The Gulf of Nicoya (Costa Rica) Fisheries System: Two Decades of Change

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Abstract
In the early 1990s, ecological and fishery data from the Gulf of Nicoya (Pacific Ocean) were holistically analyzed, and a trophic model was constructed using the Ecopath modeling approach. The results indicated that this tropical estuary, which is a Costa Rican fishery hot spot, was already overexploited by shrimp trawlers and the longline fleet, and recent observations suggest further deteriorations in this system. To evaluate the ecosystem and socioeconomic changes in the Gulf of Nicoya over the last 20 years, the 1993 model was reconstructed with data from 2013 to compare both system states. Although the summary statistics of both states (i.e., 1993 and 2013) suggested that the system maintained its general functionality and even enabled the total harvest to increase by approximately 20%, a more detailed analysis of the levels of the functional groups suggested that the system was further degraded as follows: (1) most shrimp, eel, and catfish species decreased their share in the catches, with severe economic losses for the fishery; (2) of the species that substantially increased their share in the catches, most were short-lived, low-value species, such as small pelagic and small demersal fishes; and (3) catches of long-lived, high-trophic-level fish, such as rays, sharks, mackerels, and barracudas, decreased. A picture emerged in which the advancing fishery of low-trophic-level species with low economic value enabled the total harvest to increase, while valuable shrimp resources and higher-trophic-level species were depleted. These developments caused a tremendous economic loss of approximately 50%.

Coastal waters are often highly productive and support essential fisheries worldwide; thus, these waters have a high economic value (Blaber et al. 2000). The vast majority of Costa Rican fishery catches originate from the country’s relatively large Exclusive Economic Zone (10 times the terrestrial area) along the Pacific coast, a region that is known to be nutrient-rich and highly productive, and most of its target fish stocks are known to be heavily exploited (Heilman 2012; Sea Around Us Project 2014). Costa Rica’s principal fishing fleets concentrate in the Gulf of Nicoya, which accounts for a large proportion of the national catches and is among the most exploited coastal areas in Central America (Guzmán-Mora and Molina Ureña 2007). The small-scale artisanal fishing sector is historically rooted in the communities surrounding the Gulf of Nicoya, is highly socioeconomically important for securing food production and livelihoods, and has national economic benefits. Initially, the artisanal fishing activities were confined to the inner gulf and shallow waters (Charles and Herrera 1994), but the fleets...
progressively extended to pelagic, offshore, and deepwater areas in the gulf (BIOMARCC 2013b).

After a period of intense exploitation by the multi-gear artisanal fleet and small industrial fleets, which peaked in the early 2000s, catches of several commercially important species began to show clear signs of decline and are likely to follow the same downward trend as the catches of many other fish stocks in the Pacific Central American Large Marine Ecosystem (Heileman 2012; Sea Around Us Project 2014). In particular, coastal shrimp catches drastically declined, with a severe reduction of white shrimps *Litopenaeus* sp. (Trujillo et al. 2012). These developments could lead to severe ecological and socioeconomic consequences because penaeid shrimps are known to be a central food source in the Gulf of Nicoya’s trophic web (Wolff et al. 1998) and are the most sought-after target group by many local coastal communities, which are highly vulnerable to fluctuations and negative trends in the fishery catches (Bakun et al. 1999). Coastal demersal fish, which dominate the catches of many inshore artisanal fisheries in the tropical Pacific, are valuable marine resources and are also commonly overexploited (Bell et al. 2011; Trujillo et al. 2012). Similarly, in the Gulf of Nicoya, large- and medium-sized drums and croakers (Perciformes: Sciaenidae) have always constituted a substantial and profitable proportion of the artisanal catches, but currently they are caught less frequently. The decline of high-value coastal species in the Gulf of Nicoya has caused (1) the semi-industrial fleet effort to shift toward other, low-value target groups, such as small pelagic fish species; and (2) the artisanal effort to shift toward smaller-sized individuals and juveniles due to the augmented use of small illegal mesh sizes (6.35 cm [2.5 in]).

These developments have likely caused changes in the size and species composition within the functional groups. Hence, an updated analysis of the species and weight composition of catches appears to be important for the evaluation of ecological changes in the system and the associated socioeconomic consequences (Roessig et al. 2004; Ward and Myers 2005). The depletion of coastal resources is not only associated with economic losses for the semi-industrial sector but is also likely to threaten the livelihoods of the artisanal fishing communities surrounding the Gulf of Nicoya. Hence, there is an urgent need for an ecosystem-based fishery assessment of the gulf to provide a decision-making basis for the Costa Rican management authorities. The Gulf of Nicoya has been studied by many scientists (Vargas 1995, 2016), but fishery studies concerning commercially exploited species within the area are sparse. Since the trophic model of the Gulf of Nicoya was constructed by Wolff et al. (1998), no further attempts have been made to integrate fishery-relevant data in a holistic, ecosystem-based analysis. Since that model’s construction in the early 1990s, important resources in the system have already been considered overexploited, and a further degradation of the ecosystem has been predicted (Wolff et al. 1998). We attempted to rebuild and update the model using data obtained approximately 20 years later from collaborative studies that were complemented by additional information from the literature regarding catches of target resources to analyze the ecosystem changes that occurred over the two decades between 1993 and 2013.

Changes in the biomass that occur at one trophic level are known to affect the trophic levels above and below that level, causing trophic cascades throughout the system (e.g., Pace et al. 1999; Duarte and García 2004; Andersen and Pedersen 2009). Hence, the analysis of changes in the ecosystem over time can be particularly useful for explaining changes in trophic relationships (Coll et al. 2009) and for determining the effects of certain fishing regimes on the trophic structure of the ecosystem (e.g., Walters et al. 1997; Neira et al. 2014). Thus, we used an Ecopath approach to produce mass-balanced snapshots of the Gulf of Nicoya ecosystem comprising the same ecosystem components at two distinct time points (1993 and 2013) to reveal the changes in the food web of the marine community (Christensen and Walters 2004). For this analysis, we determined the differences in the biomass distribution, system flow structure, and system summary statistics for all system components, including primary producers, target species, and nontarget species (Gascuel et al. 2011). By applying the mixed trophic impact (MTI) analysis in Ecopath, we assessed the effect of the different fishing fleets and gear types on the marine community and the interactions among the species and the identified keystone species (Libralato et al. 2006) in both system states (i.e., 1993 and 2013). The assessment of keystone species can be crucial for ecosystem management, as resource conservation plans often tend to focus more on species of high commercial value than on species of high ecological value (Navia et al. 2016).

In addition, we used Ecopath software to calculate the economic profit of the fisheries during both periods. Information regarding the resource market prices and the costs of fishing (variable and fixed costs) for each of the fishing fleets was included in the Ecopath models.

**METHODS**

*General description of the Gulf of Nicoya ecosystem.*—The Gulf of Nicoya (10°N, 85°W) is a tidally influenced estuary along the northwest Pacific coast of Costa Rica (Figure 1; Wolff et al. 1998). It is one of the world’s most productive tropical estuaries, and its main port, Puntarenas, is the country’s principal fishing ground for the artisanal fishing fleet (Vargas 1995). The model area stretches from the mouth of the Tempisque River in the north to the entrance of the Pacific Ocean in the south and covers...
an area of 1,530 km². According to its shape and bathymetry, the Gulf of Nicoya can be divided into the following three regions (Figure 1): inner gulf (zone 201), intermediate gulf (zone 202), and outer gulf (zone 203; Vargas 2016). The shallow interior zone (depth < 10 m) is fringed by mangroves and mud flats and is dominated by the seasonal freshwater inflow from the Tempisque River (Proyecto Golfo 2012). The inner gulf is considered an area of high priority by the Instituto Costarricense de Pesca y Acuicultura (INCOPESCA) due to its important function as a reproduction and nursery area for commercially important fish and shrimp species (Alpízar 2011; Proyecto Golfo 2012; Vargas 2016). The intermediate zone of the gulf is mostly surrounded by sandy beaches and mangroves. The physical parameters of the water masses are subject to intense mixing processes due to the interaction between the oceanic water and freshwater from both adjacent zones (Proyecto Golfo 2012). The region comprises reproduction areas for small pelagic fish species (Clupeiformes: Clupeidae and Engraulidae), shrimps Litopenaeus spp. (Decapoda: Penaeidae), snappers Lutjanus spp. (Perciformes: Lutjanidae), and drums Cynoscion spp. (Perciformes: Sciaenidae) and serves as feeding grounds for several commercially targeted species, such as the Mexican Barracuda Sphyraena ensis (Perciformes: Sphyraena). The outer oceanic zone extends from a minimum depth of 20 m out to 200 m at the shelf edge, is surrounded by sandy beaches and rocky shores (Wolff et al. 1998), and is mainly influenced by oceanic waters and the input from the Tárcoles River. The eastern region of the outer gulf is a hatching and reproduction site for penaeid shrimps, sharks, and several other fish species (Proyecto Golfo 2012; Vargas 2016). Similar to other tropical coastal estuarine areas, mangroves contribute to primary production in the Gulf of Nicoya by providing organic matter and playing an important role in enhancing fish and invertebrate productivity; thus, mangroves strongly support the local fisheries (Wolff 2006; Silva-Benavidez 2009; Hutchison et al. 2014).

Model Construction

Modeling approach.—The previous trophic model (GN₀) that was initially developed by Wolff et al. (1998) was based on data sampled by the RV Victor Hensen Costa Rica expedition (1993–1994) and fisheries landings data (INCOPESCA, unpublished data). The GN₀ serves as a baseline for this study and represents the ecosystem state in 1993–1994. Based on new information obtained from collaborative studies, the literature, and the most recent fisheries data, a second model (GN₊₂₀) was constructed to represent the state of the ecosystem in 2013. To ensure comparability, both models comprised the same functional groups. For the modeling task, the open-source software Ecopath with Ecosim (EwE) version 6.4.4 (Christensen and Walters 2004) was used.

Ecopath with Ecosim is based on a set of linear equations for each functional group in the system through which the group’s biomass production is connected to the other model groups via a prey–predator matrix. For each compartment (i), the basic equation is as follows:
where $P_i$ is the total production rate of $i$; $Y_i$ is the total fishery catch rate; $M_i$ is the instantaneous predation rate of group $i$; $B_i$ is the biomass; $E_i$ is the net migration rate (emigration-immigration); $B_A$ is the biomass accumulation rate; $P_i(1−EE)$ represents the “other mortality” rate of $i$; and EE is the ecotrophic efficiency of $i$ and the proportion of the production that is utilized in the system (Christensen and Walters 2004; Christensen et al. 2005).

Although equation (1) allows for the balancing of the biomass production in each group with its use in the system (and the fishery), a second equation allows for estimating the energy budget of each group $i$ as follows:

\[
\text{Consumption}_i = \text{Production}_i + \text{Respiration}_i + \text{Egestion of unassimilated food}_i
\]  

The model was built around the main groups targeted by the fisheries. Species with similar sizes, diets, consumption, mortality, production rates, and habitats were grouped. The model comprised a total of 22 functional groups, including 3 primary producer groups and 10 different fish groups. The functional groups and the scientific names of all species that are included in the GN models are presented in the Appendix (Table A.1).

**Primary producers and zooplankton.**—The mangrove coverage along the Costa Rican Pacific coast was estimated to be 413 km$^2$ (Silva-Benavide 2009). In the early 1990s, the mangrove coverage surrounding the Gulf of Nicoya was estimated to be approximately 15.2 km$^2$ (Brugnoli-Olivera and Morales-Ramirez 2008). Since then, the mangrove coverage of the Gulf of Nicoya has declined by 10%, which was attributed to land use changes, such as the development of shrimp aquaculture (R. Venegas-Li, L. Morales, and D. Martínez-Fernández, paper presented at a joint meeting of the Association for Tropical Biology and Conservation and the Organization for Tropical Studies, 2013). The phytoplankton community is dominated by diatoms and flagellates, and the primary productivity of plankton is known to be exceptionally high (Brugnoli-Olivera and Morales-Ramirez 2008). Recent studies conducted by researchers from the University of Cadiz, Spain, provided information regarding the phytoplankton communities at different stations in the Gulf of Nicoya (Requejo 2011). Phytoplankton chlorophyll-$a$ (Chl-$a$) concentrations of 1–16 mg/m$^3$ were estimated (BIOMARCC 2013a, 2013b). For the phytoplankton biomass calculations, the following ratios were used: Chl-$a$ to carbon (g) = 1:100, predominantly for diatoms; carbon to dry weight organic matter (g) = 1:2.5; and dry organic matter to wet weight organic matter (g) = 1:5 (Sathyendranath et al. 2009; Parsons et al. 2013). Regional and seasonal differences were considered; thus, a minimum biomass of 15 g/m$^2$ was measured in the inner and intermediate gulf areas, which was assumed to be most appropriate for the whole gulf area. According to previous studies, the phytoplankton primary productivity in the Gulf of Nicoya averages between 0.12 and 2.76 g C·m$^{-2}$·d$^{-1}$, and the annual gross primary productivity measured in Punta Morales was 450 g C·m$^{-2}$·year$^{-1}$ (Córdoba-Muñoz 1998; Gocke et al. 2002). The phytoplankton primary productivity was assumed to be lower in other zones of the gulf according to previous samples (Wolff et al. 1998). After the RV Victor Hensen Costa Rica expedition in the early 1990s, the zooplankton composition was once more intensively studied in Punta Morales during 1997 (Brugnoli-Olivera et al. 2004); the dominance of copepods in the zooplankton community was confirmed, and large seasonal variations in the biomass were detected. An average annual zooplankton biomass of 4 g/m$^2$ of water column was assumed for both models based on the work of Brugnoli-Olivera et al. (2004).

**Fishing fleets and target resources.**—In Costa Rican Pacific waters, the tuna fleet and the large pelagic longline fleet are the most important in terms of catch volume (FAO 2007; Trujillo et al. 2012). However, inside the Gulf of Nicoya, the small-scale artisanal fishing sector is of major economic and social importance (Trujillo et al. 2012; García Lozano and Heinen 2016). Four artisanal fishing fleets operate in the gulf with different types of gear, including gill nets, lines (bottom longlines and drifting longlines), handlines, and manual gear (traps and mollusk extraction), and target a variety of demersal and coastal species (BIOMARCC 2013a, 2013b). Gill nets are prominently used, mostly with small mesh sizes (<7.62 cm [<3 in]), which are illegal in the Gulf of Nicoya. Catches are diverse but dominated by drums (Perciformes: Sciaenidae), catfishes (Siluriformes: Ariidae), snooks (Perciformes: Centropomidae), and different penaeid shrimp species (Alpízar 2015). Additionally, two semi-industrial fishing fleets operate in the gulf: shrimp trawlers and sardine purse-seiners. The purse seine vessels target small pelagic fish species in the intermediate and outer zones of the Gulf of Nicoya, while the bottom trawl fleet targets white shrimps and several other shrimp species in the outer gulf. In this fishery, the capture of nontarget (bycatch) species drastically exceeds the shrimp catches (Figure 2). Due to shrinking resources in shallow waters, the shrimp trawler fleet has progressively moved toward deeper waters outside of the gulf (Wehrmann and Nielsen-Muñoz 2009); thus, the deepwater shrimp species that are landed in Puntarenas (kolobri shrimp Solenocera agassizii, bigheaded shrimp Heterocarpus vicarious, and three-spined nylon shrimp Heterocarpus affinis) are presumably fished outside of the gulf and were excluded from the model (UNEP 2004). Bycatch species caught outside of the gulf are not included in the model, as the Costa Rican deepwater shrimp fishery discards almost the entire bycatch,
including species of commercial value (Wehrtmann and Nielsen-Munoz 2009). The landings of the six fishing fleets were entered separately into the Ecopath model.

All fish groups are targeted by at least one of the six identified fishing fleets. For each model group, the following basic input parameters were gathered: reported artisanal and semi-industrial catches, biomass ($B$), production-to-biomass ratios ($P/B$), consumption-to-biomass ratios ($Q/B$; Table 1), and the diet composition of each species or group (Table A.2). Information regarding the diet composition was obtained from Wolff et al. (1998) and the recent literature (López-Peralta and Arcila 2002; Olson and Watters 2003; Robertson and Allen 2008). For additional references, please refer to the Appendix (Table A.3). The artisanal landings data from each zone of the Gulf of Nicoya were obtained from the Costa Rican monthly national landing statistics (INCOPESCA, unpublished data). The provided time series consists of monthly records of the main target species and groups (fish and invertebrates) that were fished and landed in the Gulf of Nicoya. The landings (kg) were separated by fishing fleet and gear. The estimated bycatch of the shrimp trawlers and discard estimates were included. The monthly records of the semi-industrial landings and the fishing effort, which was measured as the number of days fishing (as well as some data about the number of fishing trips) in the Gulf of Nicoya, were provided by INCOPESCA (Departamento de Investigación y Desarrollo). Additional yearly sampling data (INCOPESCA, Departamento de Investigación y Desarrollo) were obtained to estimate the relative species composition within the target groups. To enter the data into the model, the monthly landings data, discards, and shrimp trawl bycatch data were converted into metric tons per square kilometer (based on the model area of 1,530 km$^2$) per year.

Calculations of the model parameters.—The biomass estimates in the early model (GN$_0$) were based on fishery catches and beam and otter trawl survey data. Trends in fishery catches can serve as a first indicator of the population biomass of the target resources. For the 2013 model (GN$_{20}$), the resource biomass values per unit area (metric tons/km$^2$) were calculated from the catch data ($Y$) and estimated fishing mortality ($F$) by using the following formula proposed by Beverton and Holt (1957):

$$B = Y/F.$$  

The recent exploitation rates and $F$-values for most of the fish and shrimp species were obtained from INCOPESCA stock assessment studies (Alpízar and Vásquez 2010, 2012; Alpízar 2011, 2014, 2015; Alpízar et al. 2013) and from research conducted by the Universidad Nacional Costa Rica (Aizpurúa 2014). Stock information on morays/eels, catfishes, and flatfishes is scarce, and the biomass had to be estimated from the catch data ($Y$) and estimated fishing mortality ($F$) by using the following formula proposed by Beverton and Holt (1957):

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$$B = Y/F.$$
| Group number | Functional group                        | Catch | $B_i$  | $P/B_i$ | $Q/B_i$ | EE$_i$ | $P/Q$ |
|--------------|----------------------------------------|-------|--------|---------|---------|--------|-------|
| Parameters for model GN$_0$ (1993)                   |       |        |        |         |         |        |       |
| 1            | Seabirds                               | 0.07  | 0.10   | 50      | 0.00    | 0.002  |       |
| 2            | Mackerels and barracudas               | 0.036 | 0.15   | 0.55 (0.5) | 7 (6) | 0.43  | 0.080  |
| 3            | Rays and sharks                        | 0.048 | 0.15   | 0.60    | 4       | 0.56   | 0.150  |
| 4            | Large drums and snooks                 | 0.122 | 0.60   | 0.65    | 4.5 (5) | 0.47   | 0.144  |
| 5            | Catfishes                              | 0.257 | 0.70   | 0.70 (0.65) | 6   | 0.73   | 0.117  |
| 6            | Morays and eels                        | 0.017 | 0.70   | 0.50    | 5 (5.5) | 0.48   | 0.100  |
| 7            | Carangids                              | 0.020 | 0.60   | 0.75    | 6       | 0.90   | 0.125  |
| 8            | Snappers and grunts                    | 0.179 | 0.55 (0.60) | 0.90 (1.0) | 5 (6) | 0.93   | 0.180  |
| 9            | Cephalopods                            | 0.015 | 0.50 (0.40) | 4.00    | 15      | 0.77   | 0.267  |
| 10           | Lobster                                | 0.001 | 0.25   | 1.00    | 10      | 0.49   | 0.100  |
| 11           | Flatfishes                             | 0.022 | 0.30   | 1.80    | 7       | 0.71   | 0.257  |
| 12           | Small demersals                        | 0.798 | 1.50   | 2.50    | 10      | 0.91   | 0.250  |
| 13           | Small pelagics                         | 0.560 | 1.90   | 4.00    | 20      | 0.90   | 0.200  |
| 14           | Crabs                                  | 0.011 | 0.70 (0.60) | 3.50    | 12      | 0.94   | 0.292  |
| 15           | Epibenthos                             | 0.027 | 10.00  | 4.00    | 20      | 0.47   | 0.200  |
| 16           | Endobenthos                            | 0.001 | 1.20 (1.00) | 10.00 (12.00) | 60 | 0.86   | 0.167  |
| 17           | Shrimps                                | 0.770 | 1.50   | 6.50 (7.00) | 25 | 0.65   | 0.260  |
| 18           | Zooplankton                            | 4.00  | 40.00  | 150     | 0.66   | 0.267  |
| 19           | Phytoplankton                          | 15.00 | 200.00 |         | 0.21   |       |       |
| 20           | Mangroves                              | 100   | 0.22   |         | 0.60   |       |       |
| 21           | Microphytobenthos                      | 0.50  | 125.00 |         | 0.70   |       |       |
| 22           | Detritus                               | 0.10  |       |         | 0.23   |       |       |
| Parameters for model GN$_{+20}$ (2013)                |       |        |        |         |         |        |       |
| 1            | Seabirds                               | 0.06  | 0.09   | 50      | 0.00    | 0.00   |       |
| 2            | Mackerels and barracudas               | 0.018 | 0.06   | 0.60 (0.55) | 7   | 0.50   | 0.09   |
| 3            | Rays and sharks                        | 0.028 | 0.07   | 0.75 (0.6) | 4   | 0.56   | 0.19   |
| 4            | Large drums and snooks                 | 0.132 | 0.35   | 0.70    | 4       | 0.54   | 0.18   |
| 5            | Catfishes                              | 0.171 | 0.45   | 0.80    | 6       | 0.56   | 0.13   |
| 6            | Morays and eels                        | 0.011 | 0.17 (0.15) | 0.50    | 5 (5.5) | 0.74   | 0.10   |
| 7            | Carangids                              | 0.062 | 0.50   | 0.75    | 6       | 0.99   | 0.13   |
| 8            | Snappers and grunts                    | 0.201 | 0.70   | 0.90    | 5 (5.5) | 0.98   | 0.18   |
| 9            | Cephalopods                            | 0.010 | 0.30   | 4.00    | 15      | 0.90   | 0.27   |
| 10           | Lobster                                | 0.003 | 0.10   | 1.50    | 10      | 0.67   | 0.15   |
| 11           | Flatfishes                             | 0.020 | 0.20   | 1.80    | 7       | 0.69   | 0.26   |
| 12           | Small demersals                        | 0.984 | 1.20   | 2.50    | 10      | 0.82   | 0.25   |
| 13           | Small pelagics                         | 1.511 | 1.50   | 4.00    | 20      | 0.94   | 0.20   |
| 14           | Crabs                                  | 0.020 | 0.70   | 3.50    | 12 (10) | 0.77   | 0.29   |
| 15           | Epibenthos                             | 0.005 | 5.00 (6) | 4.00    | 20      | 0.71   | 0.20   |
| 16           | Endobenthos                            | 0.000 | 1.00   | 10.00   | 60      | 0.70   | 0.17   |
| 17           | Shrimps                                | 0.310 | 0.70 (0.65) | 7.50    | 26 (25) | 0.87   | 0.29   |
| 18           | Zooplankton                            | 4.00  | 30.00  |         | 0.76   | 0.20   |
| 19           | Phytoplankton                          | 15.00 | 200.00 |         | 0.23   |       |       |
| 20           | Mangroves                              | 90.00 | 0.22   |         | 0.39   |       |       |
| 21           | Microphytobenthos                      | 0.50  | 125.00 |         | 0.39   |       |       |
| 22           | Detritus                               | 0.10  |       |         | 0.18   |       |       |
The $P/B$ values, or stock turnover rates, are equivalent to the total mortality rate ($Z$; Allen 1971) in a steady-state ecosystem. For the fish species, $Z$ was estimated based on $F$ and natural mortality ($M$) using the following relationship:

$$Z = F + M.$$ 

We estimated $M$ by using the caudal fin aspect ratio method (Pauly 1983) as follows:

$$\log_e(M) = -0.0152 - 0.279 \log_e(L_\infty) + 0.6543 \log_e(K) + 0.463 \log_e(T),$$

where $L_\infty$ is the mean asymptotic length (cm), $K$ is the growth coefficient ($\text{year}^{-1}$), and $T$ is the mean habitat temperature ($°C$).

For invertebrates and seabirds, the $P/B$ values were obtained from other studies (see Table A.3). The $Q/B$ values were obtained from physiological studies that were conducted in similar areas and ecosystems (García and Duarte 2002; Giarrizzo et al. 2013) and from the previous model. Migration rates (immigration–emigration; in metric tons-km$^{-2}$·year$^{-1}$) were set to 1 because no highly migratory fish species were included in the model. Most of the seabird species included in the model are permanently resident in the Gulf of Nicoya. To account for seasonal biomass changes of the seabird species (black storm-petrel Hydrobates melania; certain Sulidae [blue-footed booby Sula nebouxii, Peruvian booby Sula variegata]), the biomass was calculated as a yearly average. The yearly maximum of seabird biomass was estimated at 0.09 metric tons/km$^2$.

The model was balanced based on the suggestions provided by Link (2010) while considering certain general food web model diagnostics, such as the increasing biomass from the high to low trophic levels, the increasing $P/B$ and $Q/B$ with decreasing trophic level, the predator–prey biomass ratios, and the analysis of vital rate ratios. The model was balanced to achieve reasonable EE values for each functional group ranging between 0 and 1 and respiration-to-biomass ratios ($R/B$) and $P/Q$ values ranging mainly between 0.1 and 0.3 (Christensen et al. 2005). During the balancing process, a few minor modifications were made in the biomass values, $P/B$ ratios, and the diet matrix. The values that required modification are indicated in Table 1.

**Network Analysis**

**Ecosystem changes over a period of two decades.**—To investigate ecosystem changes that occurred over the two-decade period of interest (1993–2013), the most important model characteristics, such as fisheries catches and model summary statistics, were directly compared. The EwE trophic flow diagram allowed for a direct comparison of the biomass distribution in the ecosystem and provided information regarding the abundance and relative importance of certain functional groups after 20 years of intensive fishing and changes in environmental conditions. The approach is particularly useful because stock assessment studies of exploited species are scarce.

To quantify the effect of the biomass changes of one functional group on the other groups in the ecosystem, the MTI matrix was used. This method was originally used to assess economic interactions (Leontief 1951) and was later used to assess the direct and indirect ecological impacts of one group/fishery on the other groups in a system (Ulanowicz and Puccia 1990). The values were estimated for each pair of functional groups in the trophic web and indicated either positive or negative effects of the impacting group on the impacted group. Negative values can be associated with top-down effects, and positive values can be associated with bottom-up effects.

Based on the MTI, the keystone index was then calculated for each group according to Libralato et al. (2006). The keystone index describes the relative impact of each group on all of the other groups in the system and is the highest for those groups that have a high impact and a low biomass. The keystone species have keystone index values that are close to or greater than zero (Libralato et al. 2006).

The fishing-in-balance index (FiB) was calculated according to Pauly et al. (2000) as follows:

$$\text{FiB} = \log \left[ Y_k \times (1/\text{TE})^{mTL_k} \right] - \log \left[ Y_0 \times (1/\text{TE})^{mTL_0} \right].$$

where $Y_k$ is the catch in year $k$; $mTL_k$ is the mean trophic level of the catch in year $k$; $\text{TE}$ is the transfer efficiency between the trophic levels ($\text{TE} = 0.1$); and the subscript 0 refers to the year used as the baseline (1993). In combination with the mTL, the indicator can be used to assess the state of the fisheries, including masking factors, such as the geographic expansion or technological improvements in the fleet (Pauly et al. 2000).

**Economic analysis of the fishery.**—Information regarding the current market prices in Costa Rican colones per kilogram in the early 1990s and 2013 was obtained from INCOPESCA. The prices were entered separately for the artisanal and semi-industrial fleets. The average market price that was directly paid to the fishermen at the landing site was calculated for each functional group. Costa Rican colones were converted to U.S. dollars (US$) by using the respective purchasing power parity (PPP) conversion factor per international US according to the World Development Indicators (Prince and Fantom 2014). The PPP is based on the relative cost of living and inflation rates in
the country and reflects differences in the price levels of goods (e.g., Hoyt and Iniguez 2008). A PPP conversion factor of 364 was used for 2013, and a PPP conversion factor of 100 was used for 1993. The converted prices were entered into the models as off-vessel prices (US$ per kg) and were used to calculate the value of the total catches of each functional group and the profit of the fishing fleets. The costs of each fishing fleet were entered as a percentage of the fishery’s total value in the given year, leading to a percentage of the fleet’s total profit (Christensen and Walters 2004). A distinction was made between (1) fixed costs, which accrue without any fishing activity taking place and are mainly composed of the loans for the vessels and other equipment; and (2) variable costs, such as fuel and ice. The variable costs are fleet specific and directly relate to the fishing effort of the fleet. The relative percentages of the fixed costs and effort-related costs were estimated for each of the artisanal and semi-industrial fleets in the Gulf of Nicoya separately according to an economic study by Coyle et al. (2015) on the Costa Rican fishing fleet.

RESULTS

Network Analysis

The basic Ecopath input and output parameters for both balanced trophic models of the Gulf of Nicoya (GN\textsubscript{0} and GN\textsubscript{+20}) are presented in Table 1. The EE values estimated by the EwE software varied from 0.0 to 0.99 for different functional groups. The EE value is the fraction of production that is used in the system (Christensen et al. 2005). A high EE value (close to 1) indicates that a large fraction of the production is either passed up the food chain or exported out of the system by the fisheries, as is the case for shrimps, small pelagic fish species, and other mid-trophic-level fish.

The diet matrix is presented in Table A.2. The summary statistics (Table 2) that were calculated by the EwE software for both models were directly compared. The gross efficiency of the fishery and the overall catch levels increased by 21.1% and 20.8%, respectively, between 1993 and 2013, whereas the profit from the fishery decreased by 48% due to the profound changes in the fishery targets. The model output indicated that catches at the lowest and highest trophic levels decreased, while catches at trophic level 2.5 strongly increased compared to those in 1993 and represented more than 70% of all catches in the Gulf of Nicoya in 2013 (Figure 3). The mTL of the catch remained at a low value of approximately 2.8 (Table 2).

The total system biomass and size in terms of total flows (throughput) of the system declined by 12.2% and 0.5%, respectively, over the 20-year period. The functional groups that decreased or increased in biomass in 2013 compared to 1993 are shown in the trophic flow diagram (Figure 4). The functional groups are ordered according to their trophic level (1 to 4). The sizes of the nodes and lines in Figure 4 are proportional to the biomass and the flow between the functional groups, respectively. Mangroves, which hold the largest share of the biomass in the system, declined severely. The biomass comparison showed a decline in benthic invertebrates and shrimps, which are the most prominent groups in the Gulf of Nicoya food web and function as an important link between the trophic levels. Certain species commonly caught as bycatch of the shrimp trawl fisheries, such as catfishes, morays, and eels, declined over the two-decade period of interest. The top predators—rays, sharks, mackerels, and barracudas—also declined. Important trophic flows link phytoplankton with zooplankton, benthos, and small pelagic fishes. Benthos, shrimps, and small pelagics play an important role in the system as a connection between the primary producers and the upper trophic levels.

| Parameter | GN\textsubscript{0} (1993) | GN\textsubscript{+20} (2013) | Units | Change (%) |
|-----------|----------------|----------------|-------|------------|
| Total system throughput | 6,892.33 | 6,856.97 | Metric tons/km\textsuperscript{2}-year\textsuperscript{-1} | -0.52 |
| Mean trophic level of the catch | 2.797 | 2.796 | | -0.04 |
| Gross efficiency catch/net primary production | 0.00093 | 0.00113 | | 21.10 |
| Total primary production/total respiration | 6.968 | 6.844 | | -1.77 |
| Total biomass excluding detritus | 140.67 | 123.56 | Metric tons/km\textsuperscript{2} | -12.16 |
| Total catch | 2.886 | 3.488 | Metric tons/km\textsuperscript{2}-year\textsuperscript{-1} | 20.86 |
| FiB | 0.05 | 0.1 | | |
| Total market value | 15,986.3 | 7,920.26 | US$ | -50.46 |
| Total costs | 10,230.65 | 4,929.92 | US$ | -51.81 |
| Profit | 5,755.66 | 2,990.33 | US$ | -48.05 |
The MTI plot (Figure 5) suggested that the artisanal gill-net fleet, including the use of illegal mesh sizes, had the strongest negative impact on different species in the ecosystem, particularly on predatory species (e.g., large drums, snooks, mackerels, barracudas, and catfishes). Removal of the top predators by the fishing fleet can lead to positive effects on the prey species (e.g., the gill-net fleet removes predators of lobsters). The semi-industrial shrimp fleet negatively impacted its target species along with a variety of bycatch species, whereas the selective small-pelagic fishery affected only its target species.

The bottom-up effects of the prey on the predators were clearly visible. Zooplankton had a negative impact on phytoplankton (grazing), epibenthos had a negative impact on macrophytes, and cephalopods had a negative impact on flatfish. Certain species compete for the same resources, such as catfish and morays/eels as well as carangids (jacks and pompanos) and snappers/grunts.

Compared to 1993, the negative impact of the fishing fleets on sharks/rays, mackerels/barracudas, and small pelagics was greater in 2013. The shrimp trawlers increasingly impacted other nontarget species. The impact of the developing trap fishery on lobsters was evident. Furthermore, competition between the demersal fish groups increased, as indicated by the negative interactions with...
FIGURE 5. Mixed trophic impact analysis for the Gulf of Nicoya ecosystem model in (A) 1993 (GN0) and (B) 2013 (GN+), indicating the impact of one group on the other functional groups in the ecosystem. The color of the squares indicates the proportional impact (blue = positive; red = negative) of the functional group or fishing fleet listed at the right (impacting group) on the group or fleet listed along the top (impacted group; fleet types: Art. = artisanal, SI = semi-industrial).
each other on the MTI plot. Demersal groups competed for the same prey, such as epibenthos, which substantially declined in biomass.

The EwE keystone analysis (Figure 6) of both years (1993 and 2013) indicated the high relative importance of phytoplankton and zooplankton in the ecosystem and the links to the higher trophic levels, such as benthos, shrimps, and small pelagic fishes. The 2013 model suggested that certain groups, such as snappers/grunts and small demersal fishes, increased in importance within the Gulf of Nicoya ecosystem.

### Economic Analysis

The economic value of the yearly catches of all fishing fleets that operated in the Gulf of Nicoya declined by 50% in 2013 compared to that in the early 1990s (Figure 7). In 1993, shrimps accounted for the largest percentage (72%) of the total yearly value of artisanal and semi-industrial fleets. In 2013, shrimps still accounted for the largest share of the overall value; however, their contribution severely declined (by 39%). In both years, small demersal fish species were the second most important target group in terms of the yearly catch value. Small pelagic species only contributed a small share (7%) to the total value of the catch despite their large contribution to the catch biomass (20%).

### DISCUSSION

#### Ecosystem Changes

The Gulf of Nicoya has been intensively exploited for many decades by both artisanal multi-gear fisheries and sardine purse seiners in the gulf and by shrimp trawlers in the outer zone (Salas et al. 2011; Garcia Lozano 2014). This study demonstrated an increase in total fishery catches in the Gulf of Nicoya over two decades from 1993 to 2013, despite former descriptions of an overfishing state in the gulf during 1993 (Wolff et al. 1998). However, the overall increase in the catches was due to shifts in important target species in the fishing sector, which affected the trophic structure of the ecosystem.

#### Functional Groups

Functional groups are defined in Appendix Table A.1.

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**FIGURE 6.** Keystone index (keystoneness) of the functional groups in the Gulf of Nicoya during (A) 1993 and (B) 2013. Keystone species with high importance for the ecosystem are indicated by keystone index values close to zero (on the y-axis) and a relative impact close to 1 (on the x-axis). Functional groups are defined in Appendix Table A.1.
One important change was the increase in semi-industrial sardine catches, which was consistent with the severe decrease in shrimp catches. However, the semi-industrial and artisanal catches of small pelagic fish appeared to have already peaked in the early 2000s, and a declining trend since 2008 can also be observed in those catches (BIOMARCC 2013a, 2013b; FAO 2017). The model revealed that the EE of small pelagic fishes had already been reached by 2013, as almost 100% of their production was either consumed by predators or exported out of the system by the fisheries. Thus, it is likely that the maximum sustainable catch and EE of small pelagics were already exceeded in 2008 (see Figure 2). Hence, a further increase in the exploitation rate for small pelagic species would not be advisable.

Two simultaneous changes in the fishing pattern occurred in the Gulf of Nicoya: (1) catches of small and low-trophic-level species increased; and (2) the spatial scale of the fishing fleet increased. When shrimp catches dropped, the low-trophic-level fish species were increasingly targeted, which might have had severe impacts on the gulf ecosystem. The Gulf is an extremely productive, phytoplankton-dominated estuary (Gocke et al. 2002); thus, phytoplankton production is an important factor in the system, supporting the high fishery catches in the gulf. The results of the Ecopath keystone analysis indicated the high relative importance of phytoplankton, zooplankton, and the links to the higher trophic levels (benthos, shrimps, and small pelagics), suggesting a bottom-up-driven system. In a comparison of 33 Ecopath models (Libralato et al. 2006), marine mammals or sharks were often ranked the highest in “keystoneness” (e.g., Azores Archipelago: Guenette and Morato 2001; a Galapagos reef: Okey et al. 2004). However, primary producers, zooplankton, small pelagics, and benthic organisms have been frequently observed to be among the most important groups, particularly in coastal or semi-enclosed ecosystems, including Chesapeake Bay (Baird and Ulanowicz 1989), the Gulf of Maine (Heymans 2001), and the Gulf of Thailand (Christensen 1998). These previous results are consistent with our findings for the Gulf of Nicoya.

The model shows a further decline in the biomass of shrimps, which also constitute one of the keystone species in the marine community. Keystoneness is often associated with a structuring role of the species in the food web (Libralato et al. 2006), highlighting the importance of shrimps as a link between the low and high trophic levels. The high EE of shrimps shows that almost all of the biomass production is used in the system. Thus, their decline directly affects their main predators (i.e., flatfishes, lobsters, and jacks/pompanos), as shown by the MTI. These predator species all declined in biomass.

The consequences might be more severe due to the parallel decline in the biomass of benthic invertebrates, which

![Figure 7. The share of each target group in the total yearly monetary value (US$) of the fisheries in the Gulf of Nicoya, calculated from the average market prices and yearly catches (Instituto Costarricense de Pesca y Acuicultura) in 1993 and 2013.](attachment:image.png)
occurred over the 20-year period; benthic invertebrates negatively impacted the same predator groups. In the context of declining benthic biomass, the impact of the artisanal fleet should not be disregarded. The heavy exploitation of bivalves by the coastal communities (yearly average = 20 metric tons in the last 5 years) has most likely caused the severe decline in epibenthos biomass. Furthermore, over the two decades of interest, shrimp trawlers in the Gulf of Nicoya might have caused the observed decrease in biomass of slow-growing benthic invertebrates by gradually degrading the habitat. In addition to the negative effects of the fisheries, these organisms are negatively affected by the declines in mangrove habitat.

Furthermore, the ecosystem model indicates the presence of increasing fishing pressure on small pelagic fishes, which are another important link between the trophic levels and are also identified as keystone species. In the Gulf of Nicoya, which is an ecosystem with only a few planktivorous fish species, small pelagics occupy the key position in the ecosystem as foraging fish, and a further reduction in this group’s biomass might lead to trophic cascades throughout the food web (Duarte and Garcia 2004).

Shrimp trawlers are not only known to affect the target species but also affect bycatch species and often cause disturbances to marine benthic habitats (Thrush and Dayton 2002). Shrimp trawling is likely the most significant source of fishing mortality in Costa Rica’s marine ecosystem (Trujillo et al. 2012). A fraction of the bycatch is potentially discarded; however, the full extent of the discards is unclear and has been rather underestimated in our models.

The increasing bycatch of the shrimp trawlers is most likely the reason for the dramatic drop in the biomass of eels. The same trend of declining eel populations could be observed along the Pacific coast of South America. Populations of the Pacific Bearded Brotula Brotula clarkae rapidly declined by up to 30% in South America due to increased fishing pressure (Lea et al. 2010). The Conehead Eel Cynoponticus coniceps is also known to be frequently caught as bycatch of the shrimp trawlers (Lea et al. 2010). Another reason for the decline in biomass could be the habitat degradation and especially the reduction of mangrove areas.

Several other taxa, such as catfishes, rays, sharks, mackerels, and barracudas, have been affected by the shrimp trawlers due to the increasing fishing mortality, increasing catches of juvenile fish, and habitat destruction that interferes with the reproduction and nursery areas of these species inside the Gulf of Nicoya (Trujillo et al. 2012). These developments were also observed from the MTI analysis, which showed an increasing fishing impact on these species in 2013 compared to the early 1990s.

Over the two decades, an increase in crab and lobster catches was observed. This increase might be due to the development of the trap fisheries, which target crustaceans mainly for the export market. Furthermore, previous studies have shown that the removal of demersal predatory fish species can lead to an increase in benthic macroinvertebrates; thus, the substantial decrease in predator biomass in the Gulf of Nicoya could have caused trophic cascading effects (Baum and Worm 2009).

Shifts in the species composition in marine ecosystems over time are often due to anthropogenic influences, such as fishing, pollution, and environmental factors (e.g., Last et al. 2011). In the Gulf of Nicoya, changes in the fishing pattern occurred due to spatial expansion of the fishery toward the outer gulf to target more oceanic species. Similar trends could be observed in other coastal areas of Latin America (Wehrtmann and Nielsen-Muñoz 2009). However, the decreasing shrimp catches indicate that the sparse coastal shrimp resources cannot be substituted with the deepwater shrimp fisheries, as these deepwater species are more vulnerable to overexploitation due to their low capacity for recovery (Morato et al. 2006; Wehrtmann and Nielsen-Muñoz 2009). Catches of certain high-trophic-level, large pelagic predators also increased due to the offshore expansion of the fishing grounds. Not only did the species composition in the catches change but also the catches of small and juvenile sciaenids increased. A large fraction of small sciaenids are removed from the gulf at a low weight and size before they attain the weight at first maturity (Alpizar and Vásquez 2012).

Both trends—fishing more heavily on low-trophic-level species and the expansion of the spatial scale to areas where large fish are still more abundant—are common phenomena in tropical fisheries, along with improvements in the gear and modernization of the semi-industrial fleet (Corrales and Vindas 2014). Such a gear improvement occurred in the early 2000s, when a large number of illegal gill nets with smaller mesh sizes was introduced into the Gulf of Nicoya, potentially increasing the yield of smaller and juvenile fish and increasing the success of catching low-value, small coastal fish.

Catches of the lowest and highest trophic levels declined due to the decline of shrimps and large predators, and catches are now dominated by mid-trophic-level species (trophic level = 2.5; i.e., small pelagic and small demersal fishes). However, we found no overall decline in the mTL, an indicator of increasing negative impacts on the ecosystem. One has to consider that the model does not account for the possible size-class and age-class reductions of the species within the model compartments. Furthermore, the mTL of the catch is not a sufficient measure to characterize the fishing impact on the ecosystem, as trends might be masked due to the development of the fishing sector. Hence, one should consider the FiB as an additional indicator (Pauly et al. 2000). In 1993, the FiB was close to zero (0.05; i.e., close to a balanced state); in 2013,
the FiB was 0.1. The FiB index increases as fishery catches increase more rapidly than assumed according to the trophic level declines (Kleisner and Pauly 2011). It has been shown that an increase in the FiB (FiB > 0) is often due to geographic expansion of the fishing fleets (Christensen et al. 2011; Kleisner and Pauly 2011). Therefore, the values explain the constant mTL despite the strong ecological impact of the fishing fleet.

The fishing fleets that operate in the Gulf of Nicoya differ considerably in their impact on the ecosystem due to their gear selectivity. The MTI analysis reflected the selectivity of the different fishing gears. The small pelagic fish fleet operates selectively and almost exclusively catches the target species. In contrast, the shrimp trawlers have an estimated shrimp-to-bycatch ratio of at least 1:7 (Trujillo et al. 2012), and the species landed and discarded are diverse. Among the artisanal fleets, the use of gill nets has the most negative impact on the functional groups in the ecosystem. Demersal species, such as large drums, snooks, and catfishes, are particularly affected. In 1993, rays and sharks were negatively affected by the gill-net fleet; however, this effect decreased greatly in 2013, likely due to the declining biomass of those functional groups and their overall decreasing catches. Another impact factor of the fishing fleet on the ecosystem is the use of small mesh sizes. It has been suggested that since the early 2000s, at least 80% of gill nets in use consist of mesh sizes smaller than 7.62 cm (3 in; Alpízar and Vásquez 2012), which catch almost all of the white shrimp and 36% of the major fish species (Alpízar 2015).

The gross efficiency of the fisheries describes the ratio between the catch and total primary production; in the Gulf of Nicoya, the gross efficiency value for 2013 (0.00113) exceeded the weighted global average of 0.0002 (Christensen et al. 2005) but was comparable to values reported for other coastal systems (e.g., Ullah et al. 2012). Generally, higher values tend to occur in ecosystems where most fisheries’ target species are of lower trophic levels and only a few large predatory species are caught (Godinot and Allain 2003); such is the case in the Gulf of Nicoya, where shrimp and small pelagic fishes represent the bulk of the catches. The gross efficiency of the fishery increased in 2013 compared to that in 1993, most likely due to the gear improvement and the increasing catch volumes of small pelagic fishes, small demersal fishes, and invertebrate species.

Besides the fisheries, environmental factors may have caused changes in the distribution and production of certain species over time. In the Gulf of Nicoya, several environmental factors can be considered to affect shrimp catches. Substantial changes in oceanographic factors, such as sea surface temperature and salinity, could not be observed. However, the 10% loss of mangrove biomass in the Gulf of Nicoya, as an important nursing ground for coastal shrimp species, might have negatively affected shrimp production and enhanced the decline of shrimp biomass. Large-scale environmental processes, such as the El Niño–Southern Oscillation, are also known to affect environmental conditions in the study region; however, these periodical variations are unlikely to have caused the severe decline in shrimp biomass over two decades. To analyze which environmental factors influence the ecosystem, further study is needed whereby environmental information is added to the model to simulate the effects on the ecosystem.

Economics

Although the overall catches increased between 1993 and 2013, the total value and profit of the catches decreased substantially (by 50%) over the two decades of interest (Figure 7). The heavy loss of profits was due to changes in the catches toward low-value species, such as small pelagic and small demersal species. In 2013, shrimps accounted for over 28% of the total value of the catch and therefore constituted only half as much as that in 1993. However, snappers, grunts, and small pelagic fishes increased in importance.

The observed species shifts within certain functional groups did not affect the general model behavior but appeared to have strong impacts on the economy of the fishery. This was the case for the drums and croakers, with only a few species of commercial interest, among which prices vary considerably. Catches of five of the seven commercially important species have declined over the last 10 years—in some cases, by as much as 70%. Finally, changes in the size composition of the catch at the species level must be considered. Currently, a large fraction of juvenile fish, particularly drums and croakers, is believed to be caught in the Gulf of Nicoya (Alpízar 2014). These changes of ecological and socioeconomic concern were not fully revealed by our EwE model. The analysis of the relative age-class distribution indicated increasing catches of small-sized species, which were below the mean weight at first maturity.

The different fleets have different profit margins according to their vessel (engine) sizes and the type of gear in use due to the variance in daily expenses (Bolaños 2005; Gasalla et al. 2010). In some cases, artisanal fishing fleets are able to operate more profitably than semi-industrial fishing fleets due to the gear used and the lower operational and fixed costs (Lery et al. 1999; Tietze 2001; Gasalla et al. 2010). Similarly, it is assumed that the artisanal fleet in the Gulf of Nicoya could develop an advantage over the semi-industrial fleet because of the low costs of artisanal fishing and the benefits of using more selective gear. Furthermore, some artisanal fishery-caught products, such as snappers, large drums, snooks, and sharks, achieve higher market prices
To protect the marine resource in the AMUM, a coastal resources through integrated management (Melissa 1995, with the aim of protecting and conserving marine and coastal resources outside the Gulf of Nicoya and the semi-industrial longline fleet within the gulf have further increased (Arauz 2000; Wehrtmann and Nielsen-Muñoz 2009). The semi-industrial longline fleet was able to increase catches of large pelagic fish, which are a profitable target group (e.g., market prices for marlins and tunas increased by 20–35%; INCOFESCA, unpublished data). The ratio of coastal to deepwater catches shifted from 3:2 to 1:4 and mitigated the decline in coastal catches (Mug-Villanueva 2001). Eventually, the artisanal fishermen will suffer direct negative effects from the lack of coastal resources, and the socioeconomic losses for the whole country are high due to the severe decrease in Costa Rican shrimp and fish exports since the early 2000s (Cornick et al. 2014).

Management Considerations and Outlook

The results of this study confirm the urgency for the enforcement of regulations to protect the marine coastal resources in the Gulf of Nicoya. A minimum mesh size of 7.62 cm (3 in) for gill nets was implemented but with limited success. One important step would be to regulate and enforce the minimum mesh sizes for the gill-net fleet to counteract the trend of increasing catches of juvenile fish, such as sciaenids. The specimens are not only removed from the gulf before they reach the age at first maturity and before they can reproduce, but they also generate low market values for the fishermen.

Another measure is the temporal and spatial closures of certain areas in the Gulf of Nicoya. To protect the country’s large marine environment, certain conservation measures of this type have already been taken. The Gulf of Nicoya was declared a “Marine Area of Multiple Use” (Area Marina de Uso Multiple [AMUM]) by the Costa Rican government in 1995, with the aim of protecting and conserving marine and coastal resources through integrated management (Melissa 2012). To protect the marine resource in the AMUM, a “veda” (an annual 3-month period) was implemented during which the Gulf of Nicoya is closed to fisheries. The temporal closure is supposed to overlap with the reproduction peak of commercially important species to support their recovery (Coyle et al. 2015). The closure can be a good way to reduce fishing effort in general and to support the reproduction of declining species, such as shrimps, sharks, sciaenids, and others.

Due to a lack of efficient control, difficulties in the execution of the fishing ban have occurred (Coyle et al. 2015). During the seasonal closure, a reduction in fishing effort and catches in zones 201 and 202 can be observed; however, catches in the subsequent month are accordingly higher. Moreover, the subsidies given to the fishermen during the temporal closure are hardly sufficient to secure their livelihoods. Consequently, opportunities for alternative livelihood sources for fishermen need to be assessed. Another aim is to entirely ban shrimp trawlers from the coast of Costa Rica by not renewing expired shrimp trawling licenses in the future. This would be an efficient measure to gradually remove trawling. Regulations are needed to resolve the conflict between the artisanal and semi-industrial fishing fleets in terms of the competition for the same limited resources. Furthermore, measures should be taken to protect the keystone species in the ecosystem since the observed decreases in the abundance of key functional groups might have significant implications for ecosystem functioning, and a further decline should be avoided through management. An important step could be the validity control of fishing licenses to address the problem of illegal fishing. The management plans might have led to a small reduction in fishing effort; however, due to the lack of enforcement, the measures have remained primarily ineffective. Thus, it is unlikely that these measures have caused considerable changes in the ecosystem over recent decades.

The two-snapshot approach used in this study is instrumental for the assessment of the current status of the ecosystem and the major changes that occurred over the two decades of interest. Furthermore, the ecosystem-based analysis highlights the importance of certain keystone species that should be considered in management plans due to their high ecological value for the Gulf of Nicoya system (Navia et al. 2016). The models can provide the basis for further simulations to anticipate possible future trends in development (Neira et al. 2014), including fishing effort and environmental trends.

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### Appendix: Additional Data

| Functional group                | Main taxa of group                                                                 |
|--------------------------------|-----------------------------------------------------------------------------------|
| 1. Seabirds                    | Anhinga *Anhinga anhinga*, magnificent frigatebird *Fregata magnificens*, great frigatebird *Fregata minor*, black storm-petrel *Hydrobates melania*, American white pelican *Pelecanus erythrorhynchos*, brown pelican *Pelecanus occidentalis*, neotropic cormorant *Phalacrocorax brasilianus*, boobies *Sula* spp. |
| 2. Mackerels and barracudas    | Pacific Sierra *Scomberomorus sierra*, Mexican Barracuda *Sphyraena ensis*        |
| 3. Rays and sharks              | Spotted Eagle Ray *Aetobatus narinari*, Longtail Stingray *Hypanus (Dasyatis) longus*, Rasptail Skate *Raja velezi*, Peruvian Torpedo *Torpedo peruvianus*, stingrays *Urotrogon* spp., Witch Guitarfish *Zapteryx oxyrinchus*, Brown Smoothhound *Mustelus henlei*, Sicklefin Smoothhound *Mustelus humilatus*, Scalloped Hammerhead *Sphyra lewini* |
| 4. Large drums and snooks       | Queen Corvina *Cynoscion albatus*, Yellowtail Corvina *Cynoscion stolzmanni*, Black Snook *Centropomus nigrescens*, White Snook *Centropomus viridis* |
| 5. Catfishes                    | *Arius* spp., Chihuil *Bagre panamensis*, Long-barbeled Sea Catfish *Bagre pinnimaculatus*, Sculptured Sea Catfish *Notarius kessleri*, Chili Sea Catfish *Notarius troschelii* |
| 6. Morays and eels              | Pacific Bearded Brotula *Brotula clarkae*, Conehead Eel *Cynoponticus coniceps*, morays *Gymnotherax* spp., Yellow Snake Eel *Ophichthus zophochir*, and others |
| 7. Carangids (jacks and pompanos) | Green Jack *Caranx caballus*, jacks *Caranx* spp., Golden Trevally *Gnathanodon speciosus*, leatherjacks *Oligoplites* spp., Pacific Moonfish *Selene peruviana*, Almaco Jack *Seriola rivoliana* |
| 8. Snappers and grunts          | Colorado Snapper *Lutjanus colorado*, Spotted Rose Snapper *Lutjanus guttatus*, Pacific Dog Snapper *Lutjanus novemfasciatus*, *Lutjanus* spp.; Yellowstripe Grunt *Haemulopsis axillaris*, Elongate Grunt *Haemulopsis elongatus*, Mojarra Grunt *Haemulon scudderii*, *Haemulon* spp., *Pomadasys* sp., *
| 9. Cephalopods                  | Crescent octopus *Euaxoctopus panamensis*, squids *Lolliguncula* spp., common octopus *Octopus vulgaris* |
| 10. Lobster                     | Green spiny lobster *Panulirus gracilis* |
| 11. Flatfishes                  | Toothed Flounder *Cyclopes aspina*, Dappled Flounder *Paralichthys woolmani*, Beach Flounder *Syacium latifrons*, Oval Flounder *Syacium ovale*, tonguefishes *Symphurus* spp., soles *Trinectes* sp., and others |
| 12. Small demersals             | Small and juvenile Sciaenidae and Centropomidae, Mullidae, Sparidae, Blenniidae, Gerreidae, *Gobiodia*, *Scopridae*, *Serranidae*, and others |
| 13. Small pelagics              | Anchovies *Anchoa* spp., Anchoveta *Cetengraulis mysticetus*, thread herrings *Opisthonema* spp. |
| 14. Crabs and stomatopods       | Arched box crab *Calappa convexa*, *Callinectes arcuatus*, *Callinectes* spp., *Fleurancodes* sp., mantis shrimp *Squilla* sp., *Gecarcinidae*, *Grapsidae*, *Xanthidae* |
| 15. Epibenthos                  | Ark clams *Anadara* spp., Mytilidae, Ostreidae, and other bivalves; *Strombidae* and other gastropods; *Diogenidae*, *Echinodermata*, *Isopoda*, *Paguridae* |
| 16. Endobenthos                 | Polychaeta: Capitellida, *Orbiniida*, *Spionida*, Branchiostomidae, and others |
| 17. Shrimps                     | Penaeidae: *Liopenaeus* spp., *Heterocarpus* spp., *Farfantepenaeus* spp., *Xiphopenaeus riverti*, titi shrimp *Protrachyopreys* *precipua*, *Rimapenaeus* *byrdii*; *Solenoceridae*: kobori shrimp *Solenocera agassizii* |
| 18. Zooplankton                 | Copepod: Calanoida and others; *Chaetognatha*, *Crustacea larvae*, ichthypoplankton, *Bivalvia* and *Brachiopoda larvae*, *Ostracoda*, *Cladocera*, *Foraminifera*, *Appendicularia* |
| 19. Phytoplankton               | Centric and pennate diatoms, dinoflagellates, and others |
| 20. Mangroves                   | True mangroves *Rhizophora* sp., tea mangroves *Pelicicera* sp., *Avicennia* sp. |
| 21. Microphytes                 | Cyanobacteria, benthic diatoms |
| 22. Detritus                    | |
TABLE A.2. Diet matrix of all functional groups in the Gulf of Nicoya (Costa Rica) model for 2013. The numbers in parentheses indicate the initial input parameters prior to the model balancing routine.

| Group number | Prey                  | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|--------------|-----------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1            | Seabirds              |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 2            | Mackerels and barracudas |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 3            | Rays and sharks       |    |    |    |    |    |    |    | 0.005 |    |    |    |    |    |    |    |    |    |    |
| 4            | Large drums and snooks |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 5            | Catfishes             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 6            | Morays and eels       |    |    |    |    |    |    | 0.05 | 0.01 | 0.02 |    |    |    |    |    |    |    |    |    |
| 7            | Carangids             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 8            | Snappers and grunts   | 0.07 |    | 0.05 | 0.05 |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| 9            | Cephalopods           | 0.02 |    |    |    |    |    |    | 0.08 | 0.05 | 0.05 | 0.1 | 0.03 | 0.02 | 0.15 |    |    |    |
| 10           | Lobster               | 0.01 |    |    |    |    |    |    |    |    |    | 0.14 | 0.02 |    |    |    |    |    |    |
| 11           | Flatfishes            | 0.05 |    |    |    |    |    | 0.05 |    | 0.095 | 0.03 |    |    |    | 0.04 |    |    |    |    |
| 12           | Small demersals       | 0.05 |    | 0.15 | 0.1 | 0.3 | 0.1 | 0.12 |    |    |    | 0.02 | 0.02 | 0.2 |    |    |    |    |    |
| 13           | Small pelagics        | 0.4 |    |    |    |    |    |    | 0.5 | 0.05 |    |    |    | 0.35 | 0.22 | 0.2 |    |    |    |
| 14           | Crabs                 | 0.05 |    |    |    |    |    |    | 0.05 | 0.05 |    | 0.25 | 0.15 | 0.1 | 0.05 | 0.1 | 0.06 | 0.08 | 0.15 |
| 15           | Epibenthos            | 0.3 |    |    | 0.05 |    | 0.25 | 0.1 | 0.35 | 0.35 | 0.2 | 0.4 | 0.3 | 0.55 | 0.45 | 0.3 | 0.3 | 0.3 | 0.05 |
| 16           | Endobenthos           | 0.1 |    |    |    |    |    |    |    |    | 0.2 | 0.2 | 0.1 | 0.15 | 0.2 | 0.2 | 0.2 | 0.05 |
| 17           | Shrimps               | 0.05 |    | 0.2 | 0.1 | 0.15 | 0.14 | 0.12 | 0.1 |    |    |    |    | 0.15 | 0.1 | 0.1 |    |    |    |
| 18           | Zooplankton           |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 0.1 |
| 19           | Phytoplankton         |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 0.5 | 0.1 | 0.05 | 0.05 | 0.2 | 0.1 |
| 20           | Mangroves             |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 0.01 | 0.05 | 0.2 |
| 21           | Microphytobenthos     |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 0.04 | 0.1 | 0.14 | 0.05 | 0.2 |
| 22           | Detritus              |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    | 0.05 | 0.05 | 0.05 | 0.05 | 0.1 | 0.1 |

CHANGES IN THE GULF OF NICOYA FISHERIES SYSTEM
TABLE A.3. Detailed references for the input parameters (biomass \(B_i\), production-to-biomass ratio \(P_i/B_i\), consumption-to-biomass ratio \(Q_i/B_i\), and catch) of each functional group in the updated Ecopath model GN+20 (2013) for the Gulf of Nicoya, Costa Rica (INCOPESCA = Instituto Costarricense de Pesca y Acuicultura; BIOMARCC = Biodiversidad Marino Costera y Adaptación al Cambio Climático).

| Group name                          | \(B_i\)                                | \(P_i/B_i\)                  | \(Q_i/B_i\)                  | Catch                  |
|-------------------------------------|----------------------------------------|-----------------------------|-----------------------------|------------------------|
| Seabirds                            | Wolff et al. (1998), Orias (2004)      | Opitz (1996), Wolff et al. (1998), Olson and Watters (2003) | Opitz (1996), Wolff et al. (1998), Olson and Watters (2003) | INCOPESCA              |
| Mackerels and barracudas            | INCOPESCA                              | Mendoza (1993), Olson and Watters (2003) | Mendoza (1993), Wolff et al. (1998), García and Duarte (2002), Olson and Watters (2003) | INCOPESCA              |
| Rays and sharks                     | Clarke et al. (2011, 2014), Aires-da-Silva et al. (2014), INCOPESCA | Arreguín-Sánchez et al. (2002), Kitchell et al. (2002), Clarke et al. (2014) | Zanella et al. (2011) | INCOPESCA              |
| Large drums and snooks              | Alpízar (2011, 2015), Alpízar and Vásquez (2012, 2013), BIOMARCC (2013a, 2013b), INCOPESCA | INCOPESCA | García and Duarte (2002) | INCOPESCA              |
| Catfishes                           | INCOPESCA                              | Mendoza (1993)              | Mendoza (1993), Wolff et al. (1998), García and Duarte (2002), Giarrizzo et al. (2013) | INCOPESCA              |
| Morays and eels                     | INCOPESCA                              | Wolff et al. (1998)         | García and Duarte (2002), Giarrizzo et al. (2013) | INCOPESCA              |
| Carangids                           | INCOPESCA                              | Arreguín-Sánchez et al. (2002) | García and Duarte (2002), Giarrizzo et al. (2013) | INCOPESCA              |
| Snappers and grunts                 | INCOPESCA                              | Arreguín-Sánchez et al. (2002), Mendoza (1993) | Wolff et al. (1998), García and Duarte (2002), Arreguín-Sánchez et al. (2002), Giarrizzo et al. (2013) | INCOPESCA              |
| Cephalopods                         | INCOPESCA                              | Opitz (1996), Arreguín-Sánchez et al. (2002) | Opitz (1996), Wolff et al. (1998) | INCOPESCA              |
| Lobster                             | Wehrtmann and Nielsen-Muñoz (2009), INCOPESCA | Hemáñez and Wehrtmann (2014) | Opitz (1996), Wolff et al. (1998) | INCOPESCA              |
| Flatfishes                          | INCOPESCA                              | Wolff et al. (1998)         | Wolff et al. (1998), Giarrizzo et al. (2013) | INCOPESCA              |
| Small demersals                     | Alpízar (2011, 2015), Alpízar and Vásquez (2012, 2013) | Opitz (1996), Arreguín-Sánchez et al. (2002) | García and Duarte (2002), Giarrizzo et al. (2013) | INCOPESCA              |
| Small pelagics                      | Chacón et al. (2007), Alpízar (2011, 2015), Alpízar and Vásquez (2012, 2013), BIOMARCC (2013a, 2013b) | INCOPESCA | Wolff et al. (1998), García and Duarte (2002), Giarrizzo et al. (2013) | INCOPESCA              |
| Crabs                               | Fischer and Wolff (2006)               | Dittel and Epifanio (1990), Arreguín-Sánchez et al. (2002) | Fischer and Wolff (2006) | INCOPESCA              |
| Group name    | \(B_i\)                                                                 | \(P/B_i\)                                                                 | \(Q/B_i\)                                                                 | Catch             |
|--------------|------------------------------------------------------------------------|------------------------------------------------------------------------|------------------------------------------------------------------------|------------------|
| Epibenthos   | Vargas and Cortés (1999), Willis and Cortés (2001), Stem-Pirlot and Wolff (2006), Corrales (2010), INCOPESCA | Opitz (1996), Stem-Pirlot and Wolff (2006) | Opitz (1996), Wolff et al. (1998)                                      | INCOPESCA        |
| Endobenthos  | Dean (2004)                                                            | Opitz (1996)                                                            | Opitz (1996), Wolff et al. (1998)                                      | INCOPESCA        |
| Shrimps      | Tabash Blanco and Palacios (1996), Tabash Blanco (2007), Wehrtmann and Nielsen-Muñoz (2009), Trujillo et al. (2012), BIOMARCC (2013a, 2013b), INCOPESCA | INCOPEGSA                                                               | Arreguín-Sánchez et al. (2002), Wolff et al. (1998)                       | INCOPESCA        |
| Zooplankton  | Brugnoli-Olivera et al. (2004)                                          |                                                                         |                                                                         | Brugnoli-Olivera et al. (2004)                                          |
| Phytoplankton| Brugnoli-Olivera and Morales-Ramírez (2008), Soto Rojas (2013)         | Morales-Ramírez (2001), Brugnoli-Olivera et al. (2004)                   | Córdoa-Muñoz (1998), Gocke et al. (2002), Brugnoli-Olivera and Morales-Ramírez (2008), Soto Rojas (2013) | Wolff et al. (1998) |
| Mangroves    | Wolff et al. (1998), FAO (2007), Cortés et al. (2010), Venegas-Li et al., unpublished paper |                                                                         | Wolff et al. (1998), FAO (2007)                                          | Wolff et al. (1998) |
| Microphytobenthos | Wolff et al. (1998)                                                    |                                                                         |                                                                         | Opitz (1996), Wolff et al. (1998)                                        |