



A mass-balanced food web model for a kelp forest ecosystem near its southern distributional limit in the northern hemisphere

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ABSTRACT

Coastal ecosystems are influenced by a suite of drivers and interactions, resulting in complex dynamics not captured by single species, single driver approaches. Kelp forest ecosystems of the California Current region are subject to extreme environmental variability as well as a suite of fishing pressures which remove organisms throughout the food web. Here, we present a food-web model to assess ecosystem-wide effects of different fishing strategies which can also be used to estimate the effect of warming, acidification and hypoxia on the structure and function of a highly productive temperate ecosystems. We built a mass-balanced model of a kelp forest ecosystem near the southern limit of distribution in the northern hemisphere (Isla Natividad, Mexico). The model is informed by extensive ecological monitoring of fish, benthic invertebrates, and macroalgae conducted annually from 2006 to 2016 at 5 sites around the island. The model includes 40 functional groups (FG) defined on the basis of commercial interest, ecosystem function and feeding guild, including birds, marine mammals, fish (13 FG), commercial species (7 FG), macroinvertebrates (8 FG), zooplankton, the giant kelp *Macrocystis pyrifera*, six macroalgae, phytoplankton and detritus. The estimated throughput was $5477.6 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (26% consumption, 27% exports, 24% respiration and 23.7% detritus). The sum of all production was $2727.9 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, and the total primary production/total respiration ratio was 2.4. This model, based on a detailed, multi-year monitoring program in the kelp forests, provides a valuable tool for exploring drivers of change in these vulnerable marine ecosystems and fisheries.

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1. Introduction

Coastal areas around the world are densely populated because of the suite of services provided by coastal marine ecosystems (MEA (Millennium Ecosystem Assessment), 2005). Currently, marine ecosystems and the myriad of services they provide are subject to anthropogenic disturbance from overfishing, habitat destruction and pollution, as well as climate change and the associated temperature, hypoxia and acidification extremes, all of which can cause shifts in ecosystem structure and function (Doney et al., 2012; Jackson et al., 2001; Halpern, 2008). For this reason, it is extremely important to establish ecosystem baselines and approaches for exploring management

strategies that might enhance the resilience of ecosystems and the human sectors they support. Food web models have proven to be extremely useful as ecosystem-based management tools informing fisheries management (Field and Francis, 2006). However, few models have been constructed to examine the combined effects of climate variability and fisheries in coastal ecosystems, with even fewer at their distribution range limit, where ecosystems are especially vulnerable to climate change. According to Shelford's (1911) law of tolerance, the presence and success of an organism depends upon the extent to which optimal conditions are satisfied. When a species is near its limit of distribution, a slight change in environmental conditions may be devastating.

The construction of ecosystem models parameterized with ecological monitoring data is a powerful way to investigate the dynamics of natural communities and inform better management and conservation strategies, as they are based on multi-year patterns rather than snapshot

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descriptions of the ecosystem. This is especially important when multiple stressors might be affecting highly productive and complex ecosystems. The simultaneous variation of temperature, oxygen and pH in coastal ecosystems makes it difficult to assess their individual and synergistic impacts on coastal communities through manipulative field experiments, and laboratory experiments can only typically focus on one or a few species at a time. Thus, food web models can be used instead to simulate ecosystem-wide responses to environmental change and fishing pressure, especially if they are constructed with information from long-term *in situ* monitoring data spanning a range of oceanographic conditions, and use data from both fished and unfished locations.

One of the most diverse and productive marine ecosystems worldwide are the kelp forests, structured by the giant kelp *Macrocystis pyrifera* (Foster and Schiel, 1985). These marine forests are distributed in temperate zones of the western coasts of the planet dominated by cold, nutrient-rich water, characteristic of upwelling zones (Dayton, 1985). Their high diversity and productivity make them complex ecosystems which are sensitive to physical, biological and anthropogenic impacts (Carr and Reed, 2015). Despite their ecological and economic importance, there is still limited understanding of the capacity of these systems to cope with climate change (Carr and Reed, 2015; Krumhansl et al., 2016) and a critical need to develop and test new approaches integrating modeling and empirical data to address this gap of knowledge.

We focus on Isla Natividad, Baja California Sur, Mexico (Fig. 1), a small island inhabited by approximately 300 people. The *M. pyrifera* kelp forests of Isla Natividad are close to their southernmost distribution limit in the northern hemisphere (Ladah et al., 1999), and have been continuously monitored since 2006 (Micheli et al., 2012). This ecological monitoring program has generated a physical and biological time series that includes many of the species in the community (Woodson, 2017). The abalone, snail, lobster and sea cucumber fisheries are some of the most economically important fisheries in this region, with some of them also encountering their distributional limit in this area (Hernández-Velasco et al., 2015). Biogeographic theory suggests lower abundances of species at the edge of their distribution, yet interestingly, the biogeographic break between temperate and subtropical conditions around Isla Natividad has provided a highly productive environment supporting these prolific fisheries. However, this ecosystem and the ecosystem services they provide remain susceptible to sudden environmental changes.

In addition, the information from a series of ecological and socio-economic studies at Isla Natividad and nearby communities makes this site ideal for this type of work (Finkbeiner et al., 2018; Martone et al., 2017; Micheli et al., 2014; Micheli et al., 2012; Munguia-Vega et al., 2015; Revollo-Fernández et al., 2016; Rocchi et al., 2017; Rossetto et al., 2013, 2015; Shester and Micheli, 2011; Boch et al.,

2018). A food web model for this site will be able to integrate and expand our understanding of kelp forest ecosystems and their responses to fishing and climate variability, and inform the next generation of analyses and experiments for the southern limit kelp forests and for those in the entire California Current.

The particular environmental and socio-economic conditions (e.g., high vulnerability to environmental extremes and the presence of strictly controlled voluntary marine reserves), and the unique long-term physical-biological database for this location provided us with an opportunity to construct and calibrate a realistic mass-balanced food web model. To our knowledge, this is the first attempt to build such a model for this area, although there is another Ecopath model for a kelp forest area nearby in Bahia Tortugas (Morales-Zárate et al., 2011). Both of these models are kelp ecosystems food web models and can be compared and contrasted. However, our model is based on a multi-year database from monitoring, increasing its approximation to reality. Specifically, we: 1) grouped the species associated with this ecosystem in 40 functional groups, 2) synthesized ecological monitoring data to generate biomass density estimates and species interactions for each functional group, 3) developed a mass-balanced food web model using Ecopath and, 4) characterized the structure and function of a kelp forest near its southern limit.

With this, we wanted to determine how this ecosystem works by exploring the following: 1. How is the Isla Natividad kelp forest community structured? 2. What are the FG interactions inside the kelp forests of Isla Natividad? And 3. How does the biomass flow through the different FGs of the kelp forests of Isla Natividad?

1.1. Study site

Isla Natividad is located in the Mexican Pacific, in the middle of the Baja California Peninsula between 27°54'00" and 27°51'14" N and between 115°13'59" and 115°09'22" W (Fig. 1). It is a 7 km long island and is part of the Natural Protected Area of El Vizcaino (www.conanp.gob.mx/datos_abiertos/DGCD/49.pdf). The island is inhabited by approximately 300 people, who have been living from marine products for more than 75 years (Hernández-Velasco et al., 2015). The fishing concession belongs to a fishing cooperative founded in 1942 called Sociedad Cooperativa de Buzos y Pescadores de Baja California S.C.L (<https://islandpacific.com.mx/>). The main source of livelihood of Isla Natividad is the harvest of coastal invertebrates, such as abalone, lobster, sea cucumbers, snails and sea urchins, for which the local fishing cooperative holds exclusive access rights in the form of 20-year concessions (McCay et al., 2014). All these species are extremely valuable in national and international markets. The presence of the cooperative has allowed fishers to maintain a regulated and sustained extraction from the ecosystem (Hernández-Velasco et al., 2015). Until 2010, the

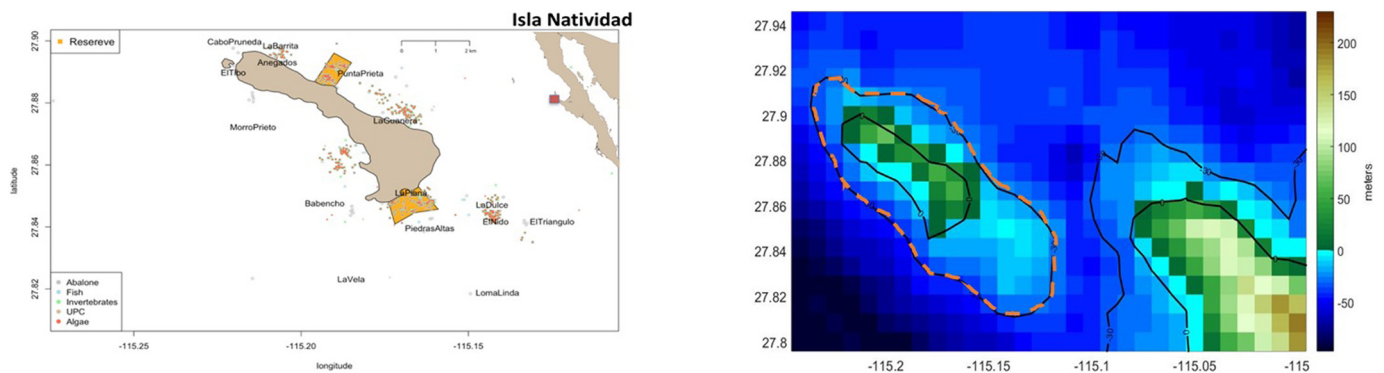


Fig. 1. Isla Natividad off the West Coast of Mexico. Left side: Dots indicate diver transects performed for the different taxonomic groups. Grey for abalone, blue for fish, green for invertebrates, light brown for reef structure and red for algae. The orange polygons indicate reserves where fishing is limited. Right side: Isla Natividad bathymetry at 30 m and 0 m. The red line represents the 30 m isobaths. We used the area inside the red line to estimate the area of the model. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

principal harvested species were the pink and green abalone (*Haliotis corrugata* and *H. fulgens*, respectively). These abalone species have recently suffered a drastic decline in their populations compared to historical records (Hernández-Velasco et al., 2015; Micheli et al., 2012). In response to abalone decline, in 2006 the cooperative created two no-take zones encompassing approx. 8% of the fishing grounds to promote recovery (Micheli et al., 2012). The design and implementation of these marine reserves followed a closed collaboration with the fishers, local NGOs and academics (Sáenz-Arroyo et al., 2012).

1.2. Ecological monitoring program

Since 2006, the non-governmental environmental organization Comunidad y Biodiversidad A.C. (COBI), the fishing cooperatives and researchers from Stanford University have conducted community-based ecological monitoring of kelp forest ecosystems in this region. The surveys are conducted once/year, in summer, following the methodology developed by Reef Check of California and adapted to this region by COBI. The protocol consists of ~20 30 × 2 m transects per site per year to measure fish density and size, kelp density and invertebrate density and size of the commercially harvested species and selected ecologically important non-commercial species. In addition, the monitoring includes uniform point contact transects (UPC) to quantify benthic cover by algae and sessile invertebrates. An area of approximately 72,000 m² is covered by these transects (60 m² × 5–6 sites × ~20 transects/site) each year. Monitoring is ongoing, but data collected between 2006 and 2016 were used here. Monitoring sites around the island were georeferenced inside and outside the marine reserves. Marine reserves at Isla Natividad were established on 2006 and thus, we build the current base model without this differentiation.

In addition to the ecological data available at Isla Natividad, there is an extensive physical oceanography monitoring program and a series of social-ecological datasets including game theory experiments and interviews. Despite none of these data is directly included in the base food web model we present in this work, it could be potentially used to design simulations and inform future questions.

2. Material and methods

2.1. Ecopath model

In order to understand the structure and function of the Isla Natividad kelp forest ecosystem, an Ecopath model was developed. Ecopath is an ecosystem modeling software that allows for the generation of a mass-balanced model of the ecosystem's trophic web. Ecopath is made up of a system of linear equations that represent each species or functional group included within the system whose inputs and outputs of biomass have to be in balance (Christensen and Pauly, 1992). The general equation of Ecopath is:

$$B_i(P/B)_i = \sum B_j Q/B_j DC_{ji} + E_i + Y_i + BA_i + B_i * PB_i(1-EE_i)$$

where B_i is the biomass of the functional group i ($t \cdot km^{-2}$), P/B_i is the biomass production ratio of i (which is considered equal to the annual mortality (Z) of i), B_j is the biomass of the predator j , Q/B_j is the biomass consumption ratio for the predator j , DC_{ji} is the fraction of the prey i within the diet of the predator j , E_i is the total export of the group i , Y_i is the fishing rate on i , BA_i is the accumulated biomass of i and EE_i is the ecotrophic efficiency of i , which indicates the proportion of i that is used in the system.

2.2. Model area determination

To delimit the total study area (Fig. 1) we used the area between 0 m (coastline) and the 30 m isobath, obtaining a total area of 31.42 km². We chose 30 m as the maximum depth for two main reasons: 1) the

ecological monitoring is performed up to this depth; and 2), the forests of *M. pyrifera* are usually found at a maximum depth of approx. 30 m (Foster and Schiel, 1985). The extent of the total area was calculated with ArcMap (version 10.3) using the island bathymetry provided by COBI.

The giant kelp forests are not uniformly distributed around the Island. Therefore, we also delimited the area occupied by *M. pyrifera* forests. We used satellite images with the best resolution of the island obtained through Google Earth Pro (version 7.1.8) from 2009. We manually delimited the most precise polygon of the *M. pyrifera* forest patches, and we obtained a total area of 5.08 km². This value was used to recalculate the observations *in situ* during the monitoring to adjust them to the model area depending on habitat preferences of each species.

2.3. Functional groups (FG)

To create a base model of the ecosystem, we wanted to use the abundance and size data obtained during the first year of monitoring from 2006, before no take zones were established. However, other species that were not registered appeared later in the monitoring years. Therefore, in order to generate a more accurate and representative model of the ecosystem with the largest number of species, we decided to use the data of the first year of registration for each FG (Heymans et al., 2016). Hence, to calculate the FG biomass we used the first abundance or annual density of all the species recorded during the 10 years of monitoring.

In ecosystem modeling, species are often grouped into functional groups (FG) to achieve a simpler and more manageable representation of the ecosystem. We used different considerations to assign the species associated with kelp forests of Isla Natividad in FG. First, in order to examine the effect of fisheries on the ecosystem, we classified species of commercial importance in separate FG. This was also done in order to be able to include the future fishing effort of the Cooperative and adjust the model with these real data. This model was created with the intention of being used and interpreted by the Isla Natividad fishing cooperative, allowing for the ability to predict the response of the ecosystem during future scenarios with ecological and human variations. We prioritized the fished species so that it would be easier to visualize and predict their responses to possible scenarios in more detail.

Species were classified based on biological aspects, such as the type of feeding or position and movement within the ecosystem. This was done to reflect the function of the species within the ecosystem. In this way, we wanted to generate a model that resembled as much as possible the structure of the real ecosystem, and that the FG will cover the greatest number of ecosystem functions.

We grouped species into FG using bibliographic sources (Supplementary Materials). In order to represent the broader food web in the model, we added five extra FG, not included in the monitoring: marine birds, marine mammals, phytoplankton, zooplankton and detritus, obtaining a total of 40 functional groups: one FG represented birds, one for marine mammals, 13 for fish, 16 for invertebrates, 8 for algae, and one for detritus. Each of the 40 FG are described through the Ecopath's parameters such as the trophic level (TL), the ecotrophic efficiency (EE), and the production/consumption ratio (P/Q) (values are shown in Table 1).

2.4. Estimated parameters

The model requires estimates of at least three of the four basic parameters: Biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) and/or ecotrophic efficiency (EE) for each FG. The biomass ($g \cdot m^{-2}$) of each functional group was calculated from the *in situ* observations (number of individuals or abundances) and fitted into the model area. As suggested by Heymans et al. (2016), we used the mean of the observed biomass along the 10 years of monitoring, in order to include all recorded species, because some species were adding

Table 1
Functional groups, species, classification criteria and input parameters sources for the kelp forest ecosystem model for Isla Natividad, Mexico. Inputs parameters are Biomass (B), production-Biomass ratio (P/B) and consumption-biomass ratio (Q/B) whilst Trophic level (TL), Ecotrophic Efficiency (EE) and the Consumption Production Ratio (PQ) were calculated by the program. The classification criteria is: 1. FG formed by species of fishing importance, 2. FG of a single species to give better resolution to the model, 3. FG of species of the same genus, 4. FG of species with similar behavior and/or similar feeding, 5. FG added to have a more representative model.

Group name	Classification	Trophic level	Biomass (t·km ⁻²)	P/B (y ⁻¹)	Q/B (y ⁻¹)	EE	P/Q (y ⁻¹)
Sea birds	5	3.39	0.01	0.31	4.50	0.02	0.07
Marine mammals	5	3.72	0.04	0.16	9.00	0.00	0.02
Lingcod	2	3.49	0.13	0.31	1.70	0.01	0.18
Giant sea bass	2	3.74	0.51	0.31	1.70	0.05	0.18
Elasmobranchia	4	3.46	0.22	0.20	2.10	0.01	0.10
Sheepheads	2	2.89	12.36	0.57	3.20	0.06	0.18
Ocean whitefish	2	2.81	1.82	0.18	6.50	0.30	0.03
Cabezon	2	3.10	0.02	0.54	4.50	0.46	0.12
Rockfishe	3	3.12	0.11	0.25	4.15	0.63	0.06
Kelp bass	3	3.13	0.99	0.19	3.70	0.57	0.05
Garibaldi	2	2.44	2.99	0.47	6.20	0.26	0.08
Blacksmith	2	2.92	1.64	1.07	7.30	0.26	0.15
Surfperch/Sargos	4	2.68	1.48	0.57	4.10	0.16	0.14
Opaleye	2	2.32	2.91	0.43	9.70	0.17	0.04
Señoritas	4	2.71	0.66	0.65	5.56	0.00	0.12
Macrocrustaceans	2	2.31	0.43	2.89	9.78	0.54	0.30
Sessile invertebrates	5	2.00	6.87	2.23	8.86	0.82	0.25
Pink abalone	1	2.00	13.43	0.31	3.50	0.89	0.09
Green abalone	1	2.00	6.50	0.19	3.50	0.89	0.05
Other abalone	3	2.00	0.27	0.31	3.50	0.48	0.09
Sea snails	1	2.00	9.60	1.48	5.00	0.48	0.30
Mobile invertebrates	5	2.22	5.28	1.69	9.51	0.70	0.18
Octopus	3	3.03	0.03	1.39	6.76	0.87	0.21
Lobster	1	2.86	2.58	0.99	4.20	0.78	0.24
Sea cucumber	1	2.00	2.66	0.70	4.50	0.81	0.16
Sea star	4	2.72	0.11	0.52	3.24	0.66	0.16
Purple sea urchin	2	2.46	1.26	3.75	12.50	0.68	0.30
Black sea urchin	2	2.22	1.24	3.75	12.50	0.84	0.30
Red sea urchin	1	2.05	1.50	3.75	12.50	0.76	0.30
Small invertebrates	5	2.08	9.88	3.41	14.00	0.88	0.24
Coralline incrusted algae	4	1.00	6.60	5.90	0.00	0.90	
Brown algae	4	1.00	2.32	17.63	0.00	0.90	
Sargassum	3	1.00	0.80	12.00	0.00	0.90	
Green algae	4	1.00	0.05	16.70	0.00	0.90	
Red algae	3	1.00	2.93	17.63	0.00	0.90	
<i>M. pyrifera</i>	1	1.00	85.12	4.71	0.00	0.24	
<i>Eklonia arborea</i>	2	1.00	8.80	7.18	0.00	0.90	
Zooplankton	5	2.00	20.00	9.50	42.50	0.20	0.22
Fitopláncton	5	1.00	35.00	52.00	0.00	0.48	

as the sampling effort increased. Therefore, some species had larger sampling size than others. The P/B value indicates how much of the production of an organism is transformed into biomass.

However, as P/B is difficult to calculate it also corresponds to the total mortality (Z). The Q/B ratio is the most common estimate of the consumption by each group (amount of food ingested) with respect to its own biomass in a determinate time period.

For the model, both of the parameters P/B and Q/B were obtained from the literature, and specifically, in the case of the fish groups, from FishBase (Froese and Pauly, 2016). In the case of the parameters B, P/B and Q/B of the functional groups formed by more than one species they were calculated using weighted averages according to the abundances or densities of each species included in the group in order to obtain a representative value of the group.

The diet matrix (Appendix A) was developed using published papers of studies performed as close as possible to the study area. The model also included catches of the island's commercial species (lobster, yellow and blue abalone, sea cucumber, red urchin, snail, kelp and red algae), provided by the 'Cooperativa de Buzos y Pescadores' of Isla Natividad. These species were included as separate FG in order to be able to simulate changes of total biomass under different fishing scenarios.

2.5. Fishing catches

To estimate catch, we used fishers' reports from 2006 to 2016 expressed in tons per year. These include information for abalone,

lobster, sea cucumber, turban snail and macroalgae. As the fishers do not limit their fishery to the area used for this model, the data were adjusted to the model area (Table 2).

2.6. Ecological indices

To better understand the structure and function of this ecosystem, we used trophic level and flow indices. These include ecosystem throughputs, connectedness and maturity. To generate the trophic web of the ecosystem, Ecopath calculates the trophic levels (TL) of each FG following a predetermined routine and gives the TL value

Table 2
Catch (tons) at Isla Natividad for 2006 and estimation of the fishery area according to species distribution inside the model area.

Fleet number	Specie	Catches (ton·year ⁻¹)	Fished area (km ²)	Fisheries inside the model area (t·km ² ·year ⁻¹)
1	Green abalone	9.99	31.42	0.318
2	Pink abalone	17.98	31.42	0.572
3	Lobster	132.84	309.00	0.430
4	Red algae	24.46	5.08	4.815
5	Snails	39.74	31.42	1.265
6	Sea cucumber	27.24	31.42	0.867
7	<i>M. pyrifera</i>	12.00	5.08	2.362
8	Red sea urchin	34.41	31.42	1.095

which can be fractional (eg: 1.2, 3.5 etc.). Primary producers and detritus are always assigned a value of TL = 1. Consumers are assigned a TL following the formula: $1 + [\text{weighted average of the trophic level of their respective prey}]$ (Christensen et al., 2005).

The total ecosystem throughput is the sum of all system flows, including: total consumption, total export, total flow by respiration and total flow for detritus (Christensen et al., 2005). The value of flow is expressed in $\text{t} \cdot \text{km}^2 \cdot \text{year}^{-1}$.

The connectance index (CI) expresses the relationship between the number of real interactions and the number of possible interactions between the FG of an ecosystem (without considering cannibalism). It is expressed in the following way: $(N - 1)^2$, where N is the number of living groups and is a dimensionless value (Christensen et al., 2005).

The maturity of an ecosystem is not easy to determine, since it depends on many factors such as biomass, the number of functional groups or the interactions between them. However, the maturity of an ecosystem can be estimated through parameters such as the primary production/respiration ratio (P/R), which tends to zero in mature ecosystems, the CI or the total flows of the system (Christensen, 1995). In addition, we estimated mixed trophic impacts (MTI, Ulanowicz and Puccia, 1990) to observe interactions between functional groups and between these and the fishing fleets, as follows:

$$\text{MTI}_{ij} = \text{DC}_{ij} - \text{FC}_{ji}$$

where DC_{ij} is the composition of the diet that expresses how much of group j contributes to the diet of group i ; and FC_{ji} is a term for the composition of the prey, which describes the proportion of predation on j produced by i as a predator. When calculating the term FC_{ji} , fishing fleets are introduced as predators. The values can be positive or negative, depending on whether the change in the biomass of a FG causes an increase or decrease in the biomass of the other FG. In the case of detritus, the term DC_{ij} is 0, while for fishing fleets the “composition of the diet” is obtained by representing how much each group contributes to the catches.

3. Results

The trophic level (TL) of the functional groups (FG) in this system ranged from one, for the primary producers, to 3.8 for the top predator (Giant Sea Bass), with an average \pm SD of 2.3 ± 0.8 (Table 1). The EE varied between 0 and 1. It was close to zero for higher-level predators (for example, Lingcods were 0.01), and close to 1 for lower TL groups. The values of P/Q, which reflect the capacity to convert food into production, ranged from 0.02 for marine birds and mammals, to 0.3 for invertebrates.

The lobster accounts for the larger volume of the commercially important species with annual mean catches over 130 ton per year (Table 2).

Our model estimates suggest the total throughput of the system was $5477.6 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, where 26% of this was the sum of all consumption, 27% was the sum of all exports, 18% was the sum of all respiratory flows and 29% was the sum of all flows into detritus (Table 3). The estimated net system production was $1420 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, and the

production/respiration (P/R) ratio was 2.4, which was related to the maturity of the ecosystem (Christensen, 1995). In addition, to estimate the connectedness within the FG of the model, we calculated the connectance index at 0.15. Fig. 2 shows a graphic representation of the trophic web of the ecosystem, identifying the proportional biomass of each FG and their trophic interactions. This depiction highlights that a large fraction of the ecosystem biomass is in macroalgae and detritus, as well as their invertebrate consumers. The Mixed Trophic Impact matrix shows how the FG interact with each other (Fig. 3). It also shows the direct and indirect impacts that occur among the FG, and between each FG and the fishing fleets. It is evident that the FG are more affected by competition and predation than by the fishing fleets (Fig. 3).

4. Discussion

We generated a realistic food web model for a kelp forest ecosystem using an extensive 10-year monitoring data set with 40 functional groups. The model is a good representation of the island's subtidal ecosystem as it includes substantial local information. Among the research carried out on the west coast of the Baja California peninsula, there are only two food web models that have been developed. One is for estuaries of the Magdalena Lagoon complex (Cruz-Escalona et al., 2013), and another for kelp forests in Bahía Tortugas, approximately 30 km to the south of Isla Natividad (Morales-Zárate et al., 2011). There is also a model for the coral reef at Cabo Pulmo (Frausto, 2012) situated at the tip of the Baja California peninsula. These existing models provide opportunities to compare our results with those previously obtained for kelp forest and other coastal ecosystems of the Baja California Peninsula (Table 4).

First of all, the number of FGs is a very important parameter for understanding the structure of an ecosystem. It can simplify or complicate the representation of the ecosystem. This is essential, especially in highly diverse ecosystems such as kelp forests. In models similar to ours, many authors comprise between 20 and 25 FG (Cruz-Escalona et al., 2013; Frausto, 2012; Morales-Zárate et al., 2011). Compared to other models for the Mexican Pacific, ours has 40 FG, almost double that of others. This has allowed us to represent the ecosystem of Isla Natividad with more detail.

Secondly, the biomass of the FG is also a key parameter for the development of a mass-balanced trophic network model. For many models, biomass is often obtained from the literature or from monitoring efforts of short periods between 1 and 3 years, as in Cruz-Escalona et al. (2013), Frausto (2012), Morales-Zárate et al. (2011) and Ortiz (2008). Our model, on the other hand, used information from 10 years of detailed ecological monitoring. Therefore, the biomass of the FGs are more accurate, as all the species observed during 10 years of monitoring have been included. In addition, the biomass values used for our model were more precise and adjusted to the ecosystem of Isla Natividad, since they were calculated from *in situ* observations at several sampling points around the island. The biomass value, therefore, gives greater reliability in the structure of the model and in the representation of the FG of the ecosystem.

The total system throughput of our model was $5477.6 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (Table 3). This value describes the “size of the whole system in terms of flow” (Ulanowicz, 1986). Comparing our total flow with the Bahía Tortugas kelp forest flow ($553 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$) we can see a huge difference, with our total flow being almost 10 times higher.

A key difference among these three models is the primary producer biomass. In our model, *M. pyrifera* has a biomass of $85 \text{ t} \cdot \text{km}^{-2}$, while in Bahía Tortugas, the biomass of *M. pyrifera* was only $20 \text{ t} \cdot \text{km}^{-2}$, 4 times lower. However, the proportion in which this total flow was distributed in each model has some differences too. In spite of being relatively close, these two ecosystems are subject to different environmental conditions. On one hand, kelp forests are seasonal communities very sensitive to water temperatures fluctuations. Biomass estimates for each model

Table 3
Ecopath model estimations for the Isla Natividad ecosystem.

Parameters	Values	Units
Total system throughputs	5477.6	$\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$
Sum of all consumption	1421.6	$\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$
Sum of all exports	1472.8	$\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$
Sum of all respiratory flows	1005.4	$\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$
Sum of all flows into detritus	1577.2	$\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$
Sum of all production	2727.9	$\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$
Total net primary production/total respiration	2.4	Dimensionless
Connectance Index (CI)	0.15	Dimensionless

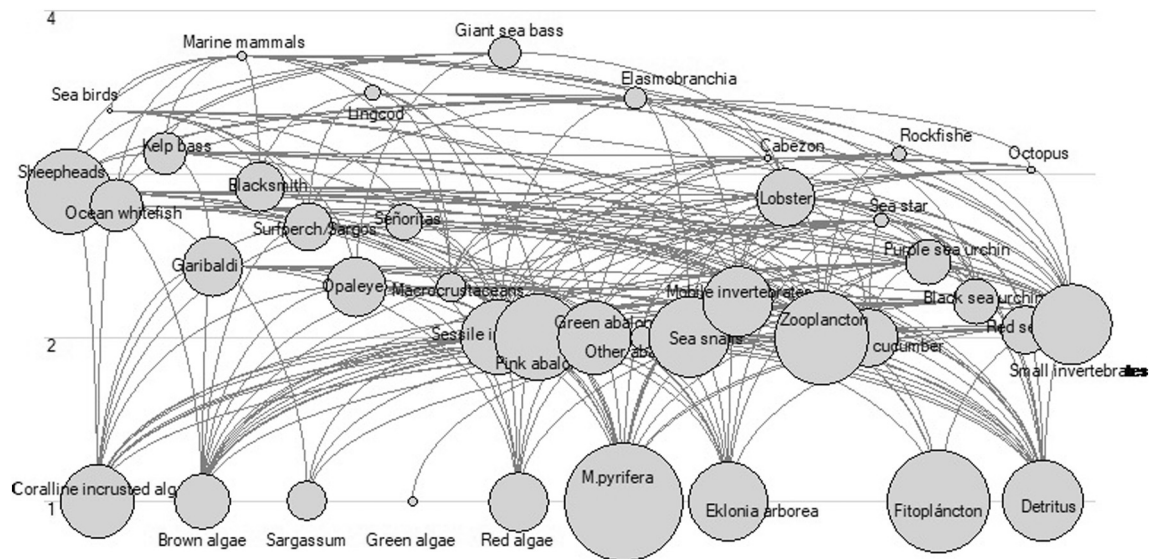


Fig. 2. Flow diagram of Isla Natividad ecosystem. The FG are represented in circles, whose size is proportional to the biomass of the FG. They are distributed along the Y axis according to the trophic levels that Ecopath calculated, and the lines that join the FG with each other are the trophic interactions existing between them.

were from different years, so that may explain the huge difference observed (Steneck et al., 2002). On the other hand, whilst Morales' model is for a semi-protected bay, Isla Natividad is an island subject to much higher environmental fluctuations, such as changes in nutrient concentrations and temperature that influence *M. pyrifera* (Reed et al., 2016).

For our model, total biomass flow was distributed with 26% of biomass towards consumption, 27% towards export out of the system, 18% for respiration and 29% towards detritus. Nevertheless, the total biomass flow for the Bahía Tortugas model was 57% to consumption, 28% to respiration, 14% to detritus and 1% to export out of the system (commercial fishing). The main differences for the flow distribution could be explained by the difference in the amount of primary producers biomass. The highest primary producer biomass at Isla Natividad is redirected as flow to detritus and consumption. In addition, the main producer *M. pyrifera* is a fishing resource, and thus the potential cause of the elevated value for exports in our model.

We also compared our model results with different ecosystem models from the Baja California peninsula, such as the models for the Cabo Pulmo coral reefs and the Bahía Magdalena lagoon complex. Cabo Pulmo showed the highest total flow value with $26,070 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ and a primary producer biomass of $111.9 \text{ t} \cdot \text{km}^{-2}$. Bahía Magdalena lagoon presented a total flow of $3361 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ which is the most similar value to our model. This last model is based on different types of algae as primary producers which add up to approximately $20 \text{ t} \cdot \text{km}^{-2}$ total. However, the flow distributions of both models have the same proportion as our model, where most of the flow goes first to consumption, followed by the respiration, then detritus and then exportation.

The value of the total primary production/respiration ratio (P/R) is generally used as a proxy of the state of maturity of an ecosystem (Christensen, 1995; Table 3). In our study, P/R was 2.4, which suggests that the ecosystem of Isla Natividad has not quite reached a state of complete maturity. This value differs to the one obtained by Morales-Zárate et al., (2011) for the Bahía Tortugas ecosystem, which presented a value lower than our model (1.34). Since both ecosystems are in a nearby area, it is logical that they show a similar maturity. On the other hand, the work of Cruz-Escalona et al. (2013) for Bahía Magdalena had the lowest value (1.14) and Frausto (2012) for Cabo Pulmo showed a higher value (1.9). The differences of the P/R values between these ecosystems and our model might be due to the specific environmental conditions of each ecosystem as they are ecologically different.

However, these differences are minimal, which would indicate that the models are comparable and can be used to study and compare the flow of biomass between these ecosystems.

The connectedness index (CI) is also used as an indicator of the maturity and stability of an ecosystem. According to Christensen et al. (2005) and Cruz-Escalona et al. (2013), an immature ecosystem presents simple linear relationships, which is reflected in a lower CI value. As the ecosystem becomes more mature, its interactions are more complex and therefore the value of CI increases. In our model, the ecosystem presented a value of 0.15, which indicates that there were only 15% of possible ecosystem connections filled (Table 3). The Bahía Tortugas kelp forest model had a value of 0.23 which is the highest of all the models compared. The main difference between both models is the number of FG, which in our model is twice as in Bahía Tortugas model. Since the CI value depends on the number of FG and its composition, the comparison of values between models may be limited (Cruz-Escalona et al., 2013). Ulanowicz and Platt (1985) mention that developing ecosystems have a maximum number of connections even when the number of species increases. For example, they mention that there are some species that appear in small proportions in relatively older and well-organized systems, which do not contribute much to connectedness, since their presence depends on certain resources or they interact with only one or a few species. Therefore, these species will only appear when the ecosystem is mature but their presence does not have a great effect on the number of ecosystem connections. All the other mentioned models presented a smaller number of FG compared to ours, which also could result in a higher value of CI. Accordingly, this occurs with the value obtained by other models for the Mexican Pacific. Both present a higher value than our model with a 0.2 for Cruz-Escalona et al. (2013) and a 0.19 for Frausto (2012) and smaller FG number with 24 and 34 FGs respectively. As we can see, the models with more FG (like this model and Frausto's model) have a lower CI value. With more FG, it is more complicated to establish the interactions between them, which may be why our model had the lowest CI. In summary, each ecosystem has a limited number of connections beyond the species that make up the ecosystem and the number of connections will depend on the development state of the ecosystem. Because of that, and comparing the CI values, we cannot say that our ecosystem is less mature than the others because of the differences in the number of FG. Instead, comparing the difference between FG and CI values, the ecosystems could be in a similar connection state.

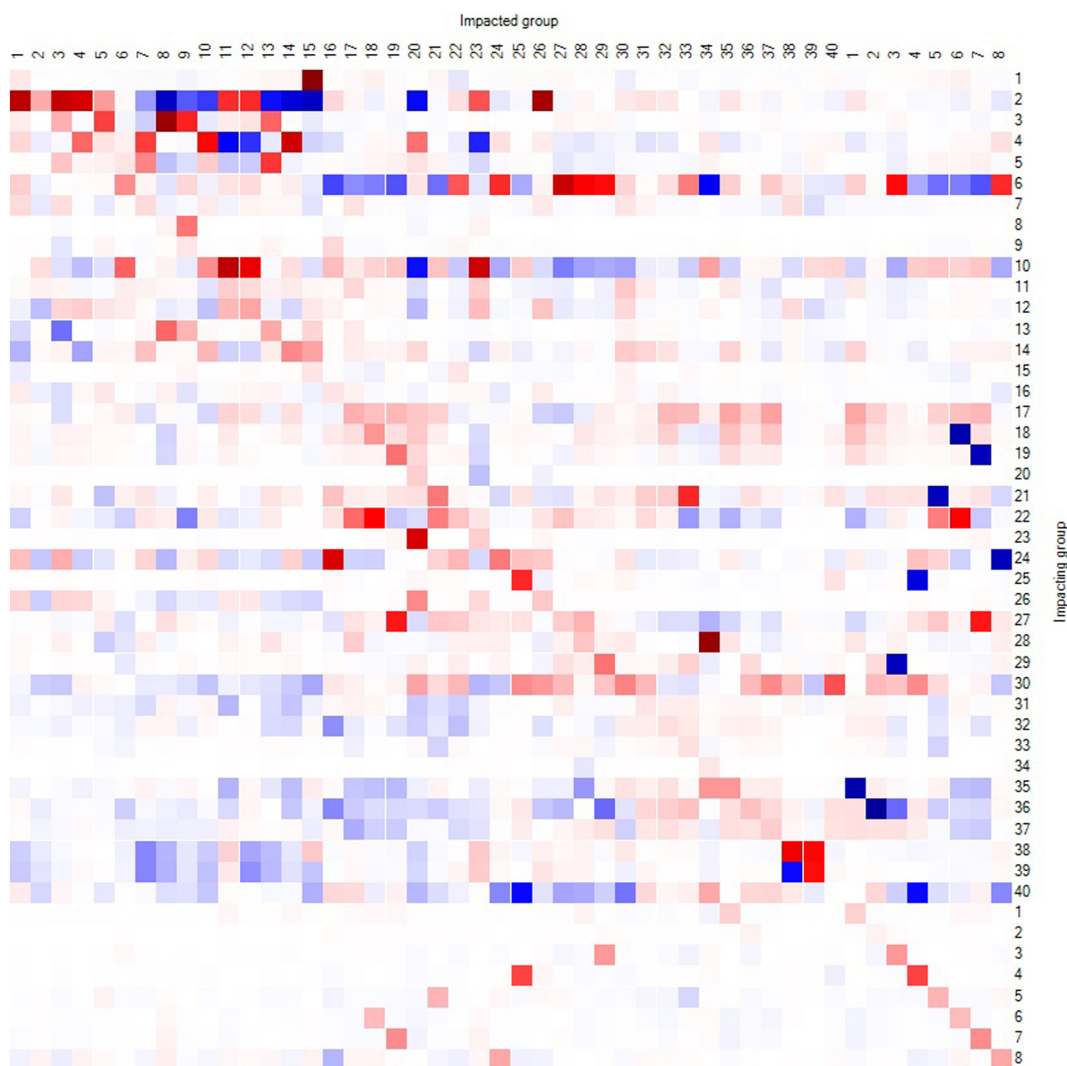


Fig. 3. Mixed Trophic Impact Matrix (MTI) of the Isla Natividad ecosystem. The blue color indicates a positive impact between FG and the red color the negative ones. The intensity of the color corresponds to the intensity of the interaction. The numbers correspond to the FG and the fisheries are included at the end of each axis (from left to right and top to bottom): 1. Birds, 2. Marine mammals, 3. Lingcods, 4. Giant sea bass, 5. Elasmobranchia, 6. Sheepheads, 7. Ocean whitefish, 8. Cabezones, 9. Rockfish, 10. Kelp basses, 11. Garibaldi, 12. Blacksmith, 13. Surfperchs/Sargos, 14. Opaleye, 15. Señoritas, 16. Macrocrustaceans, 17. Sessile invertebrates, 18. Pink abalone, 19. Green abalone, 20. Other abalone, 21. Sea snails, 22. Mobile invertebrates, 23. Octopus, 24. Lobster, 25. Sea cucumber, 26. Sea star, 27. Purple sea urchin, 28. Black sea urchin, 29. Red sea urchin, 30. Small invertebrates, 31. Coralline incrustated algae, 32. Brown algae, 33. *Sargassum*, 34. Green algae, 35. Red algae, 36. *M. pyrifera*, 37. *Ecklonia arborea*, 38. Zooplankton, 39. Phytoplankton, 40. Detritus. The last numbers. Fisheries: 1. Red algae, 2. *M. pyrifera*, 3. Sea urchin, 4. Sea cucumber, 5. Sea snail, 6. Pink abalone, 7. Green abalone, 8. Lobster. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The biomass flow at Isla Natividad showed a pyramid-shaped distribution, where primary producers or lower trophic levels had higher biomass, and this decreased as trophic level increased. For example, the

primary producers such as *M. pyrifera* and *E. arborea* were the FG with the highest biomass, while the top predators such as lingcod or giant sea bass showed lower biomass values. Other trophic network models

Table 4
Comparative of the main Ecopath statistics parameters between Isla Natividad and other models.

	Isla Natividad	Bahia Tortugas ^a	Bahia Magdalena ^b	Cabo Pulmo ^c	Units
Monitoring years	10	2	Bibliographic	1 + bibliographic	
Functional groups	40	23	24	34	
Total system throughputs	5477.6	553	3361	26,070	t · km ² · year ⁻¹
Total flow to consumption	26	57	52	36.6	%
Total flow to respiration	18	28	26	22.4	%
Export out of the system	27	1	3	20.4	%
Total flow to detritus	29	14	19	20.6	%
Mean trophic level	2.28	2.07		2.81	-
Total primary production/total respiration	1.55	1.34	1.14	1.9	t · km ² · year ⁻¹
Connectance index	0.156	0.23	0.2	0.19	-

^a Morales-Zárate et al. (2011).

^b Cruz-Escalona et al. (2013).

^c Frausto (2012).

generated in rocky environments with macroalgae also follow this type of distribution, such as the work of Morales-Zárate et al. (2011), Cruz-Escalona et al. (2013) and Beas-Luna (2014). This structure is the most common due to the rule of energy transfer, where only 10% of the energy is transferred from one trophic level to the next (Odum, 1963). Therefore, those groups that are at lower trophic levels have more biomass to allow energy to reach the highest trophic level. Other trophic structures, with large fractions of biomass at top trophic levels have also, however, been empirically described and modelled for both terrestrial and marine ecosystems (McCauley et al., 2018; Stevenson et al., 2007; Woodson et al., 2018), typically for unexploited systems. Thus, the question of whether the trophic structure described here is characteristic of kelp forests and other algal dominated marine ecosystems, or the result of decades of intensive exploitation, is still unanswered.

The Mixed Trophic Impact analysis shows the positive or negative interactions between the FG of the ecosystem. First, we observed how all the FG had some negative self-impact (kelp bass), which could be interpreted as intraspecific competition for resources. The most obvious positive and negative direct interactions are those of feeding between predators and prey (Sheepheads & Purple sea urchin), determined by the values of the diet matrix. Negative impacts between groups were also observed due to the competition involved in sharing the same prey (Purple sea urchin & Red sea urchin). Within the interactions between groups, there is also a positive relationship between two preys that share the same predator (Garibaldi & Blacksmith; Abrams and Matsuda, 1996). A positive indirect impact on the other hand, occurred where a predator indirectly impacts the prey, increasing its abundance because its predator is reduced through its own predation (e.g., trophic cascades). For example, sea urchins prey on macroalgae, that in turn are preyed upon by the sheephead fish. Therefore, the presence of sheephead favors the presence of macroalgae by reducing the predation pressure that the urchins exert on its prey.

Fishing fleets showed a negative direct impact on the exploited invertebrate species. However, we can also observe some positive indirect impacts on other FGs. This happens when the fleets are fishing a predator which indirectly and positively impacts to that prey. Another type of response observed was that each of the exploited species had a direct positive impact on the fleets that fish them. This interaction observed between the fleets and the FG of the ecosystem is very similar to that obtained by Morales-Zárate et al. (2011) for Bahía Tortugas. The ecosystems of both places are similar, and in both cases, the fishing fleets focus on invertebrates and algae. Therefore, it is expected that the results of the relationships between the fleets and the FG of the ecosystem are comparable.

The interactions of the fishing fleets with the FG can be compared with the results obtained by Beas-Luna (2014), who also generated a mass-balanced food web model for kelp forests in California. He observed the response of the ecosystem to different types of fishing mortality, varying also the type of organisms affected by the fisheries. He changed the fishing mortality of organisms of high trophic levels to organisms of low trophic levels. When the fishery was focused on high trophic level organisms, there was a small change in the biomass of lower trophic levels. However, when focusing fishing mortality on lower trophic level organisms, no changes were observed in the biomass of other FG. This result agrees with the results of this model, in which fishing effort is based on low trophic level organisms. Agreeing with the results obtained in Beas-Luna (2014), our Mixed Trophic Impact graphic did not show any relevant indirect impacts by the fleets towards other FG. In Beas-Luna's (2014) work, fishing mortality affects fish species of low trophic level, but not invertebrates as is the case of this model, however, the result is the same. Therefore, we can conclude that in these cases, fishing lower trophic level organisms has a less visible impact on other organisms of the ecosystem or it needs more time to be appreciated when compared to fishing higher trophic level organisms.

5. Conclusions

This work presents a mass-balanced food web model for the kelp forest ecosystem of Isla Natividad. This model was developed to better understand the structure and function of this ecosystem near its southern limit of its distribution. Climate change and populations at their limits of distribution are of great interest to the ecological and evolutionary community and therefore we believe that having a model for a kelp forest near its southern limit of distribution is quite relevant to obtain a good understanding of these ecosystems and understand future scenarios with similar conditions. This model describes the distribution of biomass in the different functional groups and trophic levels in this system. It has allowed us to better understand the most relevant interactions with the fisheries and other human impacts in this region. In addition, we estimated energy flow within functional groups, as well as the direct and indirect interactions between them and between the fishing fleets. This has led to a greater understanding of a complex coastal ecosystem with great potential to inform conservation measurements and better management practices. This model provides the basis for acquiring better knowledge of this region's ecosystems. In spite of providing descriptive information about the ecosystem, it is the first necessary step to be able to carry out further studies. In this work, we generated the base model of Island Natividad, which will be able to be used *a posteriori* for multiple comparisons or future predictions, including monitoring data that are still being collected every year.

Here in, we unified the two different techniques of ecological monitoring and models that are often used to improve the knowledge of the structure of ecosystems. We generated a model based on real data obtained through a 10-year ecological monitoring effort, allowing the results of the model to be more precise and realistic. It is very important to note that models taking into account long-term monitoring can be very useful to answer questions that would be very time consuming and expensive to answer with only monitoring data. The model was built with the idea that the Cooperative, the scientific community or governmental institutions, can use the model to explore the changes that might occur in the ecosystem under different scenarios. Environmental disturbances such as storms, heatwaves, hypoxia events and ocean acidification will continue to increase in frequency and intensity due to climate change. This model provides a valuable tool for exploring drivers of change in these vulnerable marine ecosystems and the fisheries they support.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2018.e00091>.

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