spatially explicit ECOSPACE (Walters et al. 1999) software represent strategies by which the population dynamics of the species or

functional groups, their food spectrum, trophic relationships, spatial distribution and fisheries activities are simultaneously integrated. The potential role of mass balance models for the management of different aquatic systems has previously been discussed (Christensen & Pauly 1998, Jarre-Teichmann 1998). Based on the intensity and diversity of flows the systems can be characterised by descriptors developed by Odum (1969) and Ulanowicz (1986, 1997). The second termed LOOP ANALYSIS (Levins 1974, 1998b, Puccia & Levins 1985) allows to estimate the local stability (sustainability) of the system under study and to assess the propagation of direct and indirect effects as response to external perturbations. This theoretical approach has been widely applied in different fields of the natural sciences (Li & Moyle 1981, Giavelli & Bodini 1990, Levins & Vandermeer 1990, Whitlatch & Osman 1994, Lane 1998) and has shown that it allows for high degree of predictability of natural phenomena (Briand & McCauley 1978, Lane & Bloiun 1985, Lane & Collins 1985, Lane 1986).

Fig. 1 illustrates two simplified and idealised conceptual models for the same ecological system. Both describe the essential aspects of the two theoretical frameworks. It recognises that although the quantitative strategies (at steady-state and dynamical) can integrate precise information, the human interventions are grasped just as a flow to the external domain of the model. Instead, the qualitative abstraction allows to expand our boundaries integrating other ecological relationships and further variables such as the fishermen. In the present situation it was possible also to integrate competition, mutualism and amensalism, and the fishermen were simulated under either a self-damping or self-enhancing situation. Moreover, the local stability (as sustainability measure) of the system can also be estimated by the analysis of negative and positive feedbacks.

In 1996, an intensive investigation begun in Chile to obtain biological, ecological and physical information of a benthic system in the southern part of Tongoy Bay (northern Chile). This benthic area is one of the 168 management areas along the Chilean coast, assigned to fishermen associations, who are allowed to harvest and develop man-made interventions to increase within sustainable boundaries the standing stock of the commercial species (Castilla 2000). Due to the impossibility to carry out replicated experiments to estimate the sustainability and the propagated direct and indirect effects at multispecies, community or ecosystem levels as response to external perturbations (Lewontin & Levins 1998, Maron et al. 2001), we enunciated different holistic system models (quantitative and qualitative) which captured the principal ecological interactions and the environmental heterogeneity of this subtidal area. Based on these models we characterised the food webs according to Odum's, Ulanowicz's and Levins' Theories to estimate the resistance of each system to external perturbations, and to assess the propagation of higher order effects in the systems. The objective of the present work was, therefore, to show and compare the principal results obtained by each modelling approach. Based on the findings of this study we recommend some adaptive man-made interventions. The models here presented are extension of the trophic Tongoy Bay model given by Wolff (1994).

Table 1 summarises the stability or sustainability estimations for each ecological system. Based on the results obtained by ECOPATH II, ECOSIM, ECOSPACE and LOOP ANALYSIS the sand-gravel habitat seems to be the most resistant or sustainable system. It is important to point out that the indices of Ulanowicz and Levins showed similar tendencies, but differed from the stability properties when based on Odum's indices. The coincidence between the relative *Ascendency* ($Ascendency/Capacity$), *Redundancy*, and the holistic stability measure (F_n) given by Ulanowicz (1986, 1997) and Levins (1998b) respectively, shows that these indexes might be considered as key measures of sustainability for natural

systems, taking into account that trophic and loop models capture different types of relationships and are based on independent robust theoretical frameworks.

Additionally, through LOOP ANALYSIS we could extend the ecological systems integrating the fishermen into the models. Under this condition the extended sand-gravel systems is, as in the case of the trophic model, the most sustainable system. This local stability is, however, reached only when the fishermen are self-damped, implying that the fishing effort and catch quota must be constrained. Non-linear quantitative theoretical studies that have analysed the fishery effects on multispecies systems described similar conclusions to the ones here presented (May et. al. 1979, Beddington & May 1980, Beddington & Cooke 1982, Azar et al. 1995).

The propagated direct and indirect effects as response to the removal of the predatory sea star *Meyenaster gelatinosus* are shown in the Table 2. This species is considered by fishermen as “undesirable” because it feeds on the commercial scallop *Argopecten purpuratus* (Fig. 1). For 7 species or groups the models predicted a similar response to the removal of the seastar. In the seagrass habitat the models predicted a biomass increase of scallops when starfish is removed. However, in the sand-gravel habitat the response differed: only ECOPATH II and ECOSIM models predicted a positive effect on the scallops, while the LOOP ANALYSIS predicts a negative effect. All three models predict a biomass increase of the predatory crabs *Cancer polyodon* and *Paraxanthus barbiger* in the seagrass and sand-gravel habitats respectively. Likewise the mollusc *Calyptraea trochiformis* and the snail *Tegula* sp. would be positively affected in the sand-gravel habitat. This positive response of the competitor and prey species (cascading effects) can be interpreted as the dominance of positive feedback at lower levels which may have a negative impact on the holistic stability.

Communities and ecosystems are open to several types of natural perturbations which may eventually maximise the deleterious influence of these positive feedback on the stability of the entire system, driving it to some other moving equilibrium (Levins 1998c). Thus, if our objective is not only to increase the standing stock of the commercial species, but also to conserve the natural systems in which they inhabit, this positive feedback must be avoided. One way to depress it may be by fishing both the crab *C. polyodon* and mollusc *C. trochiformis* (both have commercial importance). However, before a definitive additional harvest strategy can be established, the trajectory of both systems should be monitored under of sea star removal. Regarding the results of ECOPATH II, a removal of 50% of the sea star *M. gelatinosus* would be allowed without introducing important changes in the system’s properties.

Table 3 shows the estimations of fishing mortality at the level of maximum sustainable yield (F_{MSY}) obtained by ECOSIM dynamical simulations under top-down, mixed and bottom-up flow control mechanisms. F_{MSY} for *A. purpuratus* obtained for the seagrass, sand-gravel and the combined system under top-down and mixed control assumption are smaller than those proposed for the same species and the same study area (Stotz & González 1997) and the assumption of bottom-up control. Even though the debate of what mechanism controls the dynamic of the natural communities (top, mixed or bottom-up) is still going on, we suggest that the estimation of maximum sustainable fishing exclusively based on population models may have deleterious consequences in the dynamic of the commercial species. Therefore, we recommend to design long-term and holistic explorations as alternative and complementary strategies before to establish a definitive maximum possible fishing effort.

In summary, we have shown that a management strategy should be not defined only thinking in the target species as an isolated object from its surroundings. The models here

explored showed that more ecological information is required if our interest is to have a holistic reasoning of sustainability. Whereas the reductionistic models always will predict a sustainable level of harvest for the species, based on robust mathematical functions (see Clark 1985), this interventions may have deleterious consequences on the sustainability of the entire system. Sometimes we forget that the populations are heterogeneous and thus constituted by different organisms each of one with a defined history and function in the system. Therefore, some external perturbation like harvest could have unexpected behaviour, such as, the replacement of predator competitors species, the dominance of one or few population of preys in absence of predator. All responses widely reported for intervened and deterred systems.

Our work does not have the aim to preclude the detailed examination of parts as a legitimate research tactic, but to show that the study of isolated parts is insufficient to the understanding of the whole. Even though man-made interventions, such as the removal of “undesirable” predator species, may be theoretically sustainable under population models, these reductionistic abstractions offer us only a proximate response without the integration of ultimate and long-term effects. Thus we suggest to apply holistic approaches as a complementary way to define, develop and predict man-made intervention in complex natural system. We conclude that the theoretical frameworks followed in this study should be used in other benthic management areas along the Chilean coast, if the sustainability of different adaptive management options for multispecies fisheries is to be explored (Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999, Castilla 2000).

References

1. Azar, C. *et al. J Theor Biol* **174**, 13-19 (1995).
2. Beddington, J. & May, R. *Math Biosci* **51**, 261-281 (1980).
3. Beddington, J. & Cooke, J. *Ecol Model* **14**, 155-177 (1982).
4. Briand, F. & McCauley, E. *Nature* **273**, 228-230 (1978).
5. Castilla, J.C. *J Exp Mar Biol Ecol* **250**, 3-21 (2000).
6. Christensen, V. & Pauly, D. *Ecol Model* **61**, 169-185 (1992).
7. Christensen, V. & Pauly, D. *Ecological Applications* **8**(1), S104-S109 (1998).
8. Clark, C. *Bioeconomic modelling and fisheries management* (Wiley, NY, 1985).
9. Giavelli, G. & Bodini, A. *Oikos* **57**, 357-365 (1990).
10. Hilborn, *et al. Ann Rev Ecol Syst* **26**, 45-67(1995).
11. Jarre-Teichmann, A. *Ecological Applications* **8**(1), S93-S103 (1998).
12. Lane, P. *Ecology* **67**(1), 223-239 (1986).
13. Lane, P. in *Ecosystem Health* (eds. Raport, D. *et al.*) 129-153 (Blackwell, MA, 1998).
14. Lane, P. & Blouin, A. *Int Revue ges. Hydrobiol* **70**(2), 203-220 (1985).
15. Lane, P. & Collins, T. *J Exp Mar Biol Ecol* **94**, 41-70 (1985).
16. Larkin, P. *Trans Amer Fish soc* **106**(1), 1-11 (1977).
17. Levins, R. *Annals NY Acad Sci* **231**, 123-138 (1974).
18. Levins, R. *Annals NY Acad Sci* **740**, 260-270 (1994).
19. Levins, R. *Science as Culture* **7**(4), 557-582 (1998a).
20. Levins, R. in *Ecosystem Health* (eds. Raport, D. *et al.*) 178-204 (Blackwell, MA, 1998b).
21. Levins, R. *Science & Society* **62**(3), 375-399 (1998c).
22. Levins, R. & Vandermeer, J. in *The agroecosystem Embedded in a Complex Ecological Community* (eds. Carroll, R. *et al.*) 341-362 (McGraw-Hill, NY, 1990).
23. Levins, R. & Lopez, C. *Inter J Health Services* **29**(2), 261-293 (1999).
24. Lewontin, R. & Levins, R. *Capitalism Nature Socialism* **9**(1), 85-89 (1998).
25. Li, H. & Moyle, P. *Trans Amer Fish Soc* **110**, 772-782 (1981).
26. Maron, J. *et al. Oecologia* **126**, 595-602 (2001).

27. May, *et al.* *Science* **205**, 267-276 (1979).
28. Odum, E. P. *Science* **104**, 262-270 (1969).
29. Patten, B. *Ecol Model* **100**, 11-42 (1997).
30. Puccia, Ch. & Levins, R. *Qualitative Modelling of Complex Systems* (Harvard University Press, Boston, 1985).
31. Roberts, C. *TREE* **12**, 35-38 (1997).
32. Stotz, B. & González, S. *Fish Res* **32**, 173-183 (1997).
33. Ulanowicz, R. *Growth and development: Ecosystems phenomenology* (Springer, NY, 1986).
34. Ulanowicz, R. *Ecology, the Ascendent Perspective. Complexity in Ecological System Series* (Columbia University Press, NY, 1997).
35. Walters, C. & Hilborn, R. *Ann Rev Ecol Syst* **9**, 157-188 (1978).
36. Walters, C. & Korman, J. *Ecosystems* **2**, 411-421 (1999).
37. Walters, C. *et al.* *Rev Fish Biol Fish* **7**, 139-172 (1997).
40. Walters C. *et al.* *Ecosystems* **2**, 539-554 (1999).
41. Whitlatch, R. & Osman, R. *J Shellfish Res* **13**(1), 229-242 (1994).
42. Wolff, M. *J Exp Mar Biol Ecol* **182**, 149-168 (1994).

List of Tables and Figures

Table 1. Summarises the holistic measures of resistance to perturbations or local stability (two criteria) for each benthic system analysed. The ratios of production to respiration (P/R) and productivity to biomass (P/B) sensu Odum (1969), relative ascendancy (%) (A/C) and Redundancy (%) sensu Ulanowicz (1986, 1997), the magnitude of changes in the systems through the direct and indirect effect propagated ($D-I E$). For ECOSIM¹ the effects observed as response to remove of the sea star *M. gelatinosus*, and for ECOSPACE² as response to the impact of the total fishing activities in both benthic systems. In the seagrass habitat are exploited the scallop *A. purpuratus* and the crab *Cancer polyodon* and in the sand-gravel the scallop, the crab and the rodophyta *Chondrocanthus chamissoi*. The holistic measures of sustainability based on two criteria of local stability (sensu Levins 1974, 1998b) are also shown. (a) and (b) represent the fishermen with a self-damped and self-enhanced dynamic respectively. (1°) indicates the most resistant or sustainable system. The grey are shows similar tendencies between measurements.

Table 2. Qualitative predictions for each species of group in the seagrass and sand-gravel habitat as response to remove abundance of the predatory sea star *M. gelatinosus*. The grey areas indicate similar expected responses. *Mg*, *Hh* and *Lm* represent the sea star species *M. gelatinosus*, *Heliaster helianthus* and *Luidia magallanica* respectively, *Cp*, *Pb* and *Ta* sp. are the crabs *Cancer polyodon*, *Paraxanthus barbiger* and *Taliepus* sp. respectively, *LE* include the remainder crabs species like *Guadichaudia gaudichaudia*, *Hepatus chilense* and *Platymera gaudichaudia*, *Ap* is the scallop *A. purpuratus*, *Ct* represents the mollusc *Calyptraea trochiformis*, *Te* sp. is the snail *Tegula* sp., *Pch* represents the sea squirts *Pyura chilensis*, *SE* includes small gastropods such as *Nassarius* sp., *Nucula* sp., *Turritella* sp., *Mitrella* sp., and the polyplacophora *Chiton* sp., *I* comprises polychaetes and other buried bivalves, *Ht* is the rodophyta *Chondrocanthus chamissoi*, *R* includes other rodophyta, *Ul* sp. represents *Ulva* sp., *PP* is primary productivity, *D* represents dretritus and *F* is the fishermen.

Table 3. Maximum sustainable fishing mortality estimations (F_{MSY}) for the scallop *A. purpuratus* in the seagrass, sand-gravel and whole under top-down, mixed and bottom-up flow control mechanisms. The grey area indicates the results obtained under mixed control. Multiples means that with highest top-down controlling more than one possible value of F_{MSY} was obtained.

Fig. 1. Shows an idealised and simplified conceptual models under both theoretical framework used in the presented work. *MF* = microbial film, *PP* = primary productivity, *Ht* = the seagrass *Heterozostera tasmanica*, *Ap* = the scallop *Argopecten purpuratus*, *Mg* = the predatory sea star *Meyenaster gelatinosus*, *F* = fishermen (self-damped and self-enhanced), *f* = flow, *h* = harvest, and *m* represents an eventual management police (removal of the “undesirable” predator). Above a classic flow of matter or energy is represented, and below the qualitative interaction under the LOOP ANALYSIS.

Table 1

Indices	Ecological systems		
		Seagrass	Sand-Gravel
Odum (1969)	<i>P/R</i>	2.85(1°)	3.07(2°)
	<i>P/B</i>	10.59(1°)	9.42(2°)
Ulanowicz (1986)	<i>A/C (%)</i>	31.1(2°)	30.4(1°)
	<i>Redundancy (%)</i>	51(2°)	53.8(1°)
Walters et al (1997)	<i>ECOSIM</i> ¹	<i>D-I E</i> (2°)	<i>D-I E</i> (1°)
Walters et al (1999)	<i>ECOSPACE</i> ²	<i>D-I E</i> (2°)	<i>D-I E</i> (1)
Levins (1974,1975,1998b)	<i>LOOP ANALYSIS</i>		
	<i>Fn < 0</i>	(-) 1.0(2°)	(-) 96.0(1°)
	<i>2° criteria > 0</i>	no	no
		Extended systems	
<i>Fn < 0</i>	a)	(-) 12.0(2°)	(-) 24.0(1°)
	b)	(+) 42.0	(+) 168.0
<i>2° criteria > 0</i>	a)	yes	yes
	b)	no	no

Table 2

HABITAT	QUALITATIVE PREDICTIONS																			
	Species/groups																			
	Mg	Hh	Lm	Cp	Pb	Ta sp.	LE	Ap	Ct	Te sp.	Pch	SE	I	Ht	Chch	R	Ul sp.	PP	D	F
Seagrass																				
<i>ECOPATH II</i>	+	+	+	+	-	0	+	+				+	-	0	-	-	-	0	0	+
<i>ECOSIM</i>	-	+	0	+	+	+	+	+				+	-	0	+	0	0	0	0	+
<i>LOOP ANALYSIS</i>	0	-	-	+	-		0	+				+	-	-				+		-
Sand-gravel																				
<i>ECOPATH II</i>	+	+	+	+	+	-	+	+	+	+	+	0	-		0	0	0	-	-	0
<i>ECOSIM</i>	-	+	0	+	+	+	+	+	+	+	0	0	0		0	0	0	0	0	+
<i>LOOP ANALYSIS</i>	+	-	+	-	+	-	-	-	+	+	+	-	-		-	-	-	-		+

Table 3

Habitats		Control						
			Top-down			Mixed	Bottom-up	
Seagrass		1	0.8	0.6	0.4	0.3	0.2	0.1
<i>A.purpuratus</i>	F_{MSY}	Multiples	0.94	1.03	1.03	1.06	1.24	1.71
Sand-Gravel								
<i>A.purpuratus</i>	F_{MSY}	Multiples	0.17	0.28	0.52	0.7	1	1.5
Whole Area								
<i>A.purpuratus</i>	F_{MSY}	0.29	0.34	0.45	0.68	0.86	1.1	1.57

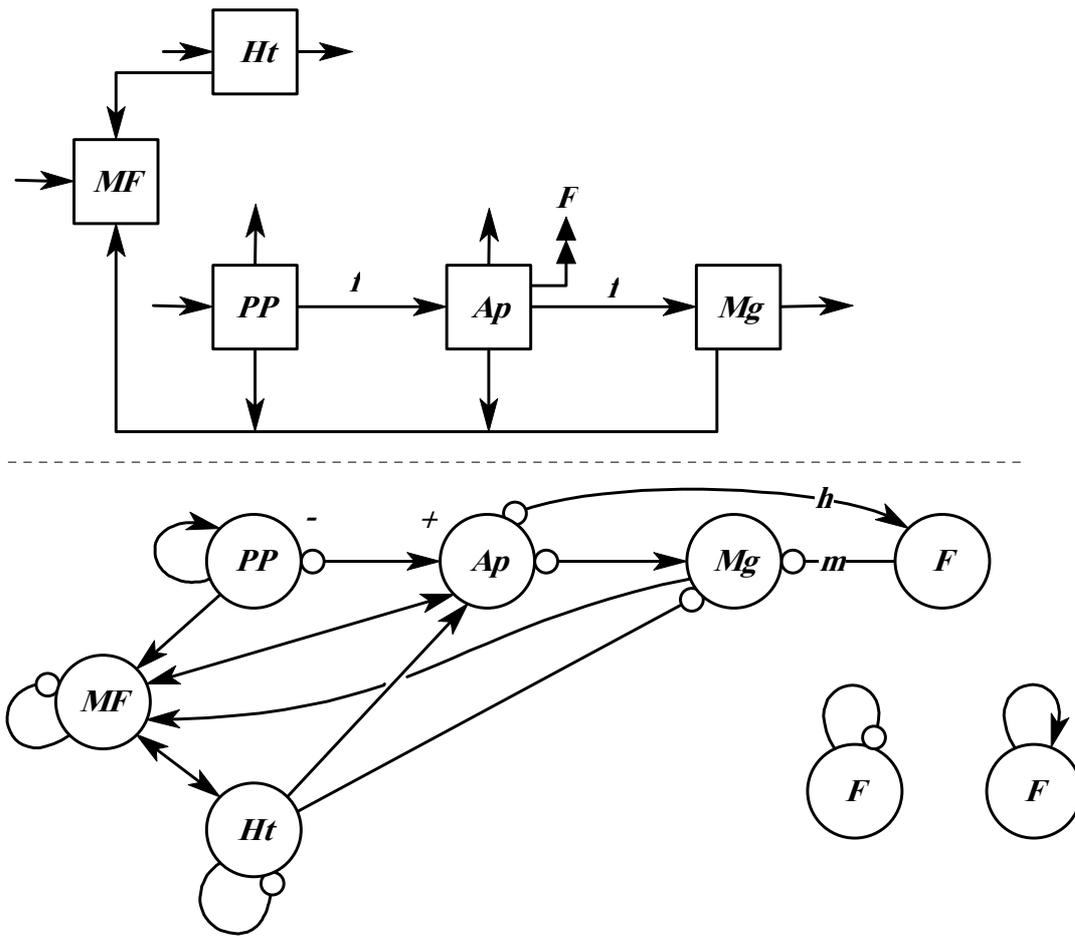


Fig. 1