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Modeling trophic flows in the wettest mangroves of the world: the case of Bahía Málaga in the Colombian Pacific coast

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Abstract The structurally most developed Neotropical mangrove forests are found along the southern and central macrotidal Colombian Pacific coast. This extremely rainy area ($>7{,}000$ mm year^{-1}) is sparsely populated and sustains a relatively small artisanal fishery. In this article, we present an ecosystem (trophic) model, built using Ecopath with Ecosim, containing 18 functional groups of a representative mangrove area of this coast. Similar to other mangrove ecosystem models, mangroves contribute most (96%) to total system biomass, providing the primary food source for other important compartments (e.g., crabs). However, most of the mangrove litterfall is constantly washed away by tidal currents, a possible reason for the very low mean transfer efficiencies to higher trophic levels and low biomass of epifauna and nekton found, compared with other Neotropical mangroves. Fish biomass is dominated by zoobenthivores (snappers, catfishes) and detritivores (mullets) which represent, together with mangrove cockles, the target resources of a low trophic level-based fishery. Very low salinities throughout the year may contribute to an impoverished community of primary and secondary consumers that is able to withstand but not flourish under these conditions. This mangrove ecosystem may be highly vulnerable to overexploitation according to the low energy reserve (overhead) of the system.

Keywords Ecosystem modeling · Tropical mangroves · Benthic productivity · Tropical Eastern Pacific · Colombia

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Introduction

Mangroves typically dominate tropical coastlines with humans benefiting from them since ancient times. Despite accelerated losses in some regions (Hamilton & Casey, 2016), mangroves worldwide are still providing the many ecosystem services that have been acknowledged in the recent decades (e.g., coastline protection against storms and hurricanes, carbon storage, food provision, climate stabilization). However, since developmental activities in coastal areas (e.g., urbanization, harbor construction, construction of aquaculture facilities, and landfilling for

agriculture) imply the need for alterations of the coastline, there is a need to understand the way mangroves and their associated ecosystems function to predict how anthropogenic actions may affect the provision of these ecosystem services.

Two biogeographical regions of mangroves are commonly identified in the literature: (1) the more diverse Indo-West Pacific (IWP) region and (2) the less diverse Atlantic-East Pacific (AEP) region (Duke et al., 1998). Eastern Pacific mangroves are concentrated in the Panama Bight eco-region (ca. 5% of the world mangroves and almost half the mangroves in the Eastern Pacific) due to suitable environmental conditions (e.g., high precipitation, large river deltas, macro- and meso-tidal regimes). The extreme precipitation regime in the Central Pacific coast of Colombia makes these mangroves probably the wettest in the world (Castellanos-Galindo et al., 2015; Fig. 1). This condition is reflected at the regional level by the lowest salinity values in the coastal areas of the entire Tropical Eastern Pacific region (from Mexico to northern Peru; Fiedler & Talley, 2006; Alory et al., 2012). Under these conditions, mangrove forests thrive (developing very dense and tall trees up to 40–50 m), but associated faunal communities seem to be depauperate both in species richness and biomass (Cantera et al., 1999; Castellanos-Galindo & Krumme, 2013).

Useful approaches for holistic descriptions of food web dynamics in marine systems such as mangroves

include mass balance models, which are based on ecological network analyses (Christensen & Pauly, 1992). The most widely used approach of this type for marine and aquatic ecosystems is Ecopath with Ecosim (EwE; >500 ecosystem models, Villasante et al., 2016). EwE uses a set of equations to parameterize its models that describe the production and the energy balance of each of a set of a priori-defined nodes (representing functional groups) within an ecosystem (Christensen et al., 2008). The use of a common framework to understand trophic links and dynamics is a major strength in EwE that now allows global food web comparisons to bring insights into the generality of marine ecosystem functioning (e.g., Christensen et al., 2014; Heymans et al., 2014; Kolding et al., 2015).

The use of EwE in mangrove ecosystems has helped us to understand the pivotal role that these ecosystems play in sustaining adjacent artisanal fisheries (e.g., North Brazil; Wolff et al., 2000; Scharler, 2011). For the AEP region, at least 10 mangrove estuarine trophic models using EwE exist, allowing for the comparison of ecosystems' functioning for systems with very different environmental characteristics (e.g., dry vs. rainy systems) within this biogeographical region.

Here we aim at (1) understanding the trophic linkages of a relative pristine mangrove ecosystem subject to particular environmental conditions in the Tropical Eastern Pacific region using a mass-balance model (EwE) and (2) comparing the resulting model to

Fig. 1 Selected mangrove localities in the world with their annual precipitation values from the lowest to highest
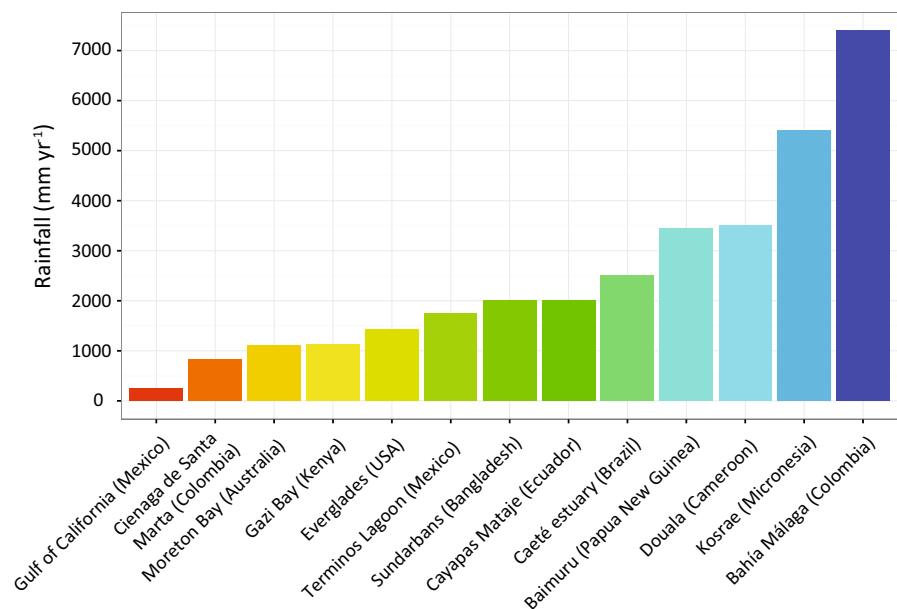
that constructed for other mangrove ecosystems in the AEP region. By doing so, we intend to identify differences and generalities of mangrove ecosystem functioning in this biogeographical region.

Materials and methods

Study area

Bahía Málaga is a bay system located in the central Colombian Pacific coast and in the southern part of the Tropical Eastern Pacific region (Fig. 2). The area is considered an estuary despite not having major rivers that drain into the coast. However, a rainfall regime reaching 7,000 mm year^{-1} causes surface salinity to stay below 28, even during dry seasons (January–April). Mangrove forests (ca. 5,000 ha) grow in the inner side of the bay and are dominated by *Rhizophora*

spp. trees attaining up to 40 m in height. The human population inside the bay is very small (<500 persons), with most villagers depending on fishing to sustain their livelihoods. Fishing is artisanal and mainly practiced using gillnets (2½″–6″ mesh sizes). Mangrove cockles [*Anadara tuberculosa* (Sowerby, 1833)] are also manually harvested, and this resource is considered overexploited (Lucero et al., 2012). In contrast to Ecuador and Peru, the semi-terrestrial mangrove crab [*Ucides occidentalis* (Ortmann, 1897)] is commonly not exploited, being only occasionally collected by locals during the mass mate-searching events (usually taking place in May–June, authors' unpublished data) and consumed locally (subsistence).

Model parameterization

EwE allows users to construct a food web composed of different functional groups (model compartments that
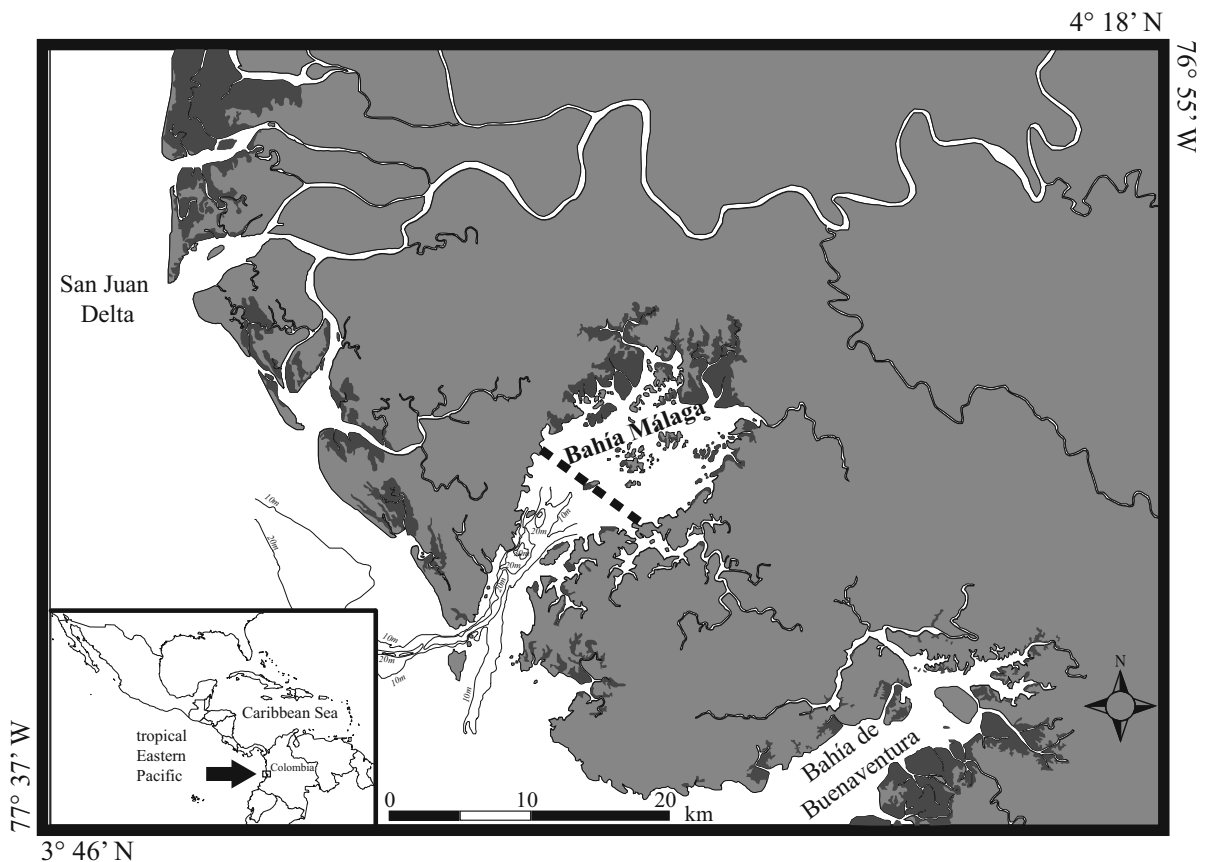

Fig. 2 Map of Bahía Málaga in the central coast of the Colombian Pacific (Tropical Eastern Pacific). Mangrove areas are represented in *dark gray*. The *black dashed line* approximately represents the ecosystem model area (interior of Bahía Málaga)

can be either single species or groups) that are trophically connected. Two equations are used to parameterize an EwE model (Christensen & Walters, 2004): the first describes the production of each group (1), and the second, the energy balance of each group (2):

$$\begin{aligned} \text{Production} = \ & \text{catch} + \text{predation mortality} \\ & + \text{net migration} \\ & + \text{biomass accumulation} \\ & + \text{other mortality} \end{aligned}$$

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

where P/B is the production-to-biomass ratio of group i, B_i is the biomass of group i, Y_i is the total fishery catch of group i, $(Q/B)_j$ is the consumption-to-biomass ratio of each predator j, DC_{ji} is the proportion of group i in the diet of predator j, E_i is the net migration rate (emigration–immigration), BA_i is the biomass accumulation rate for the group i, EE_i is the ecotrophic efficiency, and $(1 - EE_i)$ is mortality other than the one from predation and fishing.

The second equation ensures energy balance within each functional group:

$$\begin{aligned} \text{Consumption} = \ & \text{production} + \text{respiration} \\ & + \text{unassimilated food} \end{aligned}$$

$$Q_i = P_i + R_i + GS_i \times Q_i, \qquad (2)$$

where Q_i is the consumption of group i, P_i is the sum of production of group i, R_i is the respiration of group i, and $(GS_i \times Q_i)$ is the unassimilated food of group i.

With these two equations, the production of each group is linked to the consumption of all groups. The predation mortality term in Eq. 1 links the different functional groups with each other. EwE then solves a system of linear equations for each group in the system, estimating the missing parameters (Christensen et al., 2008).

Data input

Data used to construct the mass balance model developed here are drawn primarily from the published research or from supplemental data collected from the authors over the last 10 years. Supporting studies are listed in the Electronic Supplementary Material (Appendix Table 1). Therefore, the model presented here is

assumed to be a representation of annual average biomasses and trophic flows of this system from 2006 to 2016. To examine the possible effects of model construction on model's final outputs and statistics, two different models were constructed: one including mangroves as a functional group and another one which incorporates the contribution of mangrove litterfall into the detritus compartment. The latter model is presented in Table 2 and Fig. 1 in the Appendix—Electronic Supplementary Material. Model compartments (functional groups) were a priori defined based on the authors' knowledge on the ecology and biology of mangrove organisms of the area. For each functional group defined, five input parameters were collected: (1) biomass—B, (2) production rate per unit of biomass—P/B, (3) consumption rate per unit of biomass—Q/B, (4) diet composition—DC, and (5) fisheries catch rates—Y. P/B, Q/B, and catch rates are expressed in a per-year basis. Diet information for the fish groups came from the published (Ramirez-Martínez et al., 2016) and unpublished information from the authors (Castellanos-Galindo, unpublished data). Diet data from other functional groups were collected from the literature (see Table 3). In cases where input parameters for a certain functional group were not available, data from adjacent mangrove systems were used. These adjacent ecosystems were primarily located in the Colombian Pacific coast (Buenventura and Guapi), but values from the Caeté system in North Brazil were also taken. All these mangrove systems share several environmental similarities with Bahía Málaga (similar estuarine mangrove type, tidal regime, high precipitation; see Table 1 and Supplementary Material). Other parameters included in the two EwE master equations (e.g., migration, other mortality, and respiration) are calculated after solving the set of linear equations (see Christensen et al., 2008). Unassimilated food is set in EwE as 20% according to Winberg (1956).

Uncertainty associated with the input values of the model was assessed based on the pedigree index in EwE. The index that ranges between 0 and 1 takes into account the quality of all data (biomass, P/B, Q/B, and diet values) entered to calculate an overall index value.

Model statistics and indices

The flows within the ecosystem, in terms of the total production, consumption, respiration, exports, imports, and flow to detritus, were quantified to represent the

Table 1 Functional groups and principal species selected for the mangrove ecosystem model of Bahía Málaga, tropical Eastern Pacific

Functional group	Species
1. Seabirds	*Egretta caerulea, Numenius phaeopus, Butorides striatus, Nyctanassa violacea, Actitis macularius, Tringa semipalmata, Calidris mauri, Ardea alba, Charadrius semipalmatus*
2. Piscivore fish	*Caranx caninus, Caranx sexfasciatus, Strongylura scapularis*
3. Zoobenthivore fish	*Lutjanus argentiventris, Sciades seemanni, Sphoeroides rosenblatti, Centropomus armatus* and 24 more species
4. Zooplantivore fish	*Lile stolifera, Atherinella serrivomer, Chloroscombrus orqueta*
5. Herbivore-phytoplankton fish	*Opisthonema medirastre*
6. Detritivore fish	*Diapterus peruvianus, Mugil cephalus, Poeciliopsis turrobarensis*
7. Mollusks	*Littoraria* spp, *Thaisella kiosquiformis,*
	Cerithidea mazatlanica, Theodoxus luteofasciatus
8. Mangrove cockles	*Anadara tuberculosa*
9. Mangrove crabs	*Aratus pacificus, Goniopsis pulchra, Sesarma* spp., *Armases occidentale*
10. Fiddler crabs	*Leptuca oerstedi, Petruca panamensis, Leptuca tenuipedis, Leptuca umbratila*
11. Shrimps and other benthic crustaceans	*Alpheus* spp., *Panopeus* spp, *Petrolisthes zacae, Salmoneus malagensis, Eurypanopeus transversus, Axianassa darrylfelderi*
12. Semi-terrestrial mangrove crab	*Ucides occidentalis*
13. Zooplankton	Copepoda (Orden Calanoida and Poecilostomatoida), Chaetognatha (Order Aphragmophora), Eumalacostraca (Order Isopoda and Decapoda),
14. Macroalgae	*Bostrychia calliptera, Catenella*
	impudica, Boodleopsis verticillata, Caloglossa leprieurii
15. Microphytobenthos	
16. Phytoplankton	Diatoms (*Coscinodiscus* spp., *Thalassiosira* spp.), Dinoflagellates (*Gonyaulax* sp., *Ceratium* sp.),
17. Mangroves	*Rhizophora* spp., *Pelliciera rhizophorae, Mora oleifera*

mangrove ecosystem structure (Ulanowicz, 1986). A series of indices that describe community energetics, energy cycling, and system organization are calculated in EwE based on Odum (1969) and Ulanowicz (1986). Of special relevance are the following indices: (1) total system throughput (the sum of all flows within the system: consumption, exports, respiratory flows, and flows into detritus) provides a measure of the ecosystem size; (2) Finn's cycling index (Finn, 1976) is the amount of system flows that are recycled in the food web; (3) Relative Ascendency (A/C) is a measure of ecosystem development; (4) Relative overhead (O/C) is a measure of the ecosystem's "strength in reserve" to be used when experiencing unexpected perturbations; and (5) mean ecotrophic efficiency is the efficiency of energy transfer between trophic levels. These and other similar indices, as explained in Christensen et al. (2008), were calculated, compared, and discussed for the two models (with and without mangroves as functional group).

In addition, to better represent flows between trophic levels, a Lindeman spine representation was constructed. This representation shows the net amount of flows that each trophic level receives from the preceding one and also the amount that each trophic level creates for respiration, exports, and catches, and flow to detritus (Ulanowicz, 1995). Impacts within the food web were analyzed with the mixed trophic impact (MTI) routine in EwE. MTI quantifies the impacts that a theoretical change of a unit in the biomass of a functional group would have on any other group within the ecosystem's food web (Christensen et al., 2008). Through this routine, indirect trophic impacts in the food web may be detected, indicating decreases or increases in the biomass of an affected functional group. Derived from the MTI, EwE further calculates a "keystoneness index—KS_i" (Libralato et al., 2006), which is high for functional groups with relative low biomass but large effects on the food web structure of

Table 2 Input data for the Ecopath model of Bahía Malaga, central Colombian Pacific coast in the Tropical Eastern Pacific region

Trophic compartment	Biomass (ton km^{-2})	P/B (years^{-1})	Q/B (years^{-1})	Source/reference
1. Birds	0.02	0.30	60.0	Morales-Zuñiga (1998), Wolff et al. (2000)
2. Piscivore fish	0.06	0.70	4.00	Castellanos-Galindo & Krumme (2013), Froese & Pauly (2016)
3. Zoobenthivore fish	0.50	0.86	12.9	Castellanos-Galindo & Krumme (2013), Froese & Pauly (2016)
4. Zooplanktivore fish	0.15	2.57	35.9	Castellanos-Galindo & Krumme (2013), Froese & Pauly (2016)
5. Herbivore-phytoplankton fish	0.04	3.48	29.2	Castellanos-Galindo & Krumme (2013), Froese & Pauly (2016)
6. Detritivore fish	0.50	1.10	4.27	Castellanos-Galindo & Krumme (2013), Froese & Pauly (2016)
7. Mollusks	6.68	1.00	4.00	Universidad del Valle (field campaigns 2015–2016), Koch (1995, 1999)
8. Mangrove cockles	1.32	1.76	10.0	Lucero et al. (2012)
9. Mangrove crabs	1.12	2.00	11.0	Universidad del Valle (field campaigns 2015–2016)
10. Fiddler crabs	0.17	5.5	95.0	Universidad del Valle (field campaigns 2015–2016), Koch (1999)
11. Shrimps and benthic crustaceans	0.60	8.00	22.0	Universidad del Valle (field campaigns 2015–2016), Koch (1999)
12. *Ucides occidentalis*	11.83	0.250	14.0	Universidad del Valle (field campaigns 2015–2016); Rademaker (1998)
13. Zooplankton	4.00	40.00	160	
14. Macroalgae	117.5	10.5		Peña-Salamanca (2008)
15. Microphytobenthos	0.50	120		
16. Phytoplankton	6.48	252.2		Ramírez et al. (2006)
17. Mangroves	3,392	0.11		Castañeda-Moya et al. (2013), Monsalve et al. (2015)
18. Detritus				

Assumptions: the total area of the model is 165 km^2; of this area, 50 km^2 are mangroves, and the rest (115 km^2) are estuarine waters. *Ucides occidentalis* was assumed to live only in 25% of the mangroves

the ecosystem. Functional groups with KS_i values close to or higher than zero are usually considered keystone.

System characteristics and ecological network indices of the model were compared with EwE models developed for five other estuarine mangrove systems in the Neotropics (Eastern Pacific and Western Atlantic regions). Indices used for comparisons were those identified in Heymans et al. (2014) as robust to model construction.

Results

Trophic flows, trophic levels, biomasses, ecotrophic efficiencies, and catches for functional groups are shown in Table 4 and Fig. 3. Mangroves comprise

95.7% of the system biomass followed by macroalgae (3.3%) and the semi-terrestrial mangrove crab *U. occidentalis* (0.3%). The biomasses of the first- and second-order consumers (i.e., trophic level (TL) 2 and higher) are extremely low, in all cases not exceeding 1% of the total biomass within the system (Table 4; Fig. 3). The highest TL observed in this system is 3.8 (piscivore fishes). Most of the consumer's biomass is concentrated in nine functional groups from TLs 2.0–2.5 (Fig. 3).

The total system throughput, that is the sum of all flows within the system (i.e., consumption, exports, respiratory flows, and flows into detritus) and provides a measure of the ecosystem size, is 7,042.9 t km^{-2} year^{-1}. Overall transfer efficiency between trophic levels is very low (3.5%) mostly due to a very low transfer efficiency to TL 2. This is also reflected in the

Table 3 Diet composition matrix of the mangrove system in Bahía Málaga in the tropical Eastern Pacific

Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Seabirds													
2. Piscivore fish	0.025												
3. Zoobenthivore fish	0.020	0.500	0.030										
4. Zooplantivore fish	0.150	0.200	0.030										
5. Herbivore-phytoplankton fish	0.070		0.010										
6. Detritivore fish	0.020	0.300	0.030										
7. Mollusks	0.115		0.250				0.100						
8. Mangrove cockles			0.100										
9. Mangrove crabs	0.050		0.250										
10. Fiddler crabs	0.300		0.100										
11. Shrimps and other benthic crustaceans	0.200		0.100	0.050			0.100						
12. *Ucides occidentalis*	0.050		0.100										
13. Zooplankton				0.850	0.100		0.050						0.100
14. Macroalgae							0.300		0.200		0.200		
15. Microphytobenthos						0.300	0.300	0.500		0.700	0.300		
16. Phytoplankton				0.100	0.900			0.500			0.300		0.800
17. Mangroves									0.600			1.000	
18. Detritus						0.700	0.150		0.200	0.300	0.200		0.100
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

This matrix represent the proportion of functional groups within the diet of another functional group and is based on examination of stomach contents (own data and diet studies found in the literature)

Lindeman spine representation, showing that TL 1, including detritus, generates the majority of the total system throughput (88.0%, Fig. 4). Exports as catches are concentrated in the TL 2 (Fig. 4). This is confirmed by an extremely low value (0.000084) for the gross efficiency (catch/net primary production) of the fishery, and a low mean TL of the catch (2.16, Table 5). These results reflect the fact that the artisanal fishery mainly focuses on mangrove cockles and detritivore fish (mostly mullets) on the first-order consumer level. The mixed trophic impact analysis indicates a positive effect of mangroves, phytoplankton, and microphytobenthos on most functional groups. In contrast, macroalgae in this system seem to play a minor role impacting only a few functional groups. Zoobenthivore fish impact negatively most of the other functional groups (e.g., mollusks, mangrove cockles, mangrove crabs, fiddler crabs, shrimps/benthic crustaceans, U. occidentalis), which is due to its wide diet breadth (Fig. 5). Keystone groups, i.e., having low biomasses but a structuring role in the food web of Bahía Málaga (Fig. 6), are phytoplankton

(keystoneness index (KS_i) = −0.076), birds (KS_i = −0.106), and zoobenthivore fish (KS_i = −0.124).

The pedigree index obtained for the model is relatively high (0.600) mainly due to the use of data collected directly in the study system or data used from a similar system in the Neotropics (e.g., the Caeté Estuary in Brazil; Wolff et al., 2000).

Discussion

The model presented here is the first attempt to understand the trophic flow structure of a mangrove ecosystem within the Panama Bight mangrove ecoregion in the Tropical Eastern Pacific. The results reveal a surprisingly low productive system that at the same time has very little human interventions (low human population density, few artisanal fisheries, and small catches). The system studied lies probably within the rainiest area where mangroves occur in the world. Likely due to this feature, mangrove trees develop appreciably (trees of >35 m height), and

Table 4 Input (in bold) and output parameters of the mangrove system in Bahía Málaga in the Tropical Eastern Pacific

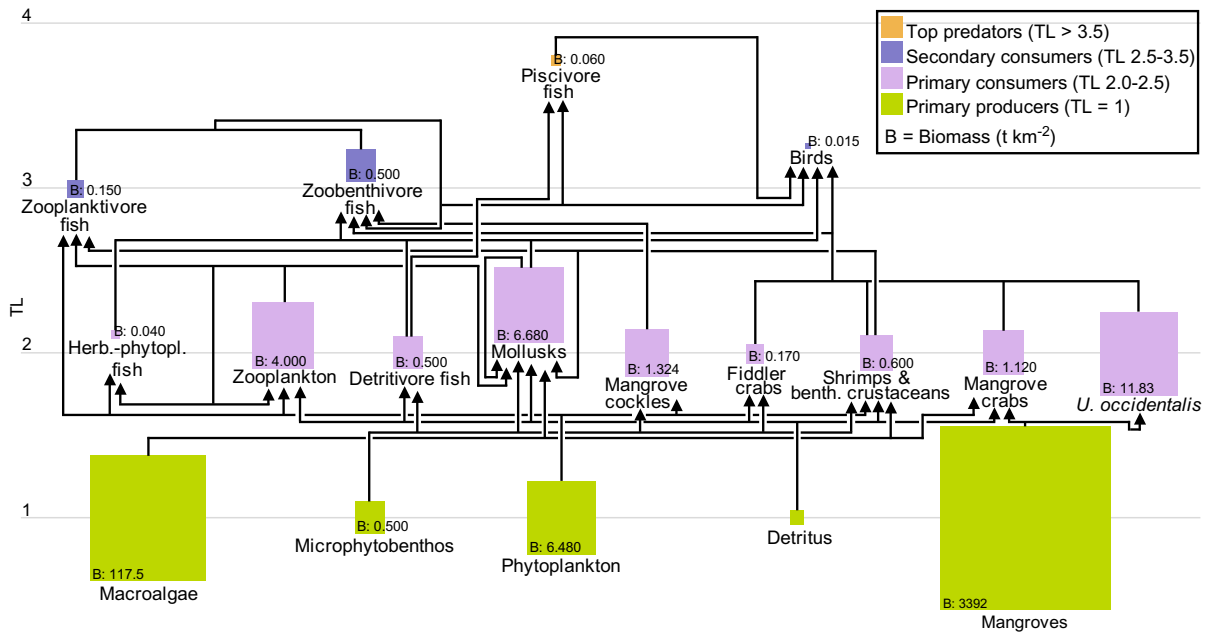| Trophic compartment	Trophic level	Biomass (ton km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE$_i$	GE$_i$ (production/ consumption)	Catch (year^{-1})	F$_i$	M0$_i$ (other mortality) (year^{-1})	M2$_i$ (predation mortality) (year^{-1})
1. Birds	3.256	**0.0150**	**0.30**	**60**	0.000	0.005			0.300	
2. Piscivore fish	3.767	**0.06**	**0.70**	**4.0**	0.869	0.175	**0.014**	0.233	0.0917	0.375
3. Zoobenthivore fish	3.136	**0.500**	**0.86**	**12.9**	0.810	0.067	**0.017**	0.034	0.163	0.663
4. Zooplanktivore fish	2.994	**0.150**	**2.570**	**35.9**	0.977	0.072			0.0600	2.510
5. Herbivore-phytoplankton fish	2.111	**0.04**	**3.484**	**29.2**	0.918	0.119		0.010	0.287	3.188
6. Detritivore fish	2.000	**0.500**	**1.095**	**4.273**	0.664	0.256	**0.080**	0.160	0.368	0.567
7. Mollusks	2.284	**6.680**	**1.000**	**4.000**	0.657	0.250			0.343	0.657
8. Mangrove cockles	2.000	**1.324**	**1.760**	**10.00**	0.348	0.176	**0.166**	0.125	1.147	0.487
9. Mangrove crabs	2.000	**1.120**	**2.000**	**11.00**	0.740	0.182			0.520	1.480
10. Fiddler crabs	2.000	**0.17**	**5.5**	**95.00**	0.979	0.058			0.118	5.382
11. Shrimps and benthic crustaceans	2.000	**0.60**	**8.000**	**22.00**	0.785	0.364			1.723	6.277
12. *Ucides occidentalis*	2.000	**11.83**	**0.250**	**14.00**	0.233	0.018			0.192	0.0583
13. Zooplankton	2.111	**4.000**	**40.00**	**160.00**	0.438	0.250			22.49	17.51
14. Macroalgae	1.000	**117.5**	**10.50**		0.011				10.39	0.112
15. Microphytobenthos	1.000	**0.500**	**120.00**		0.509				58.92	61.08
16. Phytoplankton	1.000	**6.480**	**252.22**		0.321				171.3	80.89
17. Mangroves	1.000	**3,392**	**0.11**		0.464				0.0590	0.0510
18. Detritus	1.000				0.028					

Fig. 3 Flow diagram of the estuarine mangrove system of Bahía Málaga in the Tropical Eastern Pacific as represented by its functional groups. The area of functional group's boxes is scaled to the group's biomass (B), and the y-axis describes the trophic level (TL) as calculated by EwE

Fig. 4 Lindeman spine representation of trophic flows (t km^{-2} year^{-1}) and biomasses for the mangrove system in Bahía Málaga in the Tropical Eastern Pacific region. *P* primary producers, *D* detritus, *TST%* total system throughput, *TE* transfer efficiency
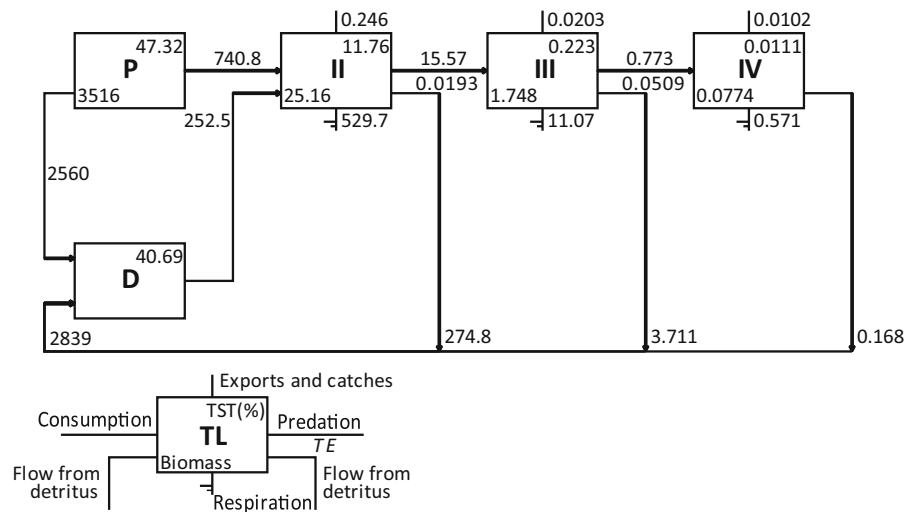
primary producer's biomass is high (i.e., mangroves and macroalgae). However, secondary production is extremely low, with the mean transfer efficiency of the entire system and the Finn cycling index being among the lowest reported in any EwE model (see Scharler, 2011; Heymans et al., 2014; and Table 6, for system comparisons). Low transfer efficiencies indicate that primary production, especially from macroalgae, is poorly integrated into the rest of the food web (see, e.g., mixed trophic impacts of these groups in Fig. 5). The fact that most of the throughput of the system is not being cycled within the system, as revealed by these indexes, could explain in part the system's low secondary production. In addition, the relative isolation of the Eastern Pacific with respect to other marine biogeographical provinces may play a role in the depauperate nature of benthic and nektonic communities as has been observed in stream communities of

Table 5 Summary statistics of two Ecopath with Ecosim (EwE) models for the Bahía Málaga mangrove system in the Tropical Eastern Pacific (with and without mangroves as functional group)

Parameter	Model with mangroves	Model with mangrove litterfall in detritus
Sum of all consumption (t km^{-2} per year)	903.529	903.529
Sum of all exports (t km^{-2} per year)	**2,759.417**	**2,386.351**
Sum of all respiratory flows (t km^{-2} per year)	541.332	541.332
Sum of all flows into detritus (t km^{-2} per year)	**2,838.592**	**2,638.538**
Total system throughput (t km^{-2} per year)	**7,042.871**	**6,469.750**
Sum of all production (t km^{-2} per year)	**3,482.241**	**3,109.175**
Mean trophic level of the catch	2.159	2.159
Gross efficiency (catch/net primary production, %)	**0.000084**	**0.000095**
Calculated total net primary production (t km^{-2} per year)	**3,300.749**	**2,927.683**
Total primary production/total respiration	**6.097**	**5.408295**
Net system production (t km^{-2} per year)	**2,759.417**	**2,386.351**
Total primary production/total biomass	**0.932**	**19.3337**
Total biomass/total throughput (per year)	**0.503**	**0.023405**
Total biomass (excluding detritus) (t km^{-2})	**3,542.939**	**151.429**
Total catches (t km^{-2} per year)	0.2774	0.2774
Connectance index decrease	**0.177**	**0.1960754**
System omnivory index	0.065	0.065
Primary production required/catch (PPR/catch)	137.9	137.9
Ascendency (%)	**46.49**	**44.03**
Finn's cycling index (%) decrease	**1.430**	**2.180**
Pedigree index	**0.600**	**0.603**

The parameter values in bold were found sensitive to the inclusion of mangroves as a functional group within the model (see section on model construction in the "Discussion")

very rainy areas of Micronesia (see Benstead et al., 2009).

Historically, the Colombian Pacific coast has had very low human population densities (5–17 persons km^{-2}; Etter et al., 2006) in part due to the lack of a coastal road that connects the region to the interior of the country. The area of Bahía Málaga is only inhabited by ca. 200–300 people (La Plata village, 1.5 inhabitants km^{-2}) who derive their livelihoods from fishing and timber extraction. Fishing is completely artisanal and performed by <100 persons in the whole area who employ predominantly gillnets as fishing gear. As a consequence, fishing mortality rates for most fisheries resources are low (Table 4). The results of the model, however, contradict the reports of overexploitation for the mangrove cockle (A. tuberculosa) in Bahía Málaga (see Lucero et al., 2012). Fishing mortalities in the EwE model are extremely low compared with the

single stock assessment made on length-converted catch curves for this species by Lucero et al. (2012). A possible explanation for these diverging results could be either an overestimation of mangrove cockle abundance or an underestimation of cockle's total catches in the present EwE model. Using an empirical formula, Lucero et al. (2012) estimated natural mortality (M) that was then used to estimate fishing mortality by subtracting total mortality (Z) from M. In contrast, in EwE, natural mortality of prey (e.g., cockles) is estimated using consumption rates of predators, the biomass of prey and the ecotrophic efficiency, and fishing mortality is calculated dividing catches by the biomass of the group. Given that the low human population density and remoteness of the mangrove areas in Bahía Málaga point to low fishery exploitation levels, it is advisable that further stock assessments of this important fishery resource are carried out integrating
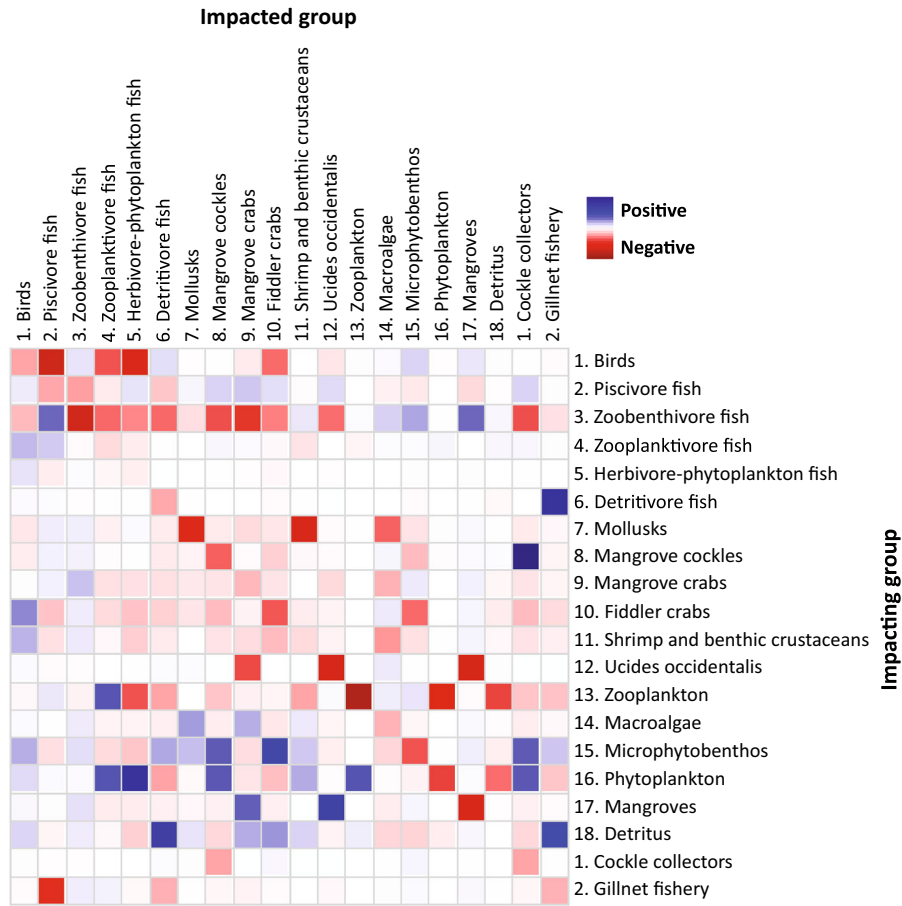
Fig. 5 Mixed trophic impact (MTI) relationships in the mangrove system of Bahía Málaga, Tropical Eastern Pacific region. The impacts are relative but comparable between groups. *Blue colors* indicate a positive impact and *red colors* a negative one. Intensity of colors reflects the strength of the

relative positive or negative impact [e.g., a very small increase in biomass of birds (*first row*) will have a high negative relative impact on the biomass of the group piscivore fish (*second column*)]

Fig. 6 Relative total impact versus keystoneness of functional groups in the food web model of Bahía Málaga, Tropical Eastern Pacific. Functional groups with high keystoneness index are those that have low biomass proportion and high overall effects on the food web (*upper right corner* in the figure; sensu Libralato et al., 2006)
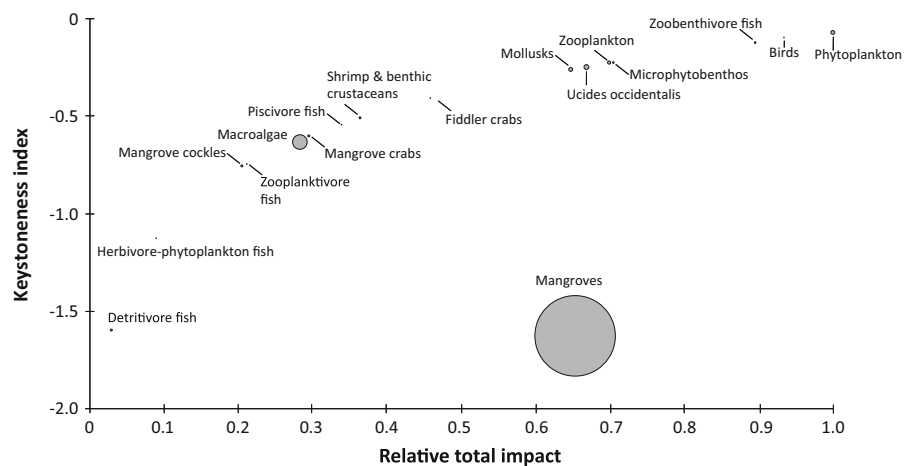
Table 6 System characteristics and ecological network analysis (ENA) indices of mangrove ecosystems for which Ecopath models have been produced in the Neotropics

System characteristics	Bahía Málaga, Colombia	Gulf of Nicoya, Costa Rica	Golfo Dulce, Costa Rica	Caeté Estuary, Brazil	Terminos Lagoon, Mexico	Huizache-Caimanero Lagoon, Mexico
Biogeographic region	Eastern Pacific	Eastern Pacific	Eastern Pacific	Western Atlantic	Western Atlantic	Eastern Pacific
Tidal regime	Macrotidal	Mesotidal	Mesotidal	Macrotidal	Microtidal	Microtidal
Size (km^2)	160	1,530	750	220	2,500	175
Mangrove area (km^2)	50	135.16	20	99	1,270	4.28
Rainfall (mm year^{-1})	8,000	2,126	3,000–5,000	2,500	1,200–2,000	800–1,200
Funtional groups	18	21	20	20	20	26
Mean trophic level of the catch	2.16	4.06	5.3	2.08	3.6	2.5
Mean transfer efficiency (%)	3.5	14.9	15	9.8	7	8.3
Finn cycling index (FCI)	1.43%	5.5%	18.9%	17.9%	7.0%	9.9%
Relative ascendancy (A/C)[a]	46.5%	26.1%	32.2%	27.4%	51.1	29.4%
Relative overhead (O/C)[a]	53.5%	73.9%	67.8%	69.6%	48.9%	70.7%
Redundancy[a]	%	56%	46.2%		36.1%	
Total system throughput (TST)[a]	7,042.9	3,049.3	1,404.6	10,558.6	3,709.5	6,668.6
Primary production/TST[a]	0.47	0.38	0.27	0.30	0.44	0.57
Consumption/TST[a]	0.13	0,38	0.48	0.35	0.11	0,31
Export/TST[a]	0.39	0.16	0.05	0,21	0.38	0.001
Total biomass of the community[a]	3,542.9	132.1	10.43	13,132.2	263.6	486.3
Reference	This study	Wolff et al. (1998)	Wolff et al. (1996)	Wolff et al. (2000)	Manickchand-Heileman et al. (1998)	Zetina-Rejón et al. (2003)

[a] Identified in Heymans et al. (2014) as robust to model construction

other sources of data (e.g., effort, catch, abundance indices) into a single analysis (Maunder & Punt, 2013).

Using ecological indicators that are robust to model construction identified in Heymans et al. (2014), it is found that Bahía Málaga represents total system throughput values within the range of those found in other estuarine mangrove systems. However, other indicators in Heymans et al. (2014), such as the relative ascendancy (A/C), the consumption/total system throughput ratio, and the total biomass of the community differ from the other systems (Table 6). The high value of relative ascendancy found in Bahía Málaga indicates a highly organized food web (internal stability) that protects itself from changes arising within the ecosystem (Saint-Béat et al., 2015). This may be explained by the very low disturbance level in this

area compared with other systems in Table 6, where fishing pressure is likely to be higher. The lower relative overhead value in this system may, on the other hand, make it more vulnerable to external perturbations (less resilient) which is in line with the low value of the Finn cycling index that also reflect an inmature and less resilient system (Christensen, 1995). Almost all other estuarine mangrove systems (as shown in Table 6) have lower A/C values but seem to be more resilient to external perturbations (i.e., have higher O/C values) than the Bahía Málaga case. The low values observed for the mean trophic level of the catch of three of the estuarine systems compared (Huizache-Caimanero Lagoon, Caeté estuary, and Bahía Málaga) seems to be a common feature of shallow-water systems (see Heymans et al., 2014) where fisheries target the highly productive low trophic level benthic organisms

(e.g., semi-terrestrial crabs, mangrove cockles, or shrimps), and juvenile estuarine fish.

Impacts of model construction on trophic network summary statistics

Most of the EwE models of estuarine systems include mangroves within the detritus compartment. The only ones that include mangroves as a functional group are the models for the Caeté estuarine system in North Brazil (Wolff et al., 2000) and the one for Bahía Málaga. This difference in model construction between estuarine EwE models was the reason to generate two alternative models for the mangrove system in Bahía Málaga. Including mangroves as a functional group (as opposed to considering the contribution of mangroves as litterfall in the detritus compartment) in the model of Bahía Málaga led to an increase in most network summary statistics calculated in EwE (see Table 5). Total system throughput was 9% higher in the model with the mangrove functional group compared with the model with mangroves included in the detritus. Considering mangroves as primary producers caused an increase in total net primary production, affecting all statistics computed from this parameter. Finally, the total biomass of the community and derived parameters changed dramatically depending on whether or not mangroves were included in the model as a functional group (more than 20-fold increase; Table 5). Similarly, Wolff et al. (2000) acknowledged that if the mangrove biomass was not included in their model as a functional group, their community biomass (132.4 t km^{-2}) would fit within the values of other tropical coastal systems (see Table 6). These results evidence the potential large effects that model construction, and further comparison with other models, might have on EwE trophic network summary statistics (Scharler, 2011). It may therefore be reasonable to include mangroves as a functional group within an EwE model for those cases where mangroves account for a large part of the habitat, since mangrove litterfall production will contribute largely to the primary production and thus form a basic food source of the ecosystem. Comparisons between mangrove EwE models should factor such differences in model construction when drawing conclusions about the functioning of these systems.

The mangrove system of the Caeté estuary in North Brazil (Wolff et al., 2000) shares a few common features with the system in Bahía Málaga that are worth considering: both (1) are dominated by extensive *Rhizophora* spp. mangrove forests, (2) are located in semi-diurnal macrotidal coasts (>4 m tidal amplitude at spring tides), and (3) present relatively high levels of annual rainfall (>3,000 mm year^{-1}). However, differences in the geomorphological settings, i.e., how mangroves develop in both areas, may well explain differences in mangrove secondary productivity (Castellanos-Galindo & Krumme, 2015), and some of the differences observed in system properties obtained from EwE. In the Caeté mangrove system, most energy is cycled within the high intertidal forest where principally the semi-terrestrial crab *Ucides cordatus* (Linnaeus, 1763) is able to process the abundant litterfall produced by mangroves (Wolff et al., 2000). This mangrove litterfall is only exported during spring tides when it is washed out to the adjacent subtidal areas. Transfer efficiencies to trophic level 2 are thus relatively higher (5.9) with the biomass of *U. cordatus* being enormously high (80 t km^{-2}). In addition, the Finn cycling index in the Caeté mangrove system is extremely high (17.9%) compared to the one in Bahía Málaga (1.43%) indicating higher energy cycling within the former mangrove system. In contrast, the mangrove system in Bahía Málaga possesses a considerably lower biomass (11.8 t km^{-2}) of the equivalent semi-terrestrial crab in the Caeté, *U. occidentalis*, the transfer efficiency to trophic level 2 is significantly lower than the one in the Brazilian system (1.93) and the Finn cycling index is only 1.43%. The most plausible explanation for these differences is the nature of the intertidal forest in Bahía Málaga that, as opposed to the Caeté mangrove system in North Brazil, is not only inundated during spring but also during neap tides. This condition may explain that most of the energy within mangroves in Bahía Málaga is not cycled in the intertidal forest but is exported into the adjacent subtidal system. The role of macroalgae in the study system remains to be understood as it accounts greatly to the total biomass of the ecosystem but does not seem to be consumed substantially by any other functional group in the system.

Caveats

This model should be taken as a first approximation to understand the functioning of this unique mangrove

system in the tropical Eastern Pacific. It should be noted that certain functional groups were not included in the model (e.g., groups belonging to subtidal rocky areas within Bahía Málaga) and that some of those already included would need to be further differentiated in future models (e.g., shrimps vs. benthic crustaceans). In addition, data for some functional groups were obtained from similar systems, and therefore further attempts should be made to collect data from this specific area. It should also be clear that this EwE model provides an annual average—a "snapshot view"—of the Bahía Málaga mangrove system. Therefore, the model is not capable, as yet, of providing insights into possible seasonal variations in trophic flows and structure of the ecosystem. Further research should investigate how parameters such as biomass vary according to seasonality in the area (wet vs. very wet seasons) and interannually in response to El Niño-Southern Oscillation events. In a next step, this model may be used to simulate scenarios of increased fishing pressure to evaluate the ecosystem response to such changes.

Conclusions

This first mangrove trophic model in the Panama Bight mangrove eco-region provides a simplified structure of the trophic flows between the main components of the food web within probably the wettest mangrove system in the world. Overall results provide a rare example of a very low productive mangrove ecosystem within a very developed mangrove forest. This low productivity is not related to overexploitation as this region is sparsely populated by humans and resource exploitation rates are very low. Explanations for these strikingly low values in a very well-developed mangrove forest may be found in the geomorphological characteristics of this tectonic bay system. Our results open an avenue of new research questions to explore this apparent productivity paradox in mangroves of this region that could help in understanding the main processes driving mangrove ecosystem function and productivity that remain as yet poorly understood.

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