



The Ecological Role of *Opisthonema libertate* and *Cetengraulis mysticetus* on Ecosystem Order in the Southeastern Gulf of California, Mexico

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Abstract

Opisthonema libertate (Pacific thread herring) and *Cetengraulis mysticetus* (Pacific anchovy) are the two most important herring stocks exploited in the south-eastern Gulf of California (SGC). The certification of these stocks is currently planned for achieving sustainable fisheries. This study analysed the role of these two species in the structure, organization and functioning of the ecosystem in this region. Twenty-four indicators of the ecosystem's structure and its organization were obtained based on the output of an Ecopath model of the SGC. The relationships of the functional groups with the ecosystem's indicators were identified using multivariate statistical techniques, and the results indicated similar roles for the Pacific thread herring and the Pacific anchovy in the ecosystem of the SGC. Both species make large contributions to the maintenance of the ecosystem's order (i.e., its structure and organization). These results are directly related to one of the criteria that are evaluated by the Marine Stewardship Council's certification process. Defining the remaining biomass level at sea after fishing would guarantee the sustainability of fisheries in the ecosystem.

Keywords: small pelagic, southeastern Gulf of California, structural indicators, degree of order.

Introduction

Herring fisheries in Mexico represent 30% of the national catch and 10% of the economic value (DOF, 2012). In the southeastern Gulf of California (SGC), large fluctuations in herring catches have been recorded since 1970 which are related to environmental variability in this area (Jacob-Cervantes, 2010). The fishery of Monterrey sardine *Sardinops sagax* (Jenyns, 1842) in the Gulf of California is certified by the Marine Stewardship Council (MSC), and this certification is planned to be expanded to other small pelagic species. This species group is important for ecosystem dynamic and plays a wasp-waist role in energy flow control (Bakun, Babcock & Santora, 2009).

Two species are the main components of the catch in the SGC: the Pacific thread herring (*Opisthonema libertate* (Günther, 1867), with small contributions of *Opisthonema bulleri* (Regan, 1904) and *Opisthonema medirastre* Berry & Barrett, 1963) and the Pacific anchovy (*Cetengraulis mysticetus* Gunther, 1868). The management of the herring fishery (including the Pacific thread herring and the Pacific anchovy) is based on the Monterrey sardine,

which is the most important species in the entire Gulf in terms of landings. The management measures consist of setting limits on the vessels and minimum legal sizes (DOF, 1993), but they do not consider the species landing structure or its spatial differences. Costanza *et al.* (1998) suggest that proper management measures must consider the ecosystem perspective and particularly environmental changes and trophic interaction within an ecosystem, which are highly relevant for wasp-waist species.

The current MSC certification processes may play an important role in achieving sustainable fisheries (Ponte, 2008; Gulbrandsen, 2009). In this context, knowledge of the ecological role of the species caught by fishing vessels is one of the criteria assessed in the MSC certification process, in addition to other criteria related to stock, harvesting rates, reference points and defining specific objectives for the fishery. This contribution focuses on the analysis of the ecological role of the Pacific thread herring and the Pacific anchovy in the ecosystem of the SGC, using holistic indicators that describe the structure and function of the ecosystem.

Materials and Methods

Study Area

Data from a previously published mass-balanced model of the SGC ecosystem was used (Hernández-Padilla, 2012; supplementary material). The study area considered in the model is located in the southeastern region of the mouth of the Gulf of California off the coast of northern Nayarit and southern Sinaloa in Mexico (Longitude 22° to 24.5° and Latitude -108° to -105°; Figure 1). This region is influenced by the following two bodies of surface water, which have unique characteristics in terms of their dynamics, productivity and structure: 1) water from the Tropical Pacific (Temperature >25°C and salinity <34‰), and 2) water from the Gulf of California (Temperature 21°-31°C and salinity >34‰) (Lavín & Marinone, 2003).

Input Data

The model represents the ecosystem state in the years 2006 and 2007 and considered 39 functional groups (Hernández-Padilla, 2012): 21 fish (including the Pacific thread herring (*Opisthonema libertate*) and the Pacific anchovy as individual functional groups), 12 invertebrates, 2 primary producers (phytoplankton and macrophytes), one birds, one sea turtles, one zooplankton and one detritus. A matrix of 24 ecosystem's indicators for each functional group was constructed to define the ecological role of the Pacific thread herring and the Pacific anchovy. Ecosystem's attributes were used as structural and ecosystem-organization indicators, particularly the degree of

order (Ulanowicz, 2009).

Indicators of Structure and Function

Attributes revealing the importance of the functional groups in the structure of the ecosystem were considered as structural indicators, including the following indicators by functional group: biomass (B), trophic level (TL), production/biomass (P/B), consumption/biomass (Q/B), production/consumption (P/Q), respiration (R), production/respiration (P/R), respiration/assimilation (R/As), respiration/biomass (R/B), and omnivory indicator (OI). In addition, four indicators were calculated using the consumption matrix based on the Ecopath model outputs: degree (D_i), closeness (CC_i), betweenness (BC_i) and keystone species (K). The D_i is considered the simplest measure of centrality; it quantifies the number of connections between groups and expresses how they are connected to the rest of the trophic network. The indicator was calculated as follows (Jordán, Benedek & Podani, 2007):

$$D_i = D_{in,i} + D_{out,i}$$

where D_i is the degree of group i , $D_{in,i}$ is the number of connections between a consumer group and its prey, and $D_{out,i}$ is the number of connections between a group and its predators.

CC_i indicator quantifies the number of connections or flow routes between a given group and all other groups (Wasserman & Galaskiewicz, 1994). The CC_i index measures how close a group is to the other groups. The standardized indicator for group i (CC_i) was calculated by the following equation

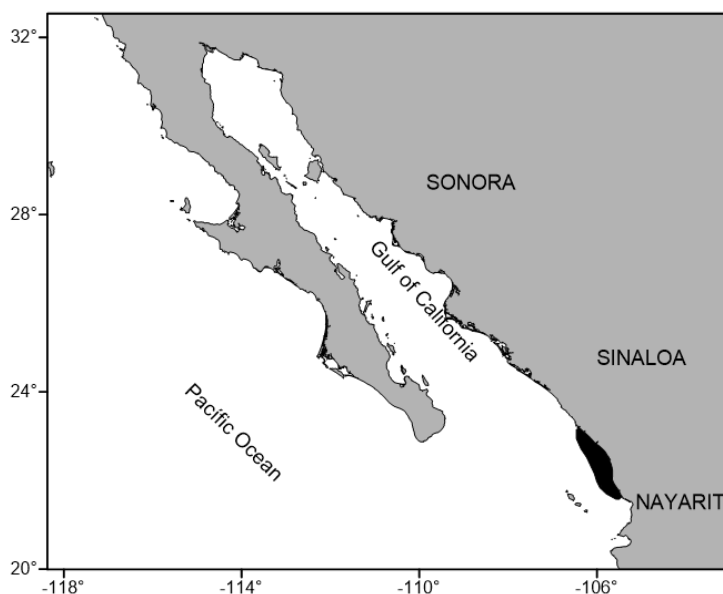


Figure 1. The study area (black area), including the ecosystem in the southeastern Gulf of California off the coast of northern Nayarit and southern Sinaloa in Mexico (Latitude: 22°-24.5°, Longitude: -105° -108°).

(Junker and Schreiber, 2008):

$$CC_i = N - 1 / \sum_{j=1}^N d_{ij}$$

where $i \neq j$, and d_{ij} is the length of the connection between groups i and j in the trophic network.

The BC_i indicator quantifies the positional significance expressed as the frequency with which group i appears in the shortest pathways or trophic routes between each pair of functional groups (Wasserman & Galaskiewicz, 1994). The standardized index for group i (BC_i) was calculated as follows (Junker & Schreiber, 2008):

$$BC_i = 2 \cdot \sum_{j < k} g_{jk}^{(i)} / g_{ik} / (N - 1)(N - 2)$$

where $i \neq j$ or k , g_{jk} is the shortest number of paths or trophic routes between the groups j and k , $g_{ik}^{(i)}$ is the number of short routes in which group i has an influence, and N is the number of functional groups.

The K indicator expresses the relative importance of each group by its participation in the system flows relative to its biomass. K for the species i was calculated as follow (Jordán et al. 2007):

$$K_i = \sum_{c=1}^n 1/d_c (1 + K_{bc}) + \sum_{e=1}^m 1/f_e (1 + K_{te})$$

where n is the number of predators consuming species i , d_c is the number of prey of the predator, K_{bc} represents the trophic effects from the bottom to the top of the trophic network of each predator, m is the number of prey consumed by species i , f_e is the number of predators of one prey, and K_{te} represents the top-down trophic effects of the trophic network of the prey. K indicator emphasizes the vertical effects on the horizontal, such as the effects of the trophic cascade (Jordán et al. 2007).

Indicators of Organization and Degree of Order

The ecosystem's order indicators were based on the concepts formalized by Ulanowicz (1986), such as the ascendancy (A_i), development capacity (C_i), overhead (Φ), average mutual information (AMI) and the effective number of roles (Ro). A_i quantifies the level of system activity and the degree of its organization and development (Ulanowicz, 2000) and it is sensitive to environmental changes (Mageau, Costanza & Ulanowicz, 1998). A_i is calculated by Ulanowicz and Norden (1990) as follows:

$$A_i = \sum_{i,j} T_{ij} \log(T_{ij}TST/T_i.T_j)$$

where T represents energy flows, i and j represent the prey and predator, respectively, and the symbol \cdot represents the sum of the flows for all prey or all predators based on their position in the notation; for example, $T_{.j}$ represents the flows of all prey to predator j and TST is the Total System Throughput and represents the growth of the ecosystem in terms of energy flow.

C_i is the highest possible value of A_i in the system, and Φ is the difference $C_i - A_i$. Φ represents a measure of the energy reserve of an ecosystem for the response to disturbances. The principal component of Φ is the redundant flows that are considered indicators of resilience (Baird & Ulanowicz, 1989). The overhead is calculated as follows:

$$\Phi = - \sum_{i,j} T_{ij} \log(T_{ij}^2/T_i.T_j)$$

The AMI measures the organization of the exchanges among different functional groups of the ecosystem. An increase in AMI signifies that the system is becoming more constrained and is channeling flows along more specific pathways (Ulanowicz & Abarca-Arenas, 1997). The AMI was calculated as follows (Ulanowicz, 1986):

$$AMI = \sum_{i,j} (T_{ij}/T_{.j}) \log(T_{ij}T_{.i}/T_i.T_j)$$

The effective number of roles (Ro) is a measure of the degree to which the system has become differentiated into distinct function: $\log R = AMI$ (Zorach & Ulanowicz, 2003). (Ro) was calculated for each group as $Ro = e^{AMI}$.

Changes in the degree of the ecosystem's order can be expressed as the relative ascendancy ratio (A_i/C_i) (Platt, Man & Ulanowicz, 1981). The ecological role of the Pacific thread herring and the Pacific anchovy was analysed by using tree indicators proposed by Riofrío-Lazo, Arreguín-Sánchez, Zetina-Rejón and Escobar-Toledo (2013) which were obtained by simulating the extraction of each group i and re-estimating the ecosystem order. The A/C_{exti} is the relative change in the ascendancy expresses the system order without group i . The $((A/C)_{exti}/(A_i/C_i))$ is the relative change in the system's order due to the absence of group i with respect to the original order (A_i/C_i). The A_{exti}/A_0 is the relative change in the ascendancy due to absence of group i with respect to the original ascendancy. These indicators describe the topology and energy flows between the species in the food web.

Data Analysis

A multicollinearity analysis was performed among the 24 indicators, thus some of them were discarded when the variables showed a correlation of

0.9. Then, the similarity between the structural and organization indicators was estimated and verified using a non-metric multidimensional scaling (MDS) test. This analysis was performed using the Bray-Curtis similarity indicator. The MDS represents all indicators in two dimensions such that the relative distances between all points are within the same rank order. The indicators that are more similar to each other are compared with those farther away (Clarke & Gorley, 2006). Additionally, a principal component analysis (PCA) was conducted using the same indicators, which summarized the information about the structural and organization ecosystem's indicators for each functional group according to its variation. The values of all indicators were previously standardized. The Spearman's rank correlation coefficient was applied using only those indicators that are related to the Pacific thread herring and the Pacific anchovy (TL, $((A/C)_{\text{extil}}/(A_i/C_i))$, A/C_{extil} , D_i , A_i/C_i and Biomass). However, only those relationships that contributed to the description of the ecological role of the Pacific thread herring and the Pacific anchovy were plotted.

Results

The input and estimated data from the Ecopath model are described in the supplementary information. Table 1 shows the values of the structural, functional and organization ecosystem's indicators for each functional group which were used in this analyses.

In general, the biomass and the effective number of roles (Ro) of the functional groups were higher in the lower trophic levels and decreased towards the higher trophic levels. The OI was higher in the intermediate trophic levels (TL=2.4 to 2.7), which suggests that the Scorpaenidae/Triglidae, Polynemidae/Mullidae and Sciaenidae groups had a higher diversity in their diet than the other groups. Detritus had the highest number of connections (related to D_i) and also supplied important intermediary information in the system according to BC_i values. This suggests that detritus is a fundamental source of nutrients in the ecosystem for the primary consumers (Gerreidae, Stomatopoda, Porifera, Haemulidae, Polychaeta and Gastropoda). The Pacific anchovy, Rajiformes, Birds and Coryphaenidae groups had high values of K indicator, which indicates their importance in energy transfer through flows of the food web.

The MDS analysis identified the relative ranks of the similarities between the variables with a stress level of 0.04 (Figure 2) (see Warwick and Clarke, 1993). At 60% similarity, the MDS analysis revealed the following five groups: group 1) Φ , TST and R ; group 2) Ro , AMI , TL , $((A/C)_{\text{extil}}/(A_i/C_i))$, Q/B , R/B , and P/B ; group 3) B ; group 4) R/As ; and group 5) D_i , $(A/C)_{\text{extil}}$, (A_i/C_i) , K , P/Q , P/R and OI (Figure 3). At 80% similarity, the groups become fragmented and

fifteen groups were formed.

Figure 3 shows the arrangement of the indicators considering the first two principal components, which account for 53% of the total variance. The PCA constructed using the indicators with greater variance explained and functional groups showed six groupings, which represent similar roles and provide stability to the ecosystem: 1) TL , $((A/C)_{\text{extil}}/(A_i/C_i))$, and $(A/C)_{\text{extil}}$; 2) K , R , R/B and Q/B ; 3) R/As , P/B , Φ , and TST ; 4) B , D_i and A_i/C_i ; 5) Ro and AMI ; and 6) OI , P/Q and P/R . The Pacific thread herring and the Pacific anchovy were related to the first group that indicates the importance of these species in maintaining the ecosystem's order when these species were removed from the Ecopath model (changes in the attribute values, $((A/C)_{\text{extil}}/(A_i/C_i))$, and $(A/C)_{\text{extil}}$ in the Ecosim simulation). Although the PCA revealed different groupings of functional groups associated with ecosystem indicators, only the arrangements related to the Pacific thread herring and the Pacific anchovy were analysed in detail. Sixty-three percent of the total variance was explained by the first three components (PCs) (PC1=30%, PC2=18, and PC3=15%). The groups with the highest contributions to the variance of these PCs (Table 2) were: Phytoplankton (29.9%) and Zooplankton (18.6%) to PC1, Zooplankton (33.2%) and Birds (16.8%) to PC2; and Porifera (29.7%) and Zooplankton (18.7%) to PC3. The Pacific thread herring and the Pacific anchovy had the smallest contributions to the variance of PC1 (0.2% and 0.1%, respectively), PC2 (0.7% and 0.5%, respectively) and PC3 (1% and 0.5%, respectively).

A positive and significant correlations was found between TL and $((A/C)_{\text{extil}}/(A_i/C_i))$, (Spearman rank correlation $r_s = 0.5$, $P < 0.05$) (Figure 4a). The groups with lower trophic levels, such as phytoplankton, macrophytes and detritus (numbers 37, 38 and 39 in figure 4a), had lower values of $((A/C)_{\text{extil}}/(A_i/C_i))$, than those for the Pacific thread herring and the Pacific anchovy (numbers 35 and 34 in figure 4a, respectively), which suggests a loss of ecosystem's order when the groups of intermediate and higher trophic levels were removed from the Ecopath model. In particular, the Pacific thread herring and the Pacific anchovy had higher values of $((A/C)_{\text{extil}}/(A_i/C_i))$ indicator. In addition, when some functional groups were removed, those that are higher than 1 in $((A/C)_{\text{extil}}/(A_i/C_i))$ indicator contributed to increased ecosystem's order, while those that are lower than 1 in the same indicator contributed to entropy or loss of ecosystem's order. These results suggest that the Pacific thread herring and the Pacific anchovy contribute to the maintenance of ecosystem's order. A positive and significant correlations was found between B and $(A/C)_{\text{extil}}$ (Spearman rank correlation $r_s = 0.45$, $P < 0.05$; Figure 4d). This figure shows that the groups with relatively higher magnitudes of biomass (Phytoplankton, Macrophytes, Detritus, Zooplankton and Other clupeoides) had larger contributions to the

Table 1. Indicators for the SGC ecosystem for each functional group used in the analysis to identify the ecological role of the Pacific thread herring and the Pacific anchovy

	Functional group	TL	B	P/B	Q/B	P/Q	OI	R	R/As	P/R	R/B	D _i	CC _i	BC _i
1	Coryphaenidae	3.50	0.36	0.85	3.43	0.25	0.13	0.69	0.69	0.45	1.90	0.55	0.07	0.04
2	Lutjanidae	3.30	0.15	0.92	7.89	0.12	0.15	0.83	0.85	0.17	5.39	0.32	0.00	0.00
3	Synodontidae	3.29	0.21	2.05	8.52	0.24	0.22	1.01	0.70	0.43	4.77	0.24	0.00	0.00
4	Birds	3.23	0.02	0.39	88.70	0.00	0.14	1.48	0.99	0.01	70.57	0.16	0.00	0.00
5	Rajiformes	3.18	0.38	0.94	7.02	0.13	0.06	1.76	0.83	0.20	4.68	0.24	0.20	0.02
6	Palinura	3.14	11.23	0.10	2.70	0.04	0.07	23.08	0.95	0.05	2.06	0.18	0.07	0.01
7	Cephalopoda	3.14	0.01	0.93	7.58	0.12	0.23	0.04	0.85	0.18	5.13	0.53	0.41	0.03
8	Cheloniidae	3.13	0.06	1.20	7.28	0.17	0.16	0.28	0.79	0.26	4.62	0.32	0.03	0.01
9	Scombridae	3.12	0.14	1.19	11.95	0.10	0.09	1.16	0.88	0.14	8.37	0.13	0.06	0.01
10	Serranidae	3.11	0.01	4.51	17.98	0.25	0.05	0.11	0.69	0.46	9.88	0.26	0.16	0.01
11	Tetraodontidae	3.10	0.11	1.74	9.77	0.18	0.21	0.68	0.78	0.29	6.08	0.29	0.11	0.01
12	Pleuronectiformes	3.07	0.67	1.44	4.77	0.30	0.20	1.59	0.62	0.61	2.38	0.40	0.08	0.01
13	Carangidae	3.06	1.04	0.88	10.40	0.08	0.06	7.71	0.90	0.12	7.44	0.26	0.06	0.01
14	Centropomidae	3.00	0.47	1.14	5.05	0.23	0.17	1.37	0.72	0.39	2.90	0.18	0.00	0.01
15	Coelenterata	2.98	1.20	3.18	10.99	0.29	0.16	6.72	0.64	0.57	5.62	0.18	0.29	0.01
16	Ariidae	2.84	1.13	0.81	8.48	0.10	0.21	6.75	0.88	0.14	5.97	0.26	0.06	0.00
17	Portunidae	2.80	0.47	2.56	6.59	0.39	0.32	1.27	0.51	0.95	2.71	0.40	0.20	0.00
18	Scorpaenidae/Triglidae	2.79	0.05	0.99	7.55	0.13	0.35	0.27	0.84	0.20	5.05	0.13	0.06	0.00
19	Polynemidae/Mullidae	2.71	0.31	0.92	8.51	0.11	0.41	1.83	0.87	0.16	5.89	0.21	0.03	0.01
20	Sciaenidae	2.44	1.11	1.05	6.23	0.17	0.33	4.35	0.79	0.27	3.94	0.16	0.11	0.00
21	Mugilidae	2.40	0.26	0.94	16.46	0.06	0.27	3.15	0.93	0.08	12.23	0.24	0.08	0.00
22	Echinodermata	2.39	0.07	1.04	3.38	0.31	0.30	0.11	0.62	0.62	1.67	0.42	0.09	0.02
23	Gerreidae	2.34	1.50	0.99	9.39	0.11	0.30	9.77	0.87	0.15	6.53	0.16	0.06	0.00
24	Bivalvia	2.23	4.70	2.65	10.67	0.25	0.19	27.63	0.69	0.45	5.88	0.42	0.32	0.01
25	Penaeidae	2.20	2.49	5.26	20.22	0.26	0.16	27.14	0.68	0.48	10.91	0.50	0.42	0.02
26	Other fish	2.18	2.49	1.54	7.41	0.21	0.17	10.91	0.74	0.35	4.38	0.50	0.38	0.03
27	Haemulidae	2.14	1.49	0.97	7.39	0.13	0.14	7.37	0.84	0.20	4.94	0.21	0.06	0.00
28	Stomatopoda	2.12	0.03	2.32	9.34	0.25	0.16	0.13	0.69	0.45	5.15	0.32	0.31	0.03
29	Zooplankton	2.06	22.39	18.95	87.81	0.22	0.06	1148.76	0.73	0.37	51.30	0.50	0.50	0.01
30	Other macrocrustacean	2.06	15.79	1.29	6.23	0.21	0.06	58.35	0.74	0.35	3.69	0.74	0.68	0.01
31	Porifera	2.03	29.13	1.06	12.89	0.08	0.03	269.50	0.90	0.11	9.25	0.16	0.14	0.00
32	Polychaeta	2.02	0.23	1.60	12.43	0.13	0.02	1.89	0.84	0.19	8.34	0.34	0.36	0.00
33	Other cupleoidae	2.02	0.09	1.89	4.95	0.38	0.02	0.19	0.52	0.91	2.07	0.16	0.15	0.00
34	Cetengraulis mysticetus	2.02	4.11	5.90	26.58	0.22	0.02	63.18	0.72	0.38	15.36	0.16	0.27	0.00
35	Opisthonema libertate	2.00	1.67	1.48	11.87	0.13	0.00	13.41	0.84	0.19	8.02	0.13	0.08	0.00
36	Gastropoda	2.00	0.03	3.43	16.45	0.21	0.00	0.24	0.74	0.35	9.73	0.24	0.25	0.00
37	Phytoplankton	1.00	59.62	35.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.52	0.00
38	Macrophytes	1.00	87.47	7.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.55	0.00
39	Detritus	1.00	4.12	0.00	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.61	0.67	0.00

Table 1. Continued

	Functional group	<i>K</i>	<i>TST</i>	<i>AMI</i>	<i>Ro</i>	<i>A_i</i>	<i>C_i</i>	<i>A_i/C_i</i>	Φ	$(A/C)_{exit}$	A_{exit}/A_0	$(A/C)_{exit}/(A/C)_i$
1	Coryphaenidae	0.49	1.24	1.96	7.12	2.43	17.49	0.14	15.06	0.33	3744.93	2.39
2	Lutjanidae	0.34	1.21	1.22	3.38	2.25	23.81	0.09	14.75	0.33	6198.80	3.66
3	Synodontidae	0.10	1.80	1.25	3.49	1.47	16.22	0.09	21.56	0.33	4046.67	3.51
4	Birds	0.46	1.86	1.36	3.89	2.53	23.52	0.11	20.99	0.33	3593.91	3.08
5	Rajiformes	0.73	2.64	1.20	3.30	3.16	32.54	0.10	29.38	0.33	2880.85	3.42
6	Palinura	0.22	30.28	1.28	3.58	0.07	1.05	0.14	228.80	0.33	234.44	2.31
7	Cephalopoda	0.03	0.06	1.24	3.45	38.63	267.50	0.07	0.98	0.33	127381.53	4.86
8	Cheloniidae	0.03	0.44	2.03	7.58	0.89	6.69	0.13	5.80	0.33	10252.79	2.50
9	Scombridae	0.06	1.66	1.43	4.17	0.20	3.33	0.11	19.51	0.33	3834.98	3.06
10	Serranidae	0.02	0.20	1.00	2.71	2.37	21.88	0.06	3.13	0.33	45933.91	5.56
11	Tetraodontidae	0.19	1.09	1.82	6.17	1.99	15.41	0.13	13.42	0.33	4567.11	2.56
12	Pleuronectiformes	0.25	3.19	2.03	7.61	6.47	41.27	0.16	34.80	0.33	1404.95	2.11
13	Carangidae	0.37	10.77	1.38	3.96	14.81	111.90	0.13	97.12	0.33	613.12	2.51
14	Centropomidae	0.06	2.39	1.11	3.05	2.66	29.99	0.09	27.33	0.33	3416.93	3.74
15	Coelenterata	0.04	13.14	1.89	6.64	24.88	141.70	0.18	116.80	0.33	364.56	1.89
16	Ariidae	0.23	9.59	1.23	3.43	11.81	100.40	0.12	88.64	0.33	769.12	2.82
17	Portunidae	0.27	3.09	1.85	6.35	5.70	41.70	0.14	36.00	0.33	1593.51	2.42
18	Scorpaenidae/Triglidae	0.01	0.40	1.48	4.37	0.59	6.09	0.10	5.50	0.33	15414.44	3.42
19	Polynemidae/Mullidae	0.14	2.65	1.49	4.42	3.94	32.98	0.12	29.04	0.33	2309.75	2.78
20	Sciaenidae	0.09	6.88	1.29	3.62	8.85	76.70	0.12	67.86	0.33	1026.93	2.88
21	Mugilidae	0.05	4.23	1.41	4.10	5.98	50.02	0.12	44.04	0.33	1520.69	2.77
22	Echinodermata	0.12	0.22	2.47	11.85	0.54	3.69	0.15	3.15	0.33	16717.96	2.25
23	Gerreidae	0.23	14.05	1.31	3.71	18.41	141.80	0.13	123.30	0.33	493.03	2.56
24	Bivalvia	0.23	50.10	1.49	4.45	74.75	447.50	0.17	372.80	0.33	120.67	2.00
25	Penaeidae	0.31	50.28	1.42	4.12	71.15	463.50	0.15	392.30	0.33	126.83	2.18
26	Other fish	0.22	18.44	1.70	5.49	31.40	196.40	0.16	165.00	0.33	288.65	2.08
27	Haemulidae	0.04	11.03	1.22	3.38	13.43	113.60	0.12	100.20	0.33	676.22	2.81
28	Stomatopoda	1.00	0.24	2.41	11.09	0.58	3.98	0.14	3.41	0.33	15816.59	2.29
29	Zooplankton	0.36	1966.00	0.85	2.34	1675.00	6371.00	0.26	4697.00	0.35	4.43	1.34
30	Other macrocrustacean	0.11	98.38	1.01	2.73	98.86	782.10	0.13	683.30	0.34	91.00	2.67
31	Porifera	0.34	375.40	1.32	3.76	1.65	7.27	0.24	1542.00	0.34	17.30	1.39
32	Polychaeta	0.00	2.81	0.95	2.59	155.00	847.00	0.08	32.52	0.33	3399.04	4.36
33	Other cupleoidae	0.06	0.46	3.56	35.26	497.10	2039.00	0.23	5.62	0.33	5524.58	1.46
34	Cetengraulis mysticetus	0.40	109.30	1.42	4.13	2.68	35.19	0.18	692.00	0.34	57.68	1.84
35	Opistonema libertate	0.01	19.85	0.96	2.61	19.05	192.30	0.10	173.20	0.33	476.43	3.36
36	Gastropoda	0.01	0.41	2.12	8.29	0.86	6.38	0.14	5.52	0.33	10562.43	2.45
37	Phytoplankton	0.37	2120.00	1.07	2.91	2262.00	5804.00	0.39	3542.00	0.32	3.02	0.81
38	Macrophytes	0.31	627.80	2.51	12.27	1574.00	3264.00	0.48	1690.00	0.31	4.78	0.64
39	Detritus	0.00	1524.00	1.61	5.01	2457.00	5685.00	0.43	3228.00	0.30	2.70	0.71

TL_i, trophic level; *B_i*, biomass; *P/B_i*, production/biomass ratio; *Q/B_i*, consumption/biomass ratio; *OI_i*, omnivory index; *R_i*, respiration; *R/As_i*, respiration/assimilation ratio; *P/R_i*, production/respiration ratio; *R/B_i*, respiration/biomass ratio; *D_i*, degree indicator; *CC_i*, closeness indicator; *BC_i*, betweenness indicator; *K_i*, keystone species indicator; *TST*, Total System Throughput; *AMI*, average mutual information; *Ro*, effective number of roles; *A_i/C_i*, relative ascendancy ratio that express the proportion of contribution of each group to the system's order; Φ , overhead; $(A/C)_{exit}$, relative change in the relative ascendancy ratio when group *i* is removed from the system; A_{exit}/A_0 , relative change in the ascendancy when group *i* is removed from the system with respect to the original ascendancy; $(A/C)_{exit}/(A/C)_i$, proportional change due to $(A/C)_{exit}$ with respect to the original $(A/C)_0$ ratio.

initial order of the ecosystem. No significant correlations were found between the degree indicator (D_i) and biomass (B) (Figure 4b) and between D_i and A_i/C_i (Figure 4c) (Spearman rank correlations $r_s = 0.15$ and 0.17 , respectively; $p > 0.05$). In both cases, the number of connections of the functional groups does not depend on their level of biomass or their contribution to the ecosystem's order.

Discussion

The analysis of the holistic indicators demonstrated that the Pacific thread herring (*Opisthonema libertate*) and the Pacific anchovy (*Cetengraulis mysticetus*) have similar ecological roles and maintain the order of the ecosystem; in addition, due of its participation in the system flows (according to its K values), the Pacific anchovy might

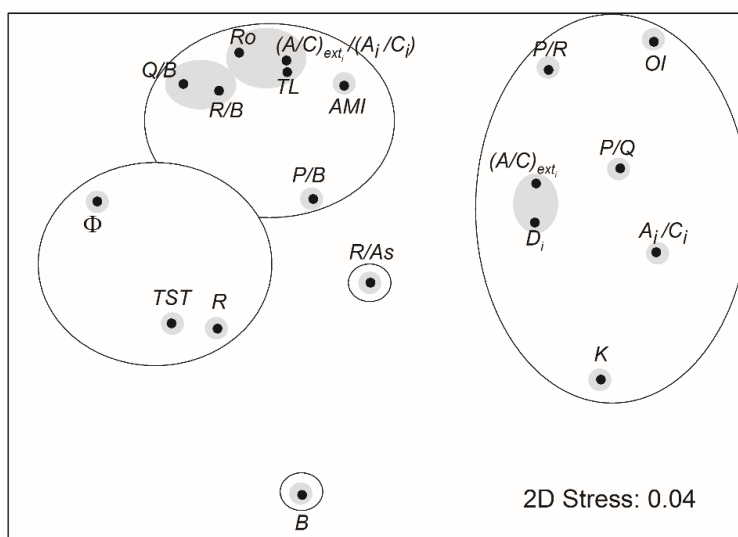


Figure 2. Percentage of similarity between variables in the non-metric multidimensional scaling analysis. The proximity of one variable to another represents similarity. Circles represent the rank orders of similarity between the variables. Open circles indicate variables with 60% similarity, and gray circles indicate 80% similarity. The data were log (x + 1) transformed. Stress level: 0.04.

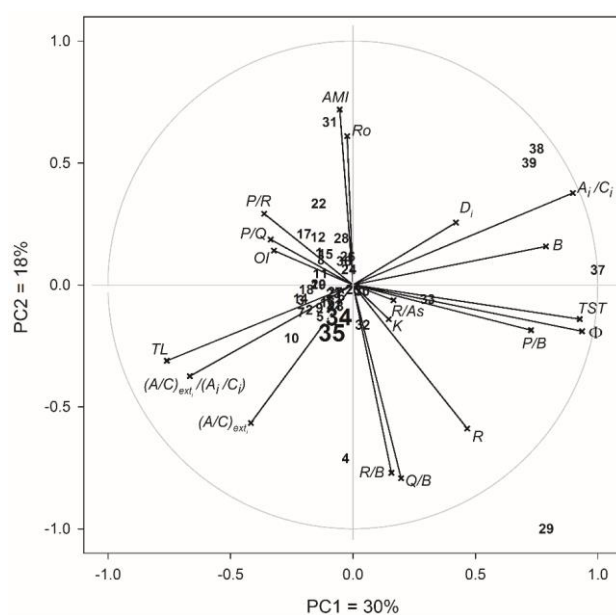


Figure 3. PCA representing the projection of functional groups (numbers) and ecosystem's indicators (initial). The projection shows the formation of sets of similar functional groups and their relationships with the ecosystem indicators. The Pacific thread herring (35) and the Pacific anchovy (34) are highlighted by large fonts and are in similar sets associated with similar ecosystem's indicators (see Table 1 for the identification key of the functional groups and ecosystem's indicators).

Table 2. Relative contributions of the groups to the variance of a PC based on correlations (%). The values of the three PCs that explain the major percentages of variance are shown; the higher the contribution of a case, the more it weighs on the PC

PC1		PC2		PC3		
Functional groups	%	Functional groups	%	Functional groups	%	
1	Phytoplankton	29.9	Zooplankton	33.2	Porifera	29.7
2	Zooplankton	18.6	Birds	16.8	Zooplankton	18.7
3	Macrophytes	16.8	Porifera	14.8	Detritus	10.1
4	Detritus	15.5	Macrophytes	10.3	Portunidae	4.0
5	Other clupeoidae	2.8	Detritus	8.3	Stomatopoda	3.6
6	Serranidae	1.9	Equinodermata	3.7	Other clupeoidae	2.9
7	Centropomidae	1.4	Serranidae	1.6	Equinodermata	2.5
8	Synodontidae	1.4	Portunidae	1.4	Palinura	2.4
9	Cephalopoda	1.3	Pleuronectiformes	1.3	Cephalopoda	2.2
10	Portunidae	1.2	Stomatopoda	1.2	Mugilidae	2.0
11	Scorpaenidae/Triglidae	1.1	Polychaeta	0.9	Phytoplankton	2.0
12	Lutjanidae	0.9	<i>Opistonema libertate</i>	0.7	Lutjanidae	1.7
13	Pleuronectiformes	0.6	Coryphaenidae	0.6	Pleuronectiformes	1.7
14	Sciaenidae	0.6	Rajiformes	0.6	Polynemidae/Mullidae	1.5
15	Polynemidae/Mullidae	0.6	Coelenterata	0.5	Ariidae	1.5
16	Equinodermata	0.6	<i>Cetengraulis mysticetus</i>	0.5	Scorpaenidae/Triglidae	1.5
17	Coryphaenidae	0.6	Other fish	0.5	Coelenterata	1.3
18	Scombridae	0.6	Cephalopoda	0.4	Gerreidae	1.2
19	Rajiformes	0.5	Lutjanidae	0.4	Scombridae	1.1
20	Tetraodontidae	0.5	Cheloniidae	0.3	<i>Opistonema libertate</i>	1.0
21	Cheloniidae	0.5	Gastropoda	0.3	Haemulidae	1.0
22	Coelenterata	0.4	Scombridae	0.3	Macrophytes	1.0
23	Ariidae	0.3	Carangidae	0.3	Sciaenidae	0.8
24	Porifera	0.3	Mugilidae	0.2	Penaeidae	0.7
25	Gerreidae	0.2	Ariidae	0.2	Carangidae	0.7
26	Mugilidae	0.2	Bivalvia	0.1	Coryphaenidae	0.6
27	Haemulidae	0.2	Synodontidae	0.1	Gastropoda	0.6
28	<i>Opistonema libertate</i>	0.2	Phytoplankton	0.1	Polychaeta	0.6
29	Carangidae	0.1	Other clupeoidae	0.1	<i>Cetengraulis mysticetus</i>	0.5
30	<i>Cetengraulis mysticetus</i>	0.1	Centropomidae	0.1	Centropomidae	0.3
31	Palinura	0.1	Tetraodontidae	0.1	Bivalvia	0.3
32	Stomatopoda	0.1	Palinura	0.1	Rajiformes	0.3
33	Polychaeta	0.0	Gerreidae	0.0	Serranidae	0.1
34	Other macrocrustaceans	0.0	Haemulidae	0.0	Other macrocrustaceans	0.0
35	Gastropoda	0.0	Other macrocrustaceans	0.0	Other fish	0.0
36	Birds	0.0	Scorpaenidae/Triglidae	0.0	Cheloniidae	0.0
37	Other fish	0.0	Penaeidae	0.0	Synodontidae	0.0
38	Bivalvia	0.0	Sciaenidae	0.0	Tetraodontidae	0.0
39	Penaeidae	0.0	Polynemidae/Mullidae	0.0	Birds	0.0

be the key species on which the herring fishery in the SGC might be managed.

In México, the knowledge of the ecological importance of the Pacific thread herring and the Pacific anchovy in the SGC ecosystem is relevant to several groups (industry, managers, researchers and civil organizations) and is a requirement of the MSC certification process to ensure the sustainability of the fishery and reduce negative impacts on the ecosystem. In this context, the European Union encourages member states to achieve the “Good Environmental Status” objective by 2020 through a set of criteria and holistic indicators proposed by the Marine Strategy Framework Directive (European Commission, 2008). Piroddi *et al.* (2015) analysed the current capabilities of the modelling community to provide information about the indicators outlined in this framework. One

aspect that was analysed refers to the state of the ecosystem, and these indicators are generally applicable to assess the ecosystem’s dynamics; however, these indicators alone are inadequate to achieve “Good Environmental Status” (Rombouts *et al.* 2013). The use of holistic indicators is an efficient approach that can be implemented to generate multiple viable management strategies based on the regulated catch rates and conservation scenarios of marine ecosystems (Arreguín-Sánchez, Zetina-Rejón, Manickchand-Heileman, Ramírez-Rodríguez & Vidal, 2004).

The indicators of D_i , CC_i and BC_i describe the structural characteristics of the food web and are usually related to the concept of keystone species (Solé & Montoya, 2001; Dunne, Williams & Martinez, 2002). This suggests a large number of

trophic links and participation in energy flows, which is reflected in a significant contribution to the structure and function of the ecosystem (Albert, Jeon & Barabási, 2000). Our results showed that the key elements of the SGC ecosystem were the lower trophic level groups, such as Detritus, Phytoplankton, Macrophytes, Zooplankton, the Pacific anchovy, Porifera, and high-level predators in the SGC such as Coryphaenidae and Lutjanidae. A large number of links in the lower trophic level groups and primary consumers suggests a bottom-up control energy flow in the food web (Vasas, Lancelot, Rousseau & Jordán, 2007). This type of control possibly occurs in the SGC, although an ecosystem can be managed by more than one type of control depending on its status, diversity and integrity (Cury, Shannon & Shin, 2001). In addition, this type of control in the ecosystem may change depending on the environmental variability which controls the abundance and distribution of

marine population (Cury *et al.* 2001). The indicators D_i , CC_i and BC_i will allow management measures to be developed for the entire ecosystem to reduce the negative impacts on the key elements of the ecosystem and to maintain its health and productivity. This is another principle of the MSC certification process.

The development of an ecosystem is generally characterized by an increase in information and its order (Ulanowicz, 1986; Jorgensen, 2000; Marques & Jorgensen, 2002). While the objective of this study was not to describe the development of the ecosystem of the SGC, our results suggest that the Pacific thread herring and the Pacific anchovy play similar roles in terms of the structure, organization and function of the ecosystem. The Pacific thread herring and the Pacific anchovy were closely related to the indicators $(A/C)_{exti}$, $(A/C)_{exti}/(A_i/C_i)$ and TL , which suggests that these species are significantly involved in the

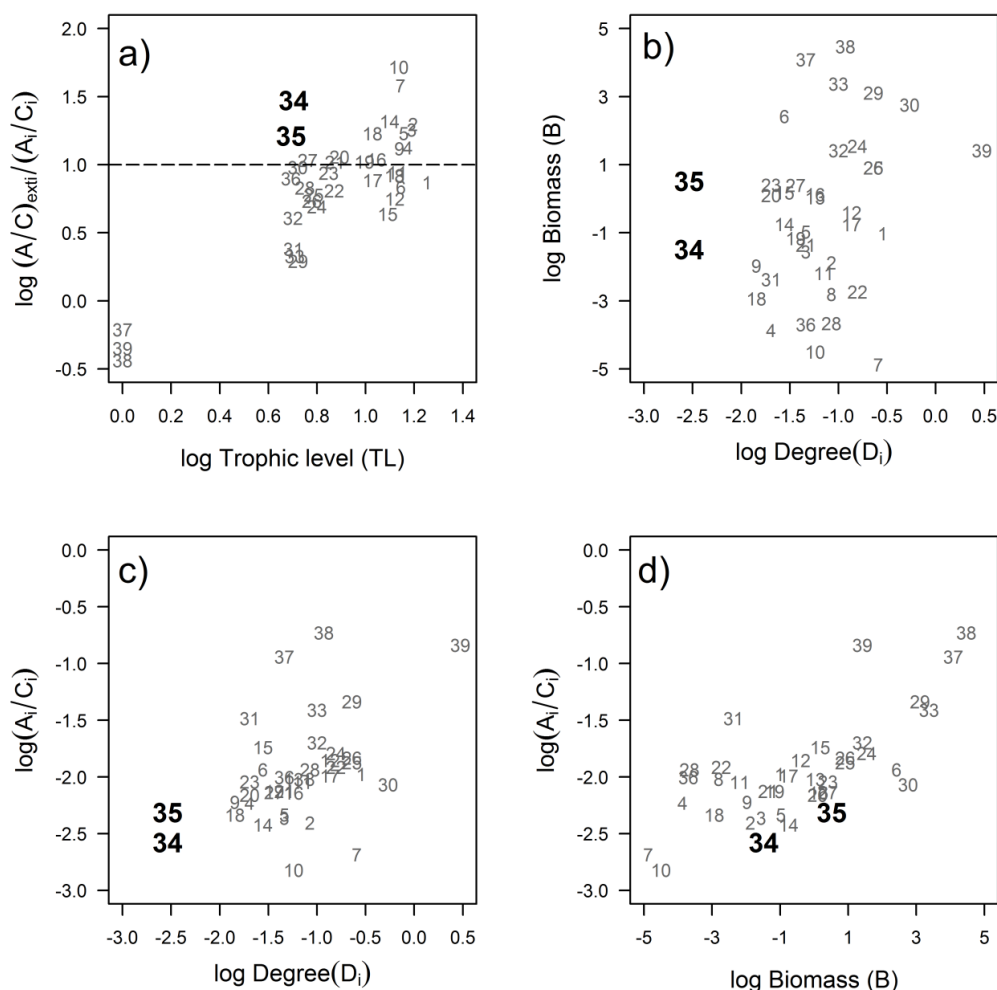


Figure 4. Scatterplots showing the different performances of the Pacific thread herring and the Pacific anchovy (numbers 35 and 34 respectively) in the SGC ecosystem. The ecosystem's indicators with the highest contributions to the variance of PC1 and those indicators with similar trends to the Pacific thread herring and the Pacific anchovy in the PCA were selected. **a)** \log TL vs. $\log(A/C)_{exti}/(A_i/C_i)$; **b)** \log degree (D_i) vs. \log biomass (B); **c)** \log degree (D_i) vs. $\log(A_i/C_i)$; and **d)** \log biomass (B) vs. $\log(A_i/C_i)$. Refer to Table 1 for the identification of the functional groups represented by numbers inside the plots.

maintenance of ecosystem's order, as was suggested by Christensen and Pauly (1995) in general terms. In addition, the relative change in the system's order was explained to be due to the absence of lower trophic level groups rather than highest trophic levels. In particular, the Pacific thread herring and the Pacific anchovy maintained higher order levels in the system compared to the other groups. The Pacific anchovy was also one of the five groups with higher values of K indicator. This is partly because even when this group has the same number of trophic links (related to D_i) to others, it participates with greater intensity in the energy transfer through the food web. This finding contrasts with that reported by Riofrío-Lazo *et al.* (2013) in the Northern Gulf of California, where small pelagic species are less important in transferring energy through the food web. In terms of ecosystem management, these results are important for the Pacific thread herring and the Pacific anchovy because attributes such as keystone species, biomass and the role in maintaining the ecosystem's order can be affected by fishing; thus, a total allowable catch would be desirable as a management strategy in the SGC but not necessarily in other regions of the Gulf. This confirms that the ecosystem-based management approach must be designed for each individual ecosystem (Arreguín-Sánchez, 2014).

The similar ecological roles of both species of herring might be partly explained by a remarkably similar distribution in the Eastern Tropical Pacific (Robertson & Allen, 2002). For that reason, the diets of the Pacific thread herring and the Pacific anchovy are not completely different (Bayliff, 1963; Jacob-Cervantes, Gallardo-Cabello, Chiappa-Carrara & Ruiz, 1992). In addition, both species of herring are considered forage species; they are characterized by high variations in their abundance and on the catch species composition during the fishing period. These factors support the similarities between the trophic levels of both herring species and might explain their topological roles in the food web, where they have the same numbers of links as predator and prey. The Pacific thread herring and the Pacific anchovy have a similar ecological role to other species groups in the SGC ecosystem, such as synodontidae (2), lutjanidae (3), birds (4), rajiformes (5), scombridae (10), centropomidae (14) and scorpaenidae/triglidae (18) (identified by numbers in Figure 4); however, these groups do not replace the two species of herring as forage species. This characteristic highlights the wasp-waist role for small pelagic species in the Gulf of California (Bakun *et al.* 2009).

The removal effect of the Pacific thread herring and the Pacific anchovy from the Ecopath model is reflected in the maintenance of ecosystem's order. If the removal does not affect the natural rate of species renewal, the ecosystem responds by restoring the energy flows to maintain its dynamic balance. When an ecosystem is developing, the entropy is high and then gradually decreases to low levels upon its

maturation (Saint-Beat *et al.* 2015). The increase in entropy may be considered a measure of the sensitivity of the ecosystem to changes in the biomass of the groups (Arreguín-Sánchez & Ruiz-Barreiro, 2014). In our simulations, the effect of drawing the ecosystem by removing the Pacific thread herring or the Pacific anchovy was partially but not completely offset by the other groups with similar ecological roles, as is indicated by their keystone indicators. In contrast, the groups that generate an increase in the ecosystem's order might provide some stability to the ecosystem over time (Margalef, 1962) and might help maintain ecosystem's resilience. Our results suggest that the Pacific thread herring and the Pacific anchovy contribute to these ecosystem's processes.

This study is relevant to the conditions of the MSC certification process that occur throughout the entire Gulf of California, which require more information about the ecological roles of herrings to achieve the ultimate goal of ensuring sustainable operation of the herring fishery. Achieving this goal will involve the consideration of several factors that affect the biological productivity of herring species in the Gulf of California. The collapse of forage species occurs because of high fishing pressure for several years before the collapse and is a cumulative effect that is caused by a sharp fall in the natural productivity of the population accompanied by a late response of policymakers to reduce fishing pressure (Essington *et al.* 2015). The results of this study suggest that allowable catch rates for the Pacific thread herring and the Pacific anchovy under an adaptability strategy might prevent undesirable effects on ecosystem sustainability.

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