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Emergy-based indicators for evaluating ecosystem health: A case study of three benthic ecosystem networks influenced by coastal upwelling in northern Chile (SE Pacific coast)

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Abstract

It has been hypothesized that ecosystem health describes the state in which all processes operating within an ecosystem are functioning at a level of optimum efficiency to maximize system empower. In this study, systems analysis of networks and information flows is used within this definition of ecosystem health to assess the condition of the benthic ecosystems in three coastal bays in northern Chile. These highly productive ecosystems are characterized by the inflow of cold, nutrient-rich waters of low oxygen concentration derived from coastal upwelling of deep waters and the interruption of upwelling flow during El Niño events when warmer waters with higher oxygen and lower nutrient concentrations enter these coastal systems. Also, these ecosystems support important artisanal benthic fisheries and are affected by industrial activities in the coastal zone. Emergy Systems Theory (EST) and Emergy Analysis¹ (EA) were applied to quantify the health of these benthic ecosystems and evaluate differences in their structure, organization and functional capacities, which are related to their emergy signatures. The marked dominance of these benthic ecosystems by nitrate from upwelling resulted in unbalanced emergy signatures, suggesting less development and system diversity compared to other coastal ecosystems with more balanced emergy signatures. Macro-descriptors and network properties, such as emergy-based ascendancy and the quality-adjusted Shannon diversity index² were highest for Mejillones Bay, followed by Antofagasta and then Tongoy Bay. The Average Mutual Information (AMI) index adjusted for energy quality³ and the emergy-based A/C (ascendancy to capacity) ratio⁴, were higher for Tongoy Bay, suggesting functional differences in health among

¹Emergy is defined as the sum of the available energy (i.e., energy with the potential to do work) of one kind, e.g., solar joules, which is used-up, directly and indirectly, within an ecosystem for the production of goods and services.

²The proportion of total system emergy flow allocated to each component.

³The number and diversity of emergy-weighted interactions among the system components.

⁴This index has been suggested as a maturity index.

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the three ecosystems. Thus, the emergy-based macro descriptors and other indicators used in our analysis indicate that the benthic networks examined have different structural and functional characteristics that lead to different characterizations of their states of health. As a result of this complexity, management policies should be implemented within a systemic context for analysis that considers all the factors determining the relative health of each ecosystem.

Keywords

Ecosystem health; Emergy; Transformity; Upwelling; Benthic ecosystems; Coastal zone; Network analysis

1 Introduction

The health of the coastal ecosystems of northern Chile is important, because as a consequence of waters rich in nutrients derived from coastal upwelling, they are some of the most productive ecosystems on Earth (Strubs et al., 1998). In addition, this high nutrient, high productivity state alternates with a lower nutrient, lower productivity state that dominates in years when the coastal upwelling circulation is curtailed by the El Niño Southern Oscillation (ENSO). A further complicating factor in assessing the health of these systems is that the frequency and intensity of upwelling regimes alternate on a multidecadal time scale driven by changes in global wind patterns (Oviatt, et al., 2015). In recent years, health assessments of the benthic systems in Mejillones, Antofagasta and Tongoy Bays have been made using trophic network models, which integrate the magnitudes of production and consumption of ecosystem compartments, the flow of energy through the network and the information distributed among model compartments (Ortiz and Wolff, 2002; Ortiz et al., 2015).

Odum (1996) pointed out that the different flows of available energy, expressed in terms of their caloric value, are not equivalent in terms of their ability to perform work. Therefore, we realized that to obtain a complete understanding of the condition of these benthic ecosystems that is grounded in thermodynamics, it was necessary to complement the conclusions gained from our ascendancy evaluation using the results of an emergy evaluation of the same systems.

Ecological studies have been pursued in at least two ways: (1) by using a reductionist approach, where each variable is studied separately based on experimental designs, population models, and models of simple interactions (e.g., predation, competition, parasitism, etc.), and (2) by using multi-species network analysis, which attempts to capture the interactions of relevant species, and from which emerge global properties that are impossible to observe and quantify in isolation (Jørgensen, 1992; Odum, 1994). In this approach, thermodynamic principles (i.e., the first and second laws of thermodynamics and the maximum [em] power principle, which has been proposed as the fourth law of thermodynamics, [Lotka, 1922 a, b; Odum, 1996])) are considered to be key principles in explaining the growth and development of ecosystems. Growth has been described as an increase in size (e.g., of the energy flow) and development as an increase in organization of the system (i.e., complexity), which is independent of size (Ulanowicz, 1986, 1997;

Jørgensen et al., 2000). In thermodynamic terms, the increase in these two properties means that ecosystems gain order and move away from the state of thermodynamic equilibrium, and these thermodynamic properties of natural systems can be used to assess the ecological condition (e.g., the health) of ecosystems (Jørgensen et al., 2005). The ecological health of ecosystems could be defined as the ability to maintain or restore optimal system function, i.e., the optimum efficiency for maximum power (Odum, 1996; Campbell, 2000), when confronted with a disturbance, which can be used as an indicator of the ecological sustainability of the system (Costanza and Mageau, 1999; Campbell, 2000; Lu et al., 2015).

Lotka (1922a, b and 1925) introduced the maximum power principle (MPP) to explain the development of self-organization in systems far from thermodynamic equilibrium. The MPP indicates that the systems that will prevail are those that capture and use (available) energy to develop configurations that maximize the inflow of useful energy (power). However, Odum (1994, 1996) showed that if energy flows alone are considered, in some cases, systems with lower levels of organization can have a greater flow of energy than those with greater organizational complexity. In this case, the MPP implies that the less organized systems will prevail in evolutionary competition over those with higher levels of organization, which is not consistent with observations and models of self-organization (Odum, 1996; Campbell, 2000; Campbell et al., 2009; Li et al., 2013). The determination of emergy (Odum, 1996) requires tracing the solar energy invested in the production of goods and services within ecosystems or economies. Therefore, Odum (1996) re-defined the MPP as the Maximum Empower Principle (MEmp) to evaluate the relative contribution of quality-adjusted power (i.e., emergy flow) to the general welfare of the system taking into account the different hierarchical levels in ecosystems. In this sense, Campbell (2000) defined ecological integrity as the emergent ecosystem structure that maximizes network empower within the context of the emergy signature received by the ecosystem, and ecosystem health as the state in which all of the processes operating within and among the components of the system are functioning at the optimum efficiency for maximum empower. Although other frameworks for evaluating ecosystem health might be chosen, Campbell (2000) provides an approach grounded in Energy Systems Theory and its metrics, such as emergy indices, which can be used as a basis for evaluating the “health” or functional integrity of any system within the context of the system’s energy and emergy signatures, including the spatial and temporal variability of the suite of forcing functions that comprise the signature.

Odum (1988, 1994 and 1996) criticized the use of energy values alone to assess the relative importance of each component of the ecosystem with respect to its function, because the flow of available energy alone does not represent the true contribution of the process or component to the functionality or “health” of the ecosystem as a whole. Odum (1996) pointed out that the different flows of available energy, expressed in terms of their caloric values, are not equivalent in terms of their ability to perform work. Therefore, as mentioned above, we realized that to obtain a complete thermodynamic understanding of the condition of these benthic ecosystems, it was necessary to complement the conclusions gained from our earlier systemic evaluations using the results of an emergy evaluation. Emergy evaluation is a methodological procedure to determine the relative efficacy of flows and storages of material, energy, and information within a system based on the normalization of

all types of available energy (i.e., energy with the potential to do work) to equivalent units as solar joules. A solar emjoule, the unit of emergy, is a solar equivalent joule that has been used-up in the past to produce the various products and services in a system. This method integrates additional information into the assessment, such as the contribution of inputs of renewable and nonrenewable energy (i.e., from the forcing functions) that until now have not been used to assess the health of coastal-benthic marine ecosystem networks.

The intention of the present study was to obtain a thermodynamic understanding of the conditions supporting these three benthic coastal ecosystems and to provide additional information on and to further develop indicators of ecosystem health by building on the framework for defining measuring and interpreting ecosystem health and ecological integrity proposed in Campbell (2000). Specifically, we wanted to 1) evaluate the ecological health of the three benthic ecosystems examined in this study using emerybased indicators that capture the effects of environmental variations, such as the El Niño Southern Oscillation (ENSO) and other factors; 2) determine the influence of these environmental factors on the growth and development of the benthic ecosystems; 3) use emergy diversity indicators to evaluate and assess the health of these benthic networks and 4) use emergy-based ascendancy (Christensen, 1994) and its related indices to assess the network properties of the benthic ecological systems of Mejillones, Antofagasta and Tongoy Bays. Furthermore, we wanted to compare macroscopic indices of the structure, organization and functional capacity of these three ecosystem networks, which are representative in their various aspects of both natural and human influences on the coastal embayment ecosystems of northern Chile. The results of our study will also be compared and contrasted with methods that use more traditional approaches based on energy and mass and others that use multiple criteria to evaluate ecosystem health.

2 Methods

2.1 Emergy signature evaluation

Forcing functions are sources of energy, matter and information from the larger system that characterize and drive ecological systems and that enter a system by flowing across its boundaries (Campbell, 2000). The major environmental forcing functions that constitute the energy signature of the three bays are solar radiation, wind, tide, waves and upwelled nitrate, which were estimated for each coastal system (Table 1 and Figure 3). The emergy signature was estimated by multiplying each available energy source by the appropriate transformity. The transformities calculated were corrected to the new baseline, which is $12\text{E}+24 \text{ seJ y}^{-1}$ (Brown et al., 2016; Campbell, 2016). It is important to clarify that Brown et al. (2016) explain that the geobiosphere baseline can only be determined by establishing equivalences between the different exergy inputs to the geobiosphere and thus it is expressed in solar equivalent joules (seJ), whereas emergy is determined by a track-sum method starting with the baseline and is expressed in emjoules (sej) as defined in section 3.2 below. The emergy base required to support primary production and consumption of species or functional groups of the ecological networks in each bay was estimated per square meter (i.e., empower density) using a procedure developed by Campbell (2004) to obtain estimates for the transformities of energy flows within the benthic ecosystems.

2.2 Emergy evaluation of benthic ecological networks

The energy flows of the ecological variables were obtained from the input parameters and flow matrices of mass balanced trophic models built by Ortiz and Wolff (2002) and Ortiz et al. (2015) that represent the interspecific relationships (prey–predator) in the benthic systems in a regime of coastal upwelling, from which the transformities were estimated using the procedure developed by Li et al. (2010).

The mass flows of the ecological variables were converted to energy using factors to convert from wet weight to dry weight ($\times 0.2$) and from dry weight to energy ($\times 5$ kcal/g dry weight and $\times 4183$ J/kcal). In this way, the interaction (consumption) matrix was expressed in energy terms ($\text{joules m}^{-2} \text{ year}^{-1}$) from which the transformities were estimated using the fundamental equation that defines emergy as the product of a flow of available energy (J_E) and the quality of that flow (transformity, tr) where $[\text{Emergy sej y}^{-1} = \text{Available Energy J y}^{-1} \times \text{Transformity sej J}^{-1}]$. The method of Li et al. (2010) allowed us to structure the equations to determine each energy flow of the ecosystem following the rules of emergy algebra, before estimating the transformities. This step, called preconditioning, is designed to prevent mistakes related to double counting in determining the value of the emergy base required for the production of each flow (see Appendix A, for the case of the Mejillones model). The first step in determining the transformities is to structure the equations from the energy systems diagram for each system (Figure 2a, b, c) using the energy flows present and considering the rules of emergy algebra (Odum, 1996; Brown and Herendeen, 1996). The transformity of an energy flow may vary according to its designation as a co-product or as a split within the ecosystem network. A co-product can be identified when the two outputs are not substitutable and in this case the entire emergy input to the production process is required for each output. On the other hand, a split occurs when the outputs of a process are substitutable and in this case the emergy input to the production of the products can be divided in proportion to the available energy on each arm of an output pathway (Odum, 1996). The implication is that these two products are functionally similar and therefore substitutable. However, sometimes in complex systems, there is not enough biological-ecological information to make an accurate determination that a particular flow is a split or a co-product (Campbell, 2004). For example, where benthic macro fauna and filter feeders ingest different living and non-living biological materials, assimilate organic matter into biomass and produce feces (detritus) and pseudo feces, which can also be used as food, distinguishing co-products and splits within a complex network of food and waste might be difficult. If products have different properties in the way that they are used in the ecosystem, they would be classified as co-products, but if the products can be used in the same manner, e.g., as food, then classification as a split is perhaps more appropriate. In this regard, we simplified the problem by assuming that there are no co-product modules in the benthic ecosystem network, based on the procedure of Brown et al. (2006) and Zarbá and Brown (2015). This simplification allowed us to more easily estimate the emergy indicators within the ecosystem networks.

The time boundary for making estimates of the flows of energy is one year. The hydrodynamic model of Moraga-Opazo et al. (2011) was used to estimate the volume of upwelled water entering Tongoy Bay per year, and the models proposed by Escribano and

Hidalgo (2001) and Marin et al. (2003) were used to estimate the volume of upwelled water entering Antofagasta and Mejillones Bays, respectively.

2.3. Network analysis: Definition of eight macro-descriptors of ecosystem network properties

Eight macroscopic indexes or descriptors were calculated to evaluate and compare the health of each benthic ecosystem. These indices are described below.

(1) Average transformity (sej/J).—The traditional ecological efficiency measure is calculated as the output energy of a process expressed as a percent of the input energy in ecological systems (Lindeman, 1942). The usual value of the Lindeman efficiency for transfers between trophic levels is about 10%. Transformity (tr) is the reciprocal of the Lindeman efficiency. The transformity is relevant, because it is a universal measure of the position of ecological variables within their system network and of systems within the hierarchy of natural processes of the biosphere. The transformity is the ratio of the emergy input to the available energy output of a process, and it is a measure of the efficiency of production processes, when the same output is produced. In this case, higher values of transformity imply a greater emergy input or a lower available energy output, and therefore the process will be less efficient compared with other production processes that are making the same amount and quality of a product using less emergy. We interpreted transformities through comparison to average values for the indicator that had been established in past studies (Ulgiati and Brown, 2002).

(2) Quality-adjusted diversity.—The energy quality-adjusted Shannon diversity index of the system (Brown et al., 2006), was used to evaluate the ecological organization (diversity) of the benthic ecosystems. This index replaces the probability of observing component i in a system of n elements with the magnitude of the Emergy Importance Value (EIV), which is defined as follows (Eq.1):

$$EIV_i = \frac{NP_i * tr_i}{\sum_j NP_j * tr_j} \quad (1)$$

which is the proportion of total system emergy flow ($sej \text{ yr}^{-1}$) allocated to each component. This formulation allowed the calculation of the ecosystem Shannon diversity index as follows (Eq. 2):

$$\sum_{i=1}^n EIV_i * \log_2(EIV_i) \quad (2)$$

where NP_i is the net production and tr_i is the transformity of component i in a system of n components. The *relative diversity* ($RD \%$) relates the Shannon diversity index of the system to the theoretical maximum diversity for the number of species present. It was calculated with the purpose of comparing the relative states of development of the different systems compared to the maximum possible for the species richness observed.

(3) Total emergy system throughput ($\text{sej m}^{-2} \text{y}^{-1}$).—Total emergy system throughput (TEST) is the sum of the magnitudes of all emergy flows on all network pathways occurring in the system, and it describes the vigor or size of a system. This descriptor represents a measure of a system's total metabolism, including consumption, flow into detritus, respiration and exports to the fishery.

(4) The average mutual information (emergy adjusted flowbits).—The average mutual information (AMI) index (Ulanowicz, 1986) adjusted for energy quality was estimated to assess the complexity of the system in terms of its flows according to Ortiz et al. (2015), in which it was established that a greater value of AMI implies less complexity. AMI measures the number and diversity of weighted interactions amongst the system components as follows:

$$\text{AMI} = \sum_{i,j} T_{ij}/T^* \log(T_{ij}^*/T_i^* T_j) \quad (3)$$

where the T_{ij} is the emergy flow out of group i and going into group j , T is the sum of the all emergy fluxes in the system, T_i is the emergy flow i and T_j is the emergy flow j .

(5) Emergy adjusted ascendancy (emergy adjusted flowbits).—The emergy-based relative ascendancy (EBA) is an index that integrates both the size (TEST) and organization of a system (AMI). Ascendancy has been related to system stability (Christensen, 1995) and maturity (Ulanowicz and Abarca-Arenas, 1997).

(6) Emergy-based development capacity (emergy adjusted flow bits).—The emergy-based Development Capacity (C) quantifies the upper limits to Ascendancy, it is calculated as:

$$C = \sum_{i,j} T_{ij} * \log \frac{T_{ij}}{T} \quad (4)$$

(7) Emergy-based overhead (emergy adjusted flow bits).—The emergy overhead (Ov) is the difference between Ascendancy and the Development Capacity, and indicates the multiplicity of information pathways such as: system input, export, dissipation and internal exchange (redundancy). This may closely relate to the capacity to withstand perturbations (Christensen, 1995).

(8) Emergy-based A/C in percent.—The emergy-based A/C (ascendancy to capacity) ratio describes the network efficiency.

The A/C ratio has been suggested as a maturity index (Costanza and Mageau, 1999). Additionally, it can also be used as an indicator of ecosystem development (Kaufman and Borrett, 2010; González et al., 2016) and as a measure of a system's ability to resist disturbances (Ulanowicz, 1986, 1997).

The unit for the (EBA), (C) and (Ov) measures is ‘flowbits’, which is given by the product of a flow (e.g., $\text{g}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) and the information in bits on the pathways given in the formulae for the relevant macrodescriptors. The ‘bit’ is an information unit defined as the amount of uncertainty associated with a single binary decision (Christensen et al., 2005).

2.4. Index for assessing health condition: The ratio between the Expected and Observed Emery Throughput (EOET)

In addition to the 8 macro-descriptors of the ecosystem network defined above, we used a 9th index as a more direct measure of ecosystem health. The ratio between the Expected and Observed Emery Throughput (EOET) from Brown et al. (2006) was used to evaluate the condition of the benthic ecosystems, since healthier ecosystems are expected to have greater evenness of flows across all components. This definition is applied within the context of a given set of forcing functions or emery signature for a system as described in Campbell (2000). The EOET is a fractional diversity index (observed diversity/ maximum diversity) as described by Eq. 3:

$$\text{EOET}_i = (\text{TET}/N)/(\text{NP}_i * t_i) \quad (5)$$

where TET is total emery throughput of the whole system and N is the number of biotic compartments. The resulting values were natural log transformed to linearize the response, where values larger than 0 indicate a component less important than the expected value of 1 and vice versa (Brown et al., 2006).

3. Results

3.1. Emery signature

The calculations and data sources for the energy signature of the coastal zones of the three bays are documented in Appendix A of Berrios et al. (2017). The energy signature shows that solar and wind energy comprised the highest percentage (> 99%) of the energy inflows (Table 1 and Figure 3a, b, c), while in the emery signature, the upwelled $\text{NO}_3\text{-N}$ contributed > 84% of the inflow in all three coastal systems (Table 1 and Figure 3d, e, f). The emery bases for the Mejillones, Antofagasta and Tongoy Bay ecosystems are comprised of the emery input in the sun, tide and upwelled nitrogen. Wave energy was not included, because the systems examined are deeper than the surf zone and wind emery supports the upwelling circulation pattern and thus would double count the nitrogen inflow, if included. The renewable empower density was higher in Mejillones Bay ($4.26\text{E}+12\text{sej m}^{-2}\cdot\text{y}^{-1}$) than in Antofagasta Bay ($3.32\text{E}+12\text{sej m}^{-2}\cdot\text{y}^{-1}$), which was higher than Tongoy Bay ($2.03\text{E}+12\text{sej m}^{-2}\cdot\text{y}^{-1}$) (Table 1).

3.2. Emery evaluation of benthic ecological networks

The network transformities are presented in Figure 5 and in Table 2. Phytoplankton had the lowest transformities (ranging between $6.35\text{E}+04\text{ sej J}^{-1}$ and $1.36\text{E}+05\text{ sej J}^{-1}$) of all primary producers and was more efficient than the brown, red and green macroalgae in all three bays. Macroalgal transformities ranged from $2.32\text{E}+05\text{ sej J}^{-1}$ to $1.96\text{E}+06\text{ sej J}^{-1}$

(Table 2). In the second trophic level, Zooplankton are the most efficient users of resources in all three bays ($3.65\text{E}+05$, Mejillones; $1.64\text{E}+05$, Antofagasta; $2.02\text{E}+05$ sej J^{-1} , Tongoy Bay). The scallop *Argopecten purpuratus* ($4.67\text{E}+05$, Mejillones; $1.84\text{E}+05$, Antofagasta; $3.27\text{E}+05$ sej J^{-1} , Tongoy Bay) is nearly as efficient as Zooplankton and it is also the second most efficient organism in using resources at the second trophic level in all three bays. Sea Urchin Species (SUS) is the least efficient user of resources at the second trophic level in Mejillones and Antofagasta Bays, $1.10\text{E}+6$ and $1.79\text{E}+6$ sej J^{-1} , respectively, but it did not appear in Tongoy Bay where the gastropod, *Tegula* sp. ($2.02\text{E}+5$ sej J^{-1}) takes its place. Between trophic levels 2 and 3, Other Sea Star Species (OSS) are more efficient in Mejillones and Antofagasta Bays, $4.17\text{E}+06$ sej J^{-1} and $4.02\text{E}+06$ sej J^{-1} , respectively, but do not appear in the list of organisms for Tongoy Bay where the tunicate *Pyura chilensis* is the most efficient organism, $3.37\text{E}+05$ sej J^{-1} . The least efficient organisms at this level are the crabs *Cancer* spp. in Mejillones Bay, $1.62\text{E}+06$ sej J^{-1} , and in Antofagasta Bay, $1.23\text{E}+06$ sej J^{-1} and *Paraxanthus barbiger* in Tongoy Bay, $1.40\text{E}+06$ sej J^{-1} . At trophic level 3 and above the cephalopod, *Octopus vulgaris*, is least efficient, $2.15\text{E}+06$ sej J^{-1} , and the sea star, *Luidia magallanica*, $2.06\text{E}+06$ sej J^{-1} , is the most efficient user of resources in Antofagasta Bay, whereas the *L. magallanica*, $2.27\text{E}+06$ sej J^{-1} , is the only trophic level 3 organism appearing in Mejillones Bay. Tongoy Bay has the greatest number of trophic level 3 organisms and within this bay the sea star, *Megenaster gelatinosus*, $1.08\text{E}+06$ sej J^{-1} , (level 3.12) is clearly more efficient at exploiting resources than is the snail *Xanthochorus cassidiformis*, $1.34\text{E}+06$ sej J^{-1} , (level 3.12) making it the most efficient user of resources at trophic level 3 in Tongoy Bay.

3.3. Network analysis: emergy system diversity index and emergy-based relative ascendency

Figure 2 and Table 3(a) present the outcomes of the emergy analysis and benthic ecosystem network analyses of the three bays. With regard to the system structure and network properties, the magnitudes of the average transformity ($9.28\text{E}+05$ sej/J), average mutual information (2.048 bits) adjusted for energy quality, and A/C (63.08) were highest in the benthic ecosystem of Tongoy Bay. In the case of the quality-adjusted Shannon diversity (76 %), total emergy system throughput ($3.55\text{E}+13$ sej $\text{m}^{-2} \text{y}^{-1}$), emergy-based relative ascendency ($4.69\text{E}+13$ flowbits), emergy capacity ($1.16\text{E}+14$ flowbits) and emergy overhead ($6.92\text{E}+13$ flowbits), the Mejillones benthic ecosystem had higher magnitudes. The Antofagasta Bay system had the same value of quality-adjusted Shannon diversity (75 %) as that of Tongoy Bay, but the latter had the lowest values of total emergy throughput, $1.23\text{E}+13$ sej $\text{m}^{-2} \text{y}^{-1}$; emergy-based relative ascendency, $2.52\text{E}+13$ flowbits; emergy capacity, $3.99\text{E}+14$ flowbits and emergy overhead, $1.47\text{E}+13$ flowbits (Table 3a).

3.4. Index for assessing health condition: The ratio between the Expected and Observed Emergy Throughput (EOET)

The expected and observed emergy throughput ratios are shown in Figure 4. The variables that exhibited the highest magnitudes of EOET were the Other Sea Star Species (OSS), the sea star *L. magallanica* and Sea Urchin Species (SUS) in Mejillones Bay, the cephalopod *O. vulgaris*, the crab *Cancer* spp. and Large Epifauna (LE) in Antofagasta Bay, and the sea star *L. magallanica*, the *X. cassidiformis* and the crab *Cancer porteri* in Tongoy Bay. All

components belong to higher trophic levels. The compartments with the lowest values of EOET in Mejillones Bay were the Detritus, Phytoplankton, the herbivorous snail *Tegula* spp. In the case of Antofagasta Bay, the Detritus, the bivalve *T. pannosa* and Phytoplankton had the lowest EOET. Finally, in Tongoy Bay Detritus, Phytoplankton and Infauna had the lowest values of this index. In all cases the ecosystem components with low EOET belong to lower trophic levels.

4. Discussion

The high productivity of the coastal zone of northern Chile has been associated with the process of coastal upwelling, which causes deeper waters, which are normally cold, rich in nutrients and of low oxygen concentration to ascend to the surface (Strubs et al., 1998). It is important to emphasize that this high productivity may also be interpreted as due to an extremely rich convergence of natural energy sources especially the nitrogen supplied from deep water, but also tides, waves, wind and solar energy similar to some other systems analyzed in the coastal zone (Campbell, 2000; Brown and Bardi, 2001; Campbell, 2004). In this context, the Energy Systems theoretical framework from past studies was used to relate the trophic models developed for Mejillones, Antofagasta and Tongoy Bays (Ortiz and Wolff, 2002 and Ortiz et al., 2015) to their basis in the inflowing environmental energies, with an emphasis on the effects of coastal upwelling. Emergy methods were applied to gain insights into benthic ecosystem health in the near shore coastal waters of Northern Chile by evaluating the physical basis for the structure, organization and functional capacity of the observed benthic ecosystem networks.

The emergy signatures estimated for the three coastal bays had empower densities of renewable resources (2020E+9, 3320E+9, 4260E+9 sej m⁻² y⁻¹) that were higher than many ecological systems cited in Brown and Bardi (2001), such as an estuary in Florida (388E+9 sej m⁻² y⁻¹), the Sea of Cortez in Mexico (39E+9 sej m⁻² y⁻¹) and Lake Okeechobee, Florida (1416E+9 sej m⁻² y⁻¹); but they are similar to that obtained for Newnans Lake, Florida (4434E+9 sej m⁻² y⁻¹) by Brandt-Williams (2000), and lower compared to the macrotidal estuarine system of Cobscook Bay, Maine USA (9553 E+9 sej m⁻² y⁻¹) studied by Campbell (2004). All emergy flows were converted to the same baseline before comparison. This finding demonstrates the relative importance of the coastal zone of northern Chile, which is dominated by coastal upwelling for much of the time, in supporting ecosystem productivity and organization when compared to other aquatic systems dominated by different sources of emergy, e.g., fresh water, a macrotidal estuary and a coastal sea. It is clear that the convergence of a combination of renewable energy sources determined by environmental, meteorological and oceanographic factors (sun, wind, tide and ocean currents), has created one of the world's highest productivity zones within the confines of a narrow coastal shelf (Marín et al., 2001). Recent studies have described these three bays, in terms of their physico-chemical and biological properties, as important and unique coastal systems in themselves (Valle-Levinson et al., 2000; Rutllant and Montecino, 2002; Cerda et al., 2010; Valdes et al., 2011, 2014). In this study, we take an integrated energy systems approach to understanding the network of interactions occurring between human beings and their environmental support systems, through evaluating the environmental conditions required to support different human activities in these coastal environments. To further

integrate the combined effects of anthropogenic and natural processes on the bays, studies such as those performed by Ulgiati and Brown (2002) and Vassallo et al. (2009) are needed to estimate processes such as the volume or mass of air or water that is required to dilute anthropic emissions to the atmosphere and sewage effluents to coastal waters to estimate the carrying capacity of these bays for different human activities. In addition, studies aimed at evaluating the minimum environmental emergy needed to support aquaculture, similar to the Odum (2000) study of salmon aquaculture in British Columbia are needed to gain an integrated understanding of the environmental, ecological and economic aspects of scallop (*Argopecten purpuratus*), kelp (*Lessonia trabeculata*) and other aquaculture operations in northern Chile.

Mejillones, Antofagasta and Tongoy Bays receive high $\text{NO}_3\text{-N}$ concentrations primarily via a natural process of upwelling and the transfer of these high nutrient waters into the nearshore zone by means of tidal exchange as hypothesized in this study and in Campbell (2004), or perhaps through internal waves or tidal bores occurring with a semidiurnal frequency (Vargas et al., 2004), rather than from municipal sewage, terrigenous particle transport (Marín et al., 1993) or non-point runoff like many other coastal ecosystems in the world (Garside and Garside, 2004). The emergy signature of the three bays is dominated by upwelled nitrogen; therefore, we suggest that tidal exchange plays an important role in dispersing upwelled N from the circulating currents within the bays into the nearshore coastal waters where the benthic ecosystems that we evaluated are found. This could be an important mechanism for delivering high concentrations of nutrients to the shallow subtidal and intertidal communities inside of the three bays as reported by Campbell (2004) for Cobscook Bay. This marked dominance of nutrients from upwelling as seen in the emergy signatures of the 3 bays (Figure 3) could constitute conditions that would support a less diverse biological system consistent with the less diverse relationships observed in Odum et al. (1974) for many other systems with unbalanced emergy signatures dominated by wastes. Coastal systems influenced by upwelling have been described as immature (Christensen, 1995; Taylor et al., 2008) and consequently they should be less diverse ecosystem according to Odum (1969). In contrast, Campbell (2004) observed high diversity of intertidal and subtidal fauna in Cobscook Bay; however, these systems are dominated by a balance of tidal effects that both increase the area of intertidal and subtidal ecosystems and bring more resources in the form of nutrients and food to support the growth and development of the macroalgae and benthic fauna found there.

Analysis of ecosystem organization using the emergy signature in the coastal areas of northern Chile is complicated by the fact that these systems are subject to a natural condition, El Niño or the Southern Oscillation (ENSO), which induces changes in the emergy signature of the benthic ecosystems establishing an alternating or pulsing temporal pattern. As a consequence of this pattern, the biological diversity of these coastal systems tends to increase during El Niño events, as the product of incremental increases in oxygen and temperature (Tarazona et al., 1996; Moreno et al., 2008). In terms of Energy Systems Theory, this change can be viewed as a consequence of changes in the emergy signature, which moves towards a more balanced profile (i.e., one with less frequent upwelling and the ascent of a water mass with different physical and chemical properties (González et al., 1998). In addition, to this natural oscillation of the prevailing emergy signature of these

coastal ecosystems, there are anthropic effects related to industrial activities and artisanal fisheries exploitation, which result in the inflow of high quality (high transformity) stressors such as pollutants and intense and unsustainable fishing, both of which have effects on the benthic ecosystems of the three bays to a greater or lesser degree. These additional aspects of the emergy signature of the benthic ecosystems in the 3 bays are not directly evaluated in this paper, where we have focused on the ecological characteristics of the upwelling regime. However, we interpret our results within the context of the general knowledge about El Niño events and their effects on the coastal ecosystems, as well as anthropic activities and their effects on these coastal systems.

Brown and Ulgiati (2004) have suggested evaluating ecological health through examining changes in the emergy signature of different biotic and abiotic elements of the ecosystem. An analysis of changes in the prevailing emergy signature (i.e., the quantity and quality of inflows) to a system may be a first predictor to identify possible changes in the health of ecosystems, if as hypothesized, the emergy signature is a holistic identifier of the expected structures and functions manifested by the organization developed under its influence (Campbell, 2000; Brown and Ulgiati, 2004).

Figures 2 and 5 show that the pathway from phytoplankton to the filter feeder groups is more efficient in capturing and processing emergy than the pathway from macroalgae to the herbivores. The average transformity of phytoplankton (all bays) had similar values to that recorded in Prince William Sound, a coastal embayment ecosystem of Alaska (Brown et al., 1993), but it was two orders of magnitude lower than the primary producers (i.e., phytoplankton and benthic diatoms) found in Cobscook Bay, a macrotidal estuary (Campbell, 2004). The macroalgae of the bays had similar transformity to the macroalgae in Cobscook Bay (Campbell, 2004). This indicates that the emergy signatures received by the three bays are effectively transferred into phytoplankton, when compared to Cobscook Bay, and they have similar properties to Cobscook Bay in the efficiency with which macroalgae are produced. Cobscook Bay is a relatively inefficient producer of phytoplankton, because of heavy tidal mixing of the water column and consequent light limitation, but it is a very effective producer of macroalgae due to high nutrient supply and tidal energy dissipated in the intertidal and subtidal zones (Campbell, 2004). The three bays influenced by upwelling have better conditions for producing phytoplankton and equally good conditions for macroalgal production as those found in a macrotidal estuary, which has higher overall emergy inflows.

It is relevant to indicate that the transfer efficiencies estimated for the network energy flows fell between 10 and 30%, which will influence the resulting quantity of energy transferred. In our analysis, as in the Cobscook Bay analysis, the input of emergy into the system through the primary producers depended on the production area and the trophic level assignments used. Both could explain why the emergy is inversely related to the amount of available energy at each trophic level, resulting in higher transformity top predators. A pattern that is consistent with the thermodynamic basis for energy transference (Odum, 1996).

The emergy-based macro-descriptors of ecosystem network properties calculated from the emergy evaluations of the three benthic coastal ecosystems are compared in Table 3(a). This comparison shows that the ecological system of Mejillones Bay is operating closest to its maximum potential diversity (i.e., it has the highest values of the Shannon relative diversity index (RD %), although this index is approximately the same for all three systems. The magnitudes of the estimated total emergy system throughput (TEST), emergy-based ascendancy (EBA), Capacity (C) and Overhead (Ov) ratios for the benthic systems of Mejillones Bay are higher than in the other two bays. In Antofagasta and Tongoy Bay these indices were lower than the comparable values in Mejillones Bay. In contrast, Tongoy Bay was somewhat less efficient in capturing and processing available energy and the emergy it delivers to the system (i.e., it had the highest value of average system transformity [Tr]). It is operating slightly farther from its maximum potential ecological diversity (RD %, 75.15%) than Mejillones Bay (RD% 75.7%), but Antofagasta Bay is further still from the maximum (74.54%). Also, Tongoy Bay is less complex in terms of emergy flow through the network (i.e., it had the highest adjusted-AMI, 2.048, which is 55% and 63% larger than in Mejillones and Antofagasta Bays, respectively. Furthermore, Tongoy Bay is a more developed system according to the emergy A/C ratio (i.e., it is closer to its maximum potential for development). Ascendancy has reached 63.1% of Capacity in Tongoy Bay compared to 36.01% for Antofagasta and 40.12% for Mejillones Bays, meaning that Tongoy Bay may be less resistant to disturbance (*sensu* Christensen, 1995) compared to Mejillones and Antofagasta Bays. In contrast, Antofagasta Bay appears to be the most efficient system in producing ecosystem organization (Tr is the lowest of the 3 bays, 5.9% lower than Mejillones and 7.31% lower than in Tongoy Bay) and it is a more complex ecosystem (i.e., it has an AMI 4.97% lower than Mejillones and 38.73% lower than Tongoy Bay). In the case of the three benthic ecosystems examined, Mejillones Bay had the highest value for the empower density supporting the benthic ecosystem, which is demonstrated by its higher values of throughput (TEST), which is a measure of a system's size or vigor. Consequently, the degree of system development and maturity (EBA) was higher, and it had better resistance against disturbances (higher Ov). However, the internal dynamic properties of Mejillones Bay, in terms of efficiency (i.e., transformity), organization (i.e., AMI) and the state of system maturity (i.e., A/C) were not optimally organized in a manner that generates the maximum empower from the emergy signature compared to the other two bays. The patterns observed in Mejillones Bay may be explained, primarily, because the throughflow dominates the ascendancy measure (Christensen, 1994; Patten, 1995; Fath et al., 2001). In terms of the emergy signature of the 3 systems, Mejillones received 111.59% more nitrate nitrogen per meter square compared to Tongoy Bay and 29.88% more than Antofagasta Bay. This interpretation is validated by the strong influence of the oxygen minimal zone that has been observed in this bay to a depth of 20 m (Gutiérrez et al., 2010), thereby constraining the respiration of organisms that comprise the benthic communities there (Escribano and Hidalgo, 2000). The Shannon ecosystem diversity indices in the three bays affected by upwelling were higher than similar indices in the Florida Everglades, USA, a system evaluated by Brown et al. (2006). These outcomes are relevant, because these bays might be expected to be more diverse as a consequence of the great magnitude of inputs to the empower base of the benthic productive systems, as demonstrated in this study and in comparison to other ecosystems (Brown and Bardi, 2001).

The three bays have very distinct ecological properties and one, Antofagasta Bay, is a semiclosed bay with an open mouth to the south exposed to winds from the south and southwest with greater habitat heterogeneity as a product of the rocky bottom and kelp forests allowing a greater abundance of other algae and invertebrate species (Ortiz, 2008). Also, Antofagasta Bay contains the La Rinconada marine reserve. Mejillones Bay has a geographical configuration that protects it from the direct action of the winds that are responsible for the coastal upwelling there. This allows longer periods between mixing and re-stratification of the surface layer in this bay (Marín and Olivares, 1999) and it is heavily influenced by industrial activities. Tongoy Bay has the same geographical configuration as Mejillones Bay and similar exposure to the wind, but it is dominated by artisanal fisheries rather than industrial activities. To a first order approximation, we may assume that these dominate characteristics of the three bays should be reflected in their observed properties on analysis.

The pattern of the EOET showed that in these systems dominated by upwelled nutrients, the lower trophic level organisms were more abundant than expected in all three systems and that the higher trophic level organisms were less abundant than expected with trophic level 3 organisms, generally, showing the greatest difference. This pattern is perhaps not unexpected given that these systems are nutrient enriched as shown by their emergy signatures. The expected and observed emergy ratios that measure ecosystem health show a clear trend with regard to their transformities, which could be interpreted as unhealthy as a consequence of the losses in the upper trophic levels reported by Brown et al. (2006). Antofagasta Bay presents a better health condition compared to Mejillones and Tongoy Bays, which is consistent with the values of the mean trophic level of the catch from Antofagasta (1.595), Mejillones (1.692) (Ortiz et al., 2015) and Tongoy Bay (2.14) (Ortiz and Wollf, 2002).

In evaluating the network and structure of mass flows in these ecological systems: the magnitude of throughput (TEST), ascendancy (A), capacity (C), overhead (Ov) and the ascendancy to capacity ratio (A/C) reported by Ortiz and Wollf (2002) and Ortiz et al. (2015) were all higher in Antofagasta Bay than in the other two embayments, with the exception of the AMI (Table 3b). These results are based on the same trophic models of the three bays used in this study, but the results of the biomass analysis differ from those of the network emergy evaluation. It is relevant to emphasize that our intention in this analysis is to complement the conclusions gained from our earlier systemic evaluations by using emergy methods to reveal uncharacterized properties of these systems, (i.e., emergy signatures, system empower, empower density, process and system efficiency, controllability (e.g., the efficacy of feedbacks), among other emergy indicators). In this regard, our approach is consistent with that proposed by Jørgensen (1992), who observed that we can obtain a more comprehensive overall picture of the ecosystem by use of a pluralistic view of models, instead of looking for the “best” model. This approach is taken, because models by their nature are only approximations and the results obtained can be the product of the essential properties of the model or of the details of its simplifying assumptions (Levins, 1969).

Campbell (2004), Brown et al. (2006), Zarbá and Brown (2015) have shown using emergybased network analysis that increasing energy quality in an ecosystem network enhances feedbacks and maximizes the empower captured by the ecosystem. Such feedbacks

of high quality energy are also responsible for the hierarchical organization of the network into trophic webs. The transformities of the system components in this study were determined within the benthic ecosystem network from the bottom-up by distributing the emergy inflows in the emergy signature up through the network to obtain the total emergy required for the available energy of each species or functional group. This approach differs from Christensen's work in terms of how to calculate the emergy values (Christensen, 1994). More specifically, this methodology allows the evaluation of empower within entire ecological network, instead of grouping by trophic level. This is important, because the maximization of network empower is hypothesized to be nature's decision criterion (Odum, 1996, Campbell, 2000, Campbell, 2001).

This procedure allowed us to gain additional insights about these benthic ecosystems with the use of EST and the emergy methods to integrate the important physical variables as forcing functions creating ecosystem organization and to model their relationships with ecological variables using the Energy Systems Language (Odum, 1994).

The use of emergy evaluation in this study allowed us to use a quality-adjusted form of the standard network indices, AMI and the A/C ratio, as a complementary tool for characterizing ecosystem network organization. Comparison of the results from these two methods resulted in increased understanding of the system based on differences between the two evaluations (Table 3a, b). These indicators have been widely used to describe and compare a variety of ecosystems with different levels of organization, spatial sizes and geographic locations based on mass balanced trophic models (Patricio et al., 2006; Vassallo et al., 2006; Ibarra-García et al., 2016; González et al., 2016; Ortiz et al., 2016).

Management of such systems requires the integration of local ecological, economic and environmental components within a systems framework (Berrios et al., 2017) to evaluate ecosystem health. In this context, the Energy Systems Theory and Emergy Analysis, which are based on ecological and general systems principles, irreversible thermodynamics and ecology (Odum, 1988, 1994, 1996) provide a powerful framework for evaluating, modeling and understanding systems and this approach offers an alternative decision criterion for determining ecosystem health, i.e., maximum empower generated in the ecosystem network. Furthermore, health assessments based on emergy have been given a strong theoretical basis as seen in Brown and Ulgiati (2004), Campbell (2000) and Campbell et al. (2014) and this approach has been modified and widely employed to characterize the condition of urban ecosystems and information systems, among others (Liu et al., 2011; Garde et al., 2007; Su et al., 2010, Campbell et al., 2014).

In the current contribution, we recognize the following uncertainties and simplifications for the assessment of emergy: (1) the emergy inflow assigned to the nitrogen and kinetic energy of upwelling in Antofagasta and Mejillones Bays requires physical oceanographic studies; however, there are no evaluations of these systems using hydrodynamic models. In this case the models proposed by Escribano and Hidalgo (2001) and Marín et al. (2003) were used to estimate the volume of upwelled water entering Antofagasta and Mejillones Bays, respectively; (2) in the benthic networks, the split strategy was applied, assuming that the contributions of feces, pseudofeces and mortality to detritus would have the same properties

and fate; (4) the effects of pollutants on the biological components of the network were not included, because the data to evaluate these effects were not available; and (5) the contributions from the economy (i.e. goods, labor and services from fishing) affecting the benthic networks were not considered.

5. Conclusions

Based on our results, the emergy signature of all three coastal bays showed an unbalanced profile dominated by $\text{NO}_3\text{-N}$ from upwelling, with Mejillones Bay showing the largest imbalance, suggesting that these three benthic ecosystems may be less biologically diverse than other comparable marine ecosystems. The emergy evaluation and analysis of benthic ecological networks used indicators, such as transformity, the emergy system diversity index, emergy-based ascendancy and an index for assessing ecosystem health (EOET), which showed that the three bays exhibit different states of ecosystem health. These findings could be related to the geographical configuration, orientation to the prevailing winds, habitat heterogeneity, community networks, fisheries and different anthropic activities taking place in each system. For example, in Tongoy Bay only artisanal fisheries and tourist activities are present, while Antofagasta Bay contains a marine reserve and Mejillones Bay is dominated by industrial activities and also contains an artisanal fishery. The outcomes are very interesting, because our understanding of these systems has increased by using different models and analysis to provide a more comprehensive overall picture of these systems to better reveal their holistic properties (Jørgensen, 1992). This is somewhat different from the conclusions reported by Patten (1995) and Fath et al. (2001) regarding the complementarity of the different analyses based on maximizing power of flows in the ecosystem networks. Despite the considerable time and data required to complete an emergy analysis, Energy Systems Theory and the emergy indicators derived from it may provide a powerful tool for improving the assessment of ecosystem health by integrating the renewable environmental resource base of ecosystems with ecological variables and network structures.

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Appendix A.

Linear equation group obtained from Mejillones Bay model. Number represents the energy flow each pathway carries and x represents the transformity of the pathway.

Equations Input = Output

Phytoplankton: $3139588 \cdot (X1) = (12725 + 76 + 982 + 4874 + 1299 + 2818 + 3099 + 1566 + 3954) \cdot (X6)$

L. trabeculata: $3118 \cdot (X2) = (348 + 15 + 1157 + 1540 + 57) \cdot (X7)$

$$\text{Chlorophyta: } 879*(X3) = (199+1+579+101)*(X8)$$

$$\text{Rhodophyta: } 1006*(X4) = (317+6+634+3020)*(X9)$$

$$\text{Phaeophyta: } 1361*(X5) = (213+3+1157+9)*(X10)$$

$$\text{Detritus: } (12725+76+982+4874+1299+2818+3099+1566+3954)*(X6)$$

$$+(348+15+1157+1540)*(X7)+(199+1+579+101)*(X8)+(317+6+6364+3320)*(9)+(213+3+1157+9)*(X10) =$$

$$(669+173+2089+497+547+671+182+1105+3+2314+669+326+231+0.9+89)*(X11)$$

$$\text{Zooplankton: } 12725*(X6) + ((669/669+9568)*(3118*(X2))) + 879*(X3) + 1006*(X4) + 1361*(X5) = (35+5993)*(X12)$$

$$\text{A. purpuratus: } 982*(X6) + (173/173+9394)*(3118*(X2)) + 879*(X3) + 1006*(X4) + 1361*(X5) = (91+0.3+56+39+59+54+242)*(X13)$$

$$\text{A. ater: } 1566*(X6) + (671/671+8896)*(3118*(X2)) + 879*(X3) + 1006*(X4) + 1361*(X5) = (60+54+1+181+56+0.1+502)*(X14)$$

$$\text{T. dombeiri: } 4874*(X6) + (4874/4874+7479)*(3118*(X2)) + 879*(X3) + 1006*(X4) + 1361*(X5) = (272+112+3+77+149+0.03+2186)*(X15)$$

$$\text{Ch. Chorus: } 2818*(X6) + (497/497+9070)*(3118*(X2)) + 879*(X3) + 1006*(X4) + 1361*(X5) = (203+56+42+77+0.8+20+868)*(X16)$$

$$\text{G. solida: } 3099*(X6) + (547/547+9020)*(3118*(X2)) + 879*(X3) + 1006*(X4) + 1361*(X5) = (77+0.6+181+8+795)*(X17)$$

$$\text{Tegula spp.: } 1157*(X7) + 579*(X8) + 6364*(X9) + 1157*(X10) + (2314/2314+7253)*(3139588*(X1)) = (30+778+0.3+214+4307)*(X18)$$

$$\text{SEH: } 1299*(X6) + 348*(X7) + 194*(X8) + 317*(X9) + 213*(X10) + (1105/1105+8463)*(3139588*(X1)) = (160+77+3+145+56+742)*(X19)$$

$$\text{SUS: } 15*(X7) + 1*(X8) + 6*(X9) + 3*(10) + (3/3+9564)*(3139588*(X1)) = (0.6+10)*(X20)$$

$$\text{OFF: } 76*(X6) + (182/182+9385)*(3139588*(X1)) = (0.6+15+30+0.6+82)*(X21)$$

$$\text{T. chocolata: } 56*(X13) + 56*(X14) + 112*(X15) + 56*(X16) + 56*(X17) = (181+0.3+39+30+0.3+282)*(X22)$$

$$\text{OSS: } 0.6*(X21) = (0.1+0.5)*(X23)$$

$$\text{LE: } 56*(X13) + 54*(X14) + 77*(X15) + 77*(X16) + 77*(X17) + 778*(X18) + 77*(X19) + 15*(X21) + 39*(X22) = (56+48+0.6+8+201)*(X24)$$

$$\text{SEC: } 91*(X13) + 181*(X14) + 272*(X15) + 203*(X16) + 181*(X17) + 214*(X18) + 145*(X19) + 181*(X22) = (18+56+0.6+636)*(X25)$$

$$\text{Cancer spp.: } 39*(X13) + 60*(X14) + 149*(X15) + 42*(X16) + 30*(X18) + 60*(X19) + 30*(X21) + 30*(X22) + 48*(X24) = (0.6+239)*(X26)$$

$$\text{L. magallanica: } 0.3(X13) + 1*(X14) + 3*(X15) + 0.8*(X16) + 0.6*(X17) + 0.3*(18) + 3*(19) + 0.6*(X20) + 0.6*(X21) + 181*(X22) + 0.1*(X23) + 0.6*(X24) + 0.6*(X25) = (0.1+5)*(X27)$$

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Highlights

- Energy Systems Theory and Emergy Analysis were applied to quantify the health of benthic ecosystems.
- Unbalanced emergy signatures, suggest less development and system diversity compared to other coastal ecosystems with more balanced emergy signatures.
- Macro-descriptors and network properties suggest functional differences in health among the three ecosystems.
- Energy Systems Theory and the emergy indicators derived from it may provide a powerful tool for improving the assessment of ecosystem health.

Figure 1.
Study areas and the location of upwelling centers of Mejillones, Antofagasta and Tongoy Bays in northern Chile.

Figure 2a.

Energy Systems Language Model of Mejillones Bay showing the energy base (underlined numbers) for the benthic ecosystem and the available energy flows along each pathway in $\text{J m}^{-2} \text{y}^{-1}$ and the energy in $\text{sej m}^{-2} \text{y}^{-1}$ required for that pathway (bold).

Figure 2b.

Energy Systems Language Model of Antofagasta Bay showing the energy base (underlined numbers) for the benthic ecosystem and the available energy flow along each pathway in $\text{J m}^{-2} \text{y}^{-1}$ and the energy in $\text{sej m}^{-2} \text{y}^{-1}$ required for that pathway (bold).

Figure 2c.

Energy Systems Language Model of Tongoy Bay showing the energy base (underlined numbers) for the benthic ecosystem and the available energy flow along each pathway in $\text{J m}^{-2} \text{y}^{-1}$ and the energy in $\text{sej m}^{-2} \text{y}^{-1}$ required for that pathway (bold).

Figure 3.

Energy sources supporting the development of the three benthic ecosystems arranged on the abscissa in order of increasing transformity. (a), (b) and (c) The energy signatures of the Mejillones, Antofagasta and Tongoy Bays, respectively, from Berrios et al. (2017). (d), (e) and (f) the emery signatures of Mejillones, Antofagasta and Tongoy Bays, respectively.

Figure 4. Expected/Observed Energy Throughput (EOET) versus Transformity for the Mejillones, Antofagasta and Tongoy Bay ecosystem networks.

Figure 5. Computed transformity values for Mejillones, Antofagasta and Tongoy bays in rank order by Trophic Level. The names of the functional groups given by number in Table 2.

Table 1.

Energy sources supporting the development of the Mejillones, Antofagasta and Tongoy Bays, the energy and emergy signature of the bays. Empower base and Empower density of the benthic production systems.

Mejillones Bay	Energy (J/y)	Transformity (sej/J)	Emergy (sej/y)	Fraction of emergy inflow	Fraction of energy inflow
(1) Solar radiation ¹	1.18E+17	1.00E+00	1.18E+17	0.1%	98.4%
(2) Wind ²	1.79E+15	1.23E+03	2.20E+18	2.6%	1.5%
(3) Wave ³	9.07E+12	3.08E+04	2.79E+17	0.3%	0.0%
(4) Tide ⁴	1.05E+14	3.09E+04	3.25E+18	3.8%	0.1%
(5) Nitrogen Upwelled ⁵	3.50E+12	2.28E+07	7.98E+19	93.2%	0.0%
Area (m ²)	1.95E+07				
Empower base of benthic productive systems		8.31E+19	(sej/y)		
Empower density base of benthic productive systems		4.26E+12	(sej/m ² /y)		

Antofagasta Bay	Energy (J/y)	Transformity (sej/J)	Emergy (sej/y)	Fraction of emergy inflow	Fraction of energy inflow
(1) Solar radiation ¹	3.21E+17	1.00E+00	3.21E+17	0.16%	98.3%
(2) Wind ²	4.86E+15	1.23E+03	5.97E+18	3.01%	1.5%
(3) Wave ³	5.26E+14	3.08E+04	1.62E+19	8.16%	0.2%
(4) Tide ⁴	2.86E+14	3.09E+04	8.83E+18	4.45%	0.1%
(5) Nitrogen Upwelled ⁵	7.33E+12	2.28E+07	1.67E+20	84.21%	0.0%
Area (m ²)	5.30E+07				
Empower base of benthic productive systems		1.76E+20	(sej/y)		
Empower density base of benthic productive systems		3.32E+12	(sej/m ² /y)		

Tongoy Bay	Energy (J/y)	Transformity (sej/J)	Emergy (sej/y)	Fraction of emergy inflow	Fraction of energy inflow
(1) Solar radiation ¹	1.48E+17	1.00E+00	1.48E+17	0.24%	98.3%
(2) Wind ²	2.41E+15	1.23E+03	2.96E+18	4.73%	1.6%
(3) Wave ³	1.36E+14	3.08E+04	4.20E+18	6.71%	0.1%
(4) Tide ⁴	8.09E+13	3.09E+04	2.50E+18	3.99%	0.1%
(5) Nitrogen Upwelled ⁵	2.31E+12	2.28E+07	5.28E+19	84.33%	0.0%
Area (m ²)	2.73E+07				

Tongoy Bay	Energy (J/y)	Transformity (sej/J)	Emergy (sej/y)	Fraction of emergy inflow	Fraction of energy inflow
Empower base of benthic productive systems		5.54E+19	(sej/y)		
Empower density base of benthic productive systems		2.03E+12	(sej/m ² /y)		
Data sources for transformities					

¹By definition.

²Transformity of wind energy dissipated in the boundary layer. New calculation Campbell and Erban (2017).

³New transformity for waves calculated relative to the new baseline, Campbell (2016).

⁴New transformity for the tide from the geobiosphere baseline paper. Brown et al. (2016).

⁵Transformity calculated relative to the new baseline, Brown et al. (2016).

Table 2.

Transformities of ecosystem flows in Mejillones, Antofagasta and Tongoy Bays based on estimates of the energy of net primary production and the annual emergy inflow to each bay.

Species/functional groups	Trophic level	Energy (J/m ² y)	Emergy (sej/m ² y)	Transformity (sej/J)
(A) Mejillones Bay				
(1) Phytoplankton	1	3.14E+07	4.26E+12	1.36E+05
(2) Lessonia trabeculata	1	3.12E+06	1.11E+12	3.56E+05
(3) Chlorophyta	1	8.79E+05	1.73E+12	1.96E+06
(4) Rhodophyta	1	1.00E+07	3.56E+12	3.56E+05
(5) Phaeophyta	1	1.38E+06	3.24E+11	2.34E+05
(6) Detritus	1	9.57E+06	1.10E+13	1.15E+06
(7) Zooplankton	2	6.03E+06	2.20E+12	3.65E+05
(8) Argopecten purpuratus	2	5.46E+05	2.55E+11	4.67E+05
(9) Aulacomya Ater	2	8.54E+05	6.84E+11	8.01E+05
(10) Tagelus dombeii	2	2.80E+06	1.89E+12	6.74E+05
(11) Choromytilus chorus	2	1.27E+06	7.32E+11	5.78E+05
(12) Gari solida	2	1.06E+06	8.05E+11	7.59E+05
(13) Tegula spp.	2	4.63E+06	5.11E+12	1.10E+06
(14) Small Epifauna Herbivore (SEH)	2	1.08E+06	8.53E+11	7.88E+05
(15) Sea urchin species (SUS)	2	1.11E+04	1.22E+10	1.10E+06
(16) Other Filter feeders (OFF)	2.12	1.29E+05	1.51E+11	1.17E+06
(17) Other Sea Star Species (OSS)	2.45	5.33E+05	2.22E+11	4.17E+05
(18) Thais chocolata	2.48	6.49E+02	6.87E+08	1.06E+06
(19) Large Epifauna (LE)	2.73	3.13E+05	3.96E+11	1.26E+06
(20) Small Epifauna Carnivore (SEC)	2.88	7.10E+05	1.05E+12	1.48E+06
(21) Cancer spp.	2.94	2.40E+05	3.89E+11	1.62E+06
(22) Luidia magallanica	3.11	4.70E+03	1.07E+10	2.27E+06
(B) Antofagasta Bay				
(1) Phytoplankton	1	5.23E+07	3.32E+12	6.35E+04
(2) Lessonia trabeculata	1	1.95E+06	1.42E+12	7.30E+05
(3) Chlorophyta	1	5.23E+05	6.33E+11	1.21E+06
(4) Rhodophyta	1	9.21E+05	8.31E+11	9.02E+05
(5) Phaeophyta	1	9.26E+05	7.68E+11	8.29E+05
(6) Detritus	1	1.35E+07	6.91E+12	5.13E+05
(7) Zooplankton	2	6.03E+06	9.90E+11	1.64E+05
(8) Argopecten purpuratus	2	2.78E+05	5.10E+10	1.84E+05
(9) Aulacomya Ater	2	4.75E+05	1.18E+11	2.48E+05
(10) Tagelus dombeii	2	1.36E+06	4.24E+11	3.13E+05
(11) Choromytilus chorus	2	3.80E+05	9.42E+10	2.48E+05
(12) Transennella pannosa	2	1.58E+07	3.43E+12	2.18E+05
(13) Protothaca thaca	2	1.90E+06	6.30E+11	3.31E+05
(14) Tegula spp.	2	5.24E+05	8.00E+11	1.53E+06

Species/functional groups	Trophic level	Energy (J/m ² y)	Emergy (sej/m ² y)	Transformity (sej/J)
(15) Small Epifauna Herbivore (SEH)	2	2.09E+06	2.55E+12	1.22E+06
(16) Sea urchin species (SUS)	2	7.72E+04	1.38E+11	1.79E+06
(17) Other Filter feeders (OFF)	2.1	3.45E+05	1.51E+11	4.38E+05
(18) Other Sea Star Species (OSS)	2.44	1.60E+05	6.41E+10	4.02E+05
(19) Thais chocolata	2.73	7.10E+05	3.31E+11	4.66E+05
(20) Large Epifauna (LE)	2.76	3.13E+04	3.24E+10	1.04E+06
(21) Small Epifauna Carnivore (SEC)	2.88	2.05E+05	2.35E+11	1.15E+06
(22) Cancer spp.	2.96	1.35E+04	1.66E+10	1.23E+06
(23) Luidia magallanica	3.06	7.32E+04	1.51E+11	2.06E+06
(24) Concholepas	3.2	3.63E+05	7.60E+11	2.09E+06
(25) Octopus vulgaris	3.3	7.83E+02	1.68E+09	2.15E+06
(C) Tongoy Bay				
(1) Phytoplankton	1	2.93E+07	2.03E+12	6.92E+04
(2) Heterostera tasmanica	1	6.91E+05	6.49E+11	9.40E+05
(3) Chondracanthus chamosi	1	1.97E+06	4.57E+11	2.32E+05
(4) Rhodophyta	1	2.53E+06	6.40E+11	2.53E+05
(5) Ulva sp.	1	1.26E+06	2.91E+11	2.32E+05
(6) Detritus	1	4.06E+06	3.96E+12	9.75E+05
(7) Zooplankton	2	5.43E+06	1.10E+12	2.02E+05
(8) Argopecten purpuratus	2	9.35E+05	3.06E+11	3.27E+05
(9) Mulinia sp.	2	3.19E+05	1.33E+11	4.18E+05
(10) Calyptraea trochiformis	2	4.33E+05	2.06E+11	4.75E+05
(11) Tegula sp.	2	6.65E+05	5.81E+11	8.74E+05
(12) Taliepus sp.	2.18	9.25E+03	9.77E+09	1.06E+06
(13) Infauna	2.21	1.84E+06	1.36E+12	7.35E+05
(14) Pyura chilensis	2.4	4.52E+05	1.53E+11	3.37E+05
(15) Small Epifauna (SE)	2.8	4.67E+05	4.25E+11	9.09E+05
(16) Paraxanthus barbiger	2.89	6.58E+04	9.20E+10	1.40E+06
(17) Luidia magallanica	3.09	7.07E+03	1.08E+10	1.53E+06
(18) Xanthochorus cassidiformis	3.12	2.36E+04	3.16E+10	1.34E+06
(19) Megenaster gelatinosus	3.12	1.99E+05	2.14E+11	1.08E+06
(20) Heliaster helianthus	3.18	4.88E+03	6.21E+09	1.27E+06
(21) Cancer porteri	3.3	2.05E+04	4.20E+10	2.05E+06
(22) Cancer polyodon	3.35	1.26E+05	2.57E+11	2.05E+06
(23) Cancer coronatus	3.36	3.87E+04	6.14E+10	1.59E+06
(24) Large Epifauna (LE)	3.47	7.25E+04	1.41E+11	1.95E+06

Table 3.

(a) Macroscopic properties (indices) quantifying system development and organization based on the emergy system diversity index and emergy-based ascendancy and percentage change (%). (b) Macroscopic properties derived from Ascendancy based on network analysis of biomass flows for Mejillones, Antofagasta and Tongoy Bays.

(a) Emergy network flow indices based on Ecopath	Mejillones ¹	Antofagasta ¹	Tongoy ¹	Bays	%	Bays	%
Total system throughput (sej m ⁻² y ⁻¹)	3.55E+13	2.38E+13	1.23E+13	M-A	32.89%	M-T	65.39%
Ascendancy adjusted (Total) Flowbits	4.69E+13	2.99E+13	2.52E+13	M-A	36.21%	M-T	46.31%
Capacity Adjusted (Total) Flowbits	1.16E+14	7.92E+13	3.99E+13	M-A	31.83%	M-T	65.65%
Overhead (Ov) Adjusted Flowbits	6.92E+13	4.93E+13	1.47E+13	M-A	28.87%	M-T	78.73%
AMI Adjusted (bits)	1.321	1.255	2.048	T-M	55.10%	T-A	63.21%
A/C (%)	40.36	37.8	63.08	T-A	36.01%	T-M	40.12%
Average transformity (sej/J)	9.14E+05	8.60E+05	9.28E+05	A-M	5.90%	A-T	7.36%
AMI adjusted (bits)	1.321	1.255	2.048	A-M	4.97%	A-T	38.73%
N per m ⁻²	4.09E+12	3.15E+12	1.93E+12	M-A	29.88%	M-T	111.59%
N as a fraction of total emergy	0.96	0.95	0.95				
Quality adjusted Diversity (bits)	3.38	3.46	3.45				
Theoretical maximum diversity (bits)	4.46	4.64	4.58				
Relative diversity (%)	75.70	74.54	75.15				
(b) Ecopath network flow indices	Mejillones ²	Antofagasta ²	Tongoy ³				
Total system throughput (g ww m ⁻² y ⁻¹)	29,429.9	37,539.8	20,593.9				
Ascendancy (Total) Flowbits	34,395.1	48,574.3	25,092.2				
Capacity (Total) Flowbits	142,897.9	170,237.0	88,686.8				
Overhead (Ov) Flowbits	108,353.1	121,434.8	62,101.9				
AMI (Average Mutual Information) (bits)	1.371	1.294	1.218				
A/C (%)	24.1	28.5	28.3				

¹This study

²Ortiz et al. (2015)

³Ortiz & Wolff (2002)