Ecosystem trophic structure and energy flux in the Northern Gulf of California, México

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Received 23 October 2002; received in revised form 13 August 2003; accepted 2 September 2003

Abstract

Using the Ecopath with Ecosim software, a trophic structure model of the Northern Gulf of California was constructed to represent the main biomass flows in the system. It was based mostly on bibliographic data and provides a snapshot of how the ecosystem operates. The model consisted of 29 functional groups. The total system throughput was 6633 tonnes/km² per year, from which 51.7% are for internal consumption, 20.0% are for respiration, 16.0% becomes detritus, and 12.2% are removed through commercial fishing. Main results show that most groups were impacted more by predation and competition than by fishing pressure, and that there are some characteristics that indicate that use of the ecosystem is balanced.

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Keywords: Ecopath; Trophic structure; Ecological model; Gulf of California; Fishery; Biosphere reserve

1. Introduction

The Northern Gulf of California (Fig. 1) has a surface area of almost 7200 km² (Nelson et al., 1980) reaching from the Colorado River Delta southward to the large islands of Tiburón and Angel de la Guarda, and have an average depth of 200 m. Nutrient enrichment is driven mainly by tidal mixing (Zeitschel, 1969), resulting in high productivity throughout the year (Lluch-Cota and Arias-Arechiga, 2000).

It is an important fishery, where 77% of the inhabitants are involved in fishing activities (INEGI, 2000), mainly harvesting blue and brown shrimp for packing and shipment from three ports at the most northern end of the Gulf (Puerto Peñasco and Santa Clara in Sonora state and San Felipe in Baja California state; Fig. 1). The northernmost area has great ecological interest because it is considered a natural refuge and nursery area for hundreds of species, including some endemic and some endangered, especially since 1993 it was designated a biosphere reserve from 31°00′ to 32°10′N and 113°30′ to 115°15′W (Gómez-Pompa and Dirzo, 1995; Fig. 1). Since 1997, some environmental organizations have proposed that the southern boundary of the reserve be expanded to the large islands (Tiburón and Angel de la Guarda), restricting the numbers of boats, and banning trawlers, arguing that these protective measures will improve the health of the upper Gulf ecosystem and increase economic opportunities for residents in the longer term (World Wildlife México, 2003). Nevertheless, if these protective measures are approved, they probably will cause a

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significant socio-economic impact on residents of the Northern Gulf of California.

Despite controversy over the conflict between exploitation and conservation in the region, no quantitative data exist on the impact of shrimp extraction, on the ecosystem and on other species. In this study, we present a trophic structure model focused on biomass flows among components and species of ecological and commercial interest, with the purpose of finding parameters that allow estimates of the impact of the fishing activity in the entire ecosystem.

2. Methods and materials

Trophic interactions and energy flux were evaluated using the Ecopath with Ecosim model (EwE; Polovina and Ow, 1983; Polovina, 1984, Christensen and Pauly, 1992). Its basic premise is that, in a given time period, the system will be in balance, that is, production is equal to consumption and is defined by the following equation:

\[ P_i - R_i M_{2i} - P_i (1 - EE_i) - EX_i = 0 \]  

(1)

where for an i group, \( P_i \) is production, \( R_i \) is biomass in tonnes wet weight, \( M_{2i} \) is mortality by predation, EE is ecotrophic efficiency, and \( EX_i \) is export. Ecotrophic efficiency is the proportion of organisms that die by predation and export, including fishing extraction. The first term represents production, the second represents losses by predation, the third represents losses that are not assigned to predation or export, and the last term represents losses by export. The equation is equal to 0 because it is at balance.

Because material transfers between groups is through trophic relationships, Eq. (1) is re-expressed:

\[ B_i \left( \frac{P_i}{B_i} \right) EE_i - \sum_{j=1}^{n} B_j \left( \frac{Q_{ji}}{B_j} \right) DC_{ji} - B_i \left( \frac{Q_{ii}}{B_i} \right) (1 - EE_i) - EX_i = 0 \]  

(2)

where subscript \( j \) represent predators, \( B_j \) is its biomass in tonnes wet weight, \( P/B \) is production to biomass ratio, which is equal to the instantaneous rate of total mortality \( Z \) at equilibrium (Allen, 1971). We used an annual base. \( EE_i \) and \( EX_i \) are the same as in Eq (1), \( Q/B \) is consumption to biomass ratio of group \( j \). Annual base and \( DC_{ji} \) is the fraction of prey \( i \) in the diet of predator \( j \).

Each group was represented by a similar equation, and a system of linear equations was established in which at least three of the four parameters \( (R, P/B, Q/B, \text{ and } EE) \) of each group was known and only one was estimated by the model, if needed. In summary, Eq. (2) describes the biomass flow balance between inputs and outputs for each group.

Most species were included in functional groups sharing similar trophic roles. Only those of particular interest were kept as individual groups: commercially important species such as blue, brown, and rocky shrimp: Litopenaeus stylirostris, Farfantepeneaus californiensis, and Sicyonia penicillata, respectively, and ecologically interesting species such as totoaba, vaquita, and sea lion: Totoaba macdonaldi, Phocoena sinus, and Zalophus californianus, respectively. Our classification resulted in 29 functional groups (Table 1).

Biomass was estimated from published reports (Table 1), and was calculated with the swept area method (Pauly, 1984a,b) that is based on the densities of fish (i.e., the weight of the fish caught per unit area covered by an experimental gear), from which the potential yield can be obtained. When possible, information for different groups came from the same source; for example, we used Pérez-Mellado (1980) for sharks.
Table 1
Sources of input parameters for Northern Gulf of California trophic model

<table>
<thead>
<tr>
<th>Group</th>
<th>Biomass</th>
<th>P/B</th>
<th>Q/B</th>
<th>EE</th>
<th>Diets</th>
</tr>
</thead>
<tbody>
<tr>
<td>Totoaba</td>
<td>4</td>
<td>13</td>
<td>13</td>
<td>–</td>
<td>15</td>
</tr>
<tr>
<td>Vachita</td>
<td>2</td>
<td>–</td>
<td>28</td>
<td>–</td>
<td>28</td>
</tr>
<tr>
<td>Sharks</td>
<td>1</td>
<td>10</td>
<td>27</td>
<td>31</td>
<td></td>
</tr>
<tr>
<td>Sea lion</td>
<td>3</td>
<td>11</td>
<td>28</td>
<td>32</td>
<td></td>
</tr>
<tr>
<td>False whales</td>
<td>3</td>
<td>12</td>
<td>28</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Hakes</td>
<td>5</td>
<td>18</td>
<td>18</td>
<td>35</td>
<td></td>
</tr>
<tr>
<td>Whales</td>
<td>3</td>
<td>12</td>
<td>28</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Croakers</td>
<td>1</td>
<td>15</td>
<td>15</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>Guitarfish</td>
<td>1</td>
<td>17</td>
<td>17</td>
<td>34</td>
<td></td>
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<tr>
<td>Groupers</td>
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<td>16</td>
<td>34</td>
<td></td>
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<td>23</td>
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<tr>
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<td>30</td>
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<tr>
<td>Rays</td>
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<td>22</td>
<td>39</td>
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<tr>
<td>Rocky shrimp</td>
<td>8</td>
<td>8</td>
<td>30</td>
<td>42</td>
<td></td>
</tr>
<tr>
<td>Flat fishes</td>
<td>1</td>
<td>19</td>
<td>19</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td>Other fishes</td>
<td>1</td>
<td>14</td>
<td>14</td>
<td>–</td>
<td>Supposed</td>
</tr>
<tr>
<td>Linter fish</td>
<td>–</td>
<td>21</td>
<td>21</td>
<td>Supposed</td>
<td>38</td>
</tr>
<tr>
<td>Blue shrimp</td>
<td>7</td>
<td>24</td>
<td>30</td>
<td>42</td>
<td></td>
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<tr>
<td>Cephalopods</td>
<td>–</td>
<td>23</td>
<td>29</td>
<td>Supposed</td>
<td>40</td>
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<tr>
<td>Polyhachites</td>
<td>–</td>
<td>26</td>
<td>30</td>
<td>Supposed</td>
<td>30</td>
</tr>
<tr>
<td>Grunts</td>
<td>1</td>
<td>14</td>
<td>14</td>
<td>34</td>
<td></td>
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<tr>
<td>Majeunas</td>
<td>1</td>
<td>14</td>
<td>14</td>
<td>33</td>
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<tr>
<td>Small pelagics</td>
<td>1</td>
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<td>20</td>
<td>37</td>
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<tr>
<td>Benthic macro-invertebrates</td>
<td>7</td>
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<td>Supposed</td>
<td>30</td>
<td></td>
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<tr>
<td>Zooplankton</td>
<td>–</td>
<td>Supposed</td>
<td>–</td>
<td>Supposed</td>
<td>Supposed</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>–</td>
<td>Supposed</td>
<td>–</td>
<td>Supposed</td>
<td>–</td>
</tr>
<tr>
<td>Algae</td>
<td>9</td>
<td>Supposed</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Detritus</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

Sources of information corresponding to numbers:

For commercially unimportant groups, P/B corresponded to the instantaneous rate of natural mortality (M). M was estimated from data in FishBase (Froese and Pauly, 2001) for fish species, using the empirical equation of Pauly (1980) and P/B = 1.5 as a first estimate because information on by-catch mortality is lacking. We used mortality values reported in the literature for the remaining functional groups.

The Q/B relation represents the amount of food ingested by a group with respect to its own biomass in a given period. Values for fish groups were computed with the empirical equation of Jarre et al. (1990), which considers environmental temperature, fish weight and size, and caudal fin morphology. The algorithm is available in FishBase (Froese and Pauly, 2001). For invertebrates, sharks, and rays, Q/B was...
taken from the literature (Table 1). For marine mammals, $Q_B$ was estimated by dividing daily ingestion weight during a year by body weight of an average individual (García-Rodríguez, 1999; IMMA, 2001). In most cases, the software computed ecotrophic efficiency, since Eq. (2) assumes balance between terms. However, we assumed a value of EE based on literature for the same or a similar species when no input data were available (Table 1). A predator-prey matrix was developed from reports of stomach contents for the different functional groups, using reports for similar species or groups when no data were available.

Fishing fleets and catches ($Y_i$) of important species were included in the model, impacting on the following groups: shrimp (three species), croakers (Sciaenides), guitar fish (Rhinobatides), groupers (Epinephelus sp.), rays (Dasyatides, Myliobatides, and Rajides), and flat fish (Pleuronectides and Paralichthys), grunts (Haemulides), mojarres (Gerreid, Sparidae), and crabs (Callinectes sp.). Data were obtained from San Felipe and Puerto Peñasco fisheries regional offices.

We used EE $< 1$ as the primary criterion to balance the model. The diet matrix was adjusted by modifying the initial values and producing small changes. We selected this approach because diet is the source of greatest uncertainty and we avoided large modifications of the feeding patterns of functional groups. For example, the vaquita mainly feeds on fish, so we changed its initial consumption of hake from 0.92 to 0.086 without modifying its diet pattern.

Consistency of the model was mainly verified by comparing trends in the respiration to biomass ratio ($R/B$), which must be higher for active species than for sedentary groups.

Once the model was balanced and consistent, we minimized residuals with the Ecotramer routine (Pauly and Christensen, 1996), which allows entry of a range and mean/mode values for all basic parameters, i.e., biomass, consumption rates, production rates, ecotrophic efficiencies, and all elements of the composition of diets. Random input variables are then drawn with specific frequency distributions selected by the user. In this case, we used normal distribution for all parameters. The resulting model was then evaluated with defined criteria and physiological and mass balance constraints. The process was repeated in a Monte-Carlo fashion included in the routine of the model runs that pass the selection criteria, the best-fitting one was chosen with a least square criterion.

$EwE$ was used also to evaluate various flow indices, such as total system ascendency (measure of ecosystem flow; Christensen, 1994, 1995; Pérez-España and Arregui-Sánchez, 2001), total system throughput (sum of flows and measure of ecosystem size; Ulanowicz and Norden, 1990), and path length (average number of groups that an inflow or outflow passes through). Additionally, mixed trophic impacts of each group and other physiological information about species groups and the ecosystem, such as transfer efficiencies, omnivore index, respiration, and assimilation, were computed (Christensen and Pauly, 1993; Vega-Cendejas and Arregui-Sánchez, 2001).

### 3. Results

Table 2 shows values of the balanced model, including those estimated by the software. The first column shows the trophic level (TL), a dimensionless index (Christensen et al., 2000). In Ecopath, TL can be an integer or a fraction, as suggested by Odum and Heald (1975). We obtain four discrete TLs, and except for grunts, all fish groups obtained a TL very close to the reported in the FishBase database (Froese and Pauly, 2003).

Other parameters shown in Table 2 are biomass in habitat area, which is the biomass in the area where the group most probably occurs. For groups that are homogeneously distributed, the biomass in area is the same of the total biomass value.

For the detritus group, a relatively low EE was obtained, meaning that biomass accumulation is greater than consumption and the difference is assumed to either end up as accumulated detritus, buried as sediment, or exported from the system (Christensen et al., 2000). In general terms, high EE resulted for primary producers (0.90) and lower values for top predators, except totuaba (0.85), probably resulting from underestimating biomass.

Table 3 shows ecological attributes estimated with the software, and used to test model consistency. Nutritional conversion efficiency ($q_i$) ranged from 0.009 to 0.488 (tonnes per year) with an inverse relationship to trophic level. The respiration to biomass ($R/B$) ratio
was consistent with other authors (Jarre-Teichmann, 1992; Arregui-Sánchez et al., 1993a,b; Olivieri et al., 1993; Pauly and Christensen, 1996; Vega-Cendejas, 1998; Zetina-Rejón, 1999). Respiration to assimilation ratio ranged from 0.390 to 0.989 tonnes/km² per year, with the highest value corresponding to high trophic level. High values of omnivory corresponded to crabs, mojarres, and grunts, suggesting that predators have a relatively narrow trophic range compared with lower levels. This was not consistent with the false whales group that had the lowest omnivory, but it was probably due to its ichthyophagous nature, and to the small differentiation between the fish groups that were considered.

Table 4 shows the adjusted predator–prey matrix. Table 5 shows the basic attributes of the system: The total system throughput was 6633 tonnes/km² per year, where internal consumption accounts for 51.7% of total flows, respiration for 20%, detritus for 16.1%, and export out of the system (commercial fishing) for 12.2%.

Total primary production to respiration ratio (TPP/R) was 1.61, indicating that TPP is approximately 60% greater than respiration. The total primary production to biomass ratio was 17.38 tonnes/km² per year, suggesting a nearly mature state because this rate is lower when the system approaches maturity (Odum, 1969; Christensen, 1995). The connectance index is the proportion of theoretically possible trophic connections, and had a value of 0.319.

Table 6 shows an ascendency (A) value of 6187.8 flow bits, with 10.9% corresponding to internal flows.

### Table 2

<table>
<thead>
<tr>
<th>Group</th>
<th>Trophic level</th>
<th>Habitat area (fraction)</th>
<th>Biomass habitat tonnes/fraction (tonnes/km²)</th>
<th>Biomass biomass tonnes/km²</th>
<th>P/B (tonnes per year)</th>
<th>Q/B (tonnes per year)</th>
<th>EE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Totoaba</td>
<td>4.20</td>
<td>0.15</td>
<td>0.010</td>
<td>0.066</td>
<td>0.400</td>
<td>5.00</td>
<td>0.847</td>
</tr>
<tr>
<td>2 Vaquita</td>
<td>4.10</td>
<td>0.30</td>
<td>0.002</td>
<td>0.005</td>
<td>0.600</td>
<td>30.00</td>
<td>0.563</td>
</tr>
<tr>
<td>3 Sharks</td>
<td>4.10</td>
<td>0.60</td>
<td>0.474</td>
<td>0.790</td>
<td>0.280</td>
<td>3.00</td>
<td>0.764</td>
</tr>
<tr>
<td>4 Sea lion</td>
<td>4.00</td>
<td>0.10</td>
<td>0.033</td>
<td>0.330</td>
<td>0.544</td>
<td>23.73</td>
<td>0.362</td>
</tr>
<tr>
<td>5 False whales</td>
<td>3.90</td>
<td>0.60</td>
<td>0.138</td>
<td>0.230</td>
<td>0.216</td>
<td>26.45</td>
<td>0.199</td>
</tr>
<tr>
<td>6 Hakes</td>
<td>3.90</td>
<td>0.30</td>
<td>0.148</td>
<td>0.490</td>
<td>0.450</td>
<td>1.85</td>
<td>0.084</td>
</tr>
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<td>7 Whales</td>
<td>3.60</td>
<td>0.50</td>
<td>0.190</td>
<td>0.380</td>
<td>0.200</td>
<td>2.92</td>
<td>0.171</td>
</tr>
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<td>8 Croakers</td>
<td>3.50</td>
<td>0.30</td>
<td>0.346</td>
<td>1.152</td>
<td>2.950</td>
<td>12.10</td>
<td>0.362</td>
</tr>
<tr>
<td>9 Guitar fish</td>
<td>3.50</td>
<td>0.30</td>
<td>0.346</td>
<td>1.152</td>
<td>2.950</td>
<td>12.10</td>
<td>0.362</td>
</tr>
<tr>
<td>10 Groupers</td>
<td>3.50</td>
<td>0.25</td>
<td>0.294</td>
<td>0.790</td>
<td>0.200</td>
<td>3.60</td>
<td>0.171</td>
</tr>
<tr>
<td>11 Squillas</td>
<td>3.30</td>
<td>0.55</td>
<td>0.264</td>
<td>0.480</td>
<td>6.300</td>
<td>12.90</td>
<td>0.945</td>
</tr>
<tr>
<td>12 Crabs</td>
<td>3.30</td>
<td>0.55</td>
<td>0.029</td>
<td>0.053</td>
<td>2.650</td>
<td>6.28</td>
<td>0.982</td>
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<td>13 Rays</td>
<td>3.20</td>
<td>0.30</td>
<td>0.563</td>
<td>1.878</td>
<td>3.450</td>
<td>18.40</td>
<td>0.944</td>
</tr>
<tr>
<td>14 Rockey shrimp</td>
<td>3.10</td>
<td>0.45</td>
<td>0.090</td>
<td>0.200</td>
<td>3.000</td>
<td>8.50</td>
<td>0.923</td>
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<tr>
<td>15 Flat fishes</td>
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<td>1.954</td>
<td>3.343</td>
<td>4.950</td>
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<td>0.499</td>
</tr>
<tr>
<td>16 Other fishes</td>
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<td>1.00</td>
<td>5.540</td>
<td>5.540</td>
<td>1.950</td>
<td>5.60</td>
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<td>0.60</td>
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<td>2.089</td>
<td>2.500</td>
<td>7.94</td>
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<td>0.026</td>
<td>0.064</td>
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<td>8.50</td>
<td>0.997</td>
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<tr>
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<td>0.50</td>
<td>0.450</td>
<td>0.900</td>
<td>4.030</td>
<td>10.20</td>
<td>0.864</td>
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<td>0.40</td>
<td>3.186</td>
<td>7.966</td>
<td>3.450</td>
<td>11.68</td>
<td>0.750</td>
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<td>1.00</td>
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<td>22.933</td>
<td>8.000</td>
<td>27.00</td>
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<td>0.40</td>
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<td>2.850</td>
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<td>1.650</td>
<td>8.20</td>
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<td>0.30</td>
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<td>0.243</td>
<td>3.980</td>
<td>10.30</td>
<td>0.981</td>
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<tr>
<td>25 Benthic macro-invertebrates</td>
<td>2.50</td>
<td>1.00</td>
<td>2.886</td>
<td>2.886</td>
<td>38.000</td>
<td>84.00</td>
<td>0.975</td>
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<td>26 Zooplankton</td>
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<td>1.00</td>
<td>39.455</td>
<td>39.455</td>
<td>27.00</td>
<td>60.00</td>
<td>0.900</td>
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<td>1.00</td>
<td>33.949</td>
<td>33.949</td>
<td>60.00</td>
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<td>28 Algae</td>
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<td>1.610</td>
<td>2.500</td>
<td>60.00</td>
<td>–</td>
<td>0.900</td>
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<td>1.00</td>
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Table 3  
Ecological attributes for the upper Gulf of California model

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<tr>
<th>Group</th>
<th>$g$ (tonnes per year)</th>
<th>$R/B$ (tonnes/km$^2$ per year)</th>
<th>Assimilation (tonnes/km$^2$ per year)</th>
<th>Respiration/assimilation (tonnes/km$^2$ per year)</th>
<th>Production (tonnes/km$^2$ per year)</th>
<th>Flow to detritus (tonnes/km$^2$ per year)</th>
<th>Omnivory index</th>
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<td>Totoaba</td>
<td>0.080</td>
<td>0.55</td>
<td>0.040</td>
<td>0.904</td>
<td>0.004</td>
<td>0.011</td>
<td>0.117</td>
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<td>7.00</td>
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<td>0.975</td>
<td>0.001</td>
<td>0.009</td>
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<td>1.138</td>
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Ascendency is a measure of the information content in the ecosystem derived from information theory (Ulanowicz and Norden, 1990), is symmetrical, and will have the same value whether calculated from input or output. The upper limit for the size of the ascendency corresponds to the development capacity (DC). In this case, DC was of 25925.3 flow bits. With those parameters, we interpreted ascendency in the current state of the ecosystem to be 24% of the development capacity ($A_{DC}$). The difference between the DC and the $A_{DC}$ is the system overhead, that is, the maximum energy reserve of the ecosystem for potential use against disturbances (Ulanowicz, 1986). We obtained a high overhead when compared with other ecosystems (i.e., 16435.8 for the Huizache-Caimanero coastal lagoon, Zetina-Rejón, 1999; 17832.4 for the Veracruz continental shelf, Cruz-Escalona, personal communication), and this was probably a result of the large amount of detritus and the relatively high flows of biomass from detritus of living groups, since detritus was considered as a group that allows modulation of trophic impacts (Pérez-España and Arreguin-Sánchez, 2001).

Fig. 2 shows the biomass flows (only flows greater than 10% of the total are shown). The size of the box is proportional to biomass for each group. Boxes are distributed on the Y-axis according to trophic level. Trophic interactions, expressed in proportions from 0 to 1, were analyzed by trophic niche overlaps (Fig. 3). Values close to unity indicate large trophic

...
Table 4
Adjusted diet matrix for upper Gulf of California model

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<th>6</th>
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<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
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<tr>
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</tr>
</tbody>
</table>

| 1 - Totoaba | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 2 - Vaquita | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 3 - Shark | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 4 - Sea lion | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 5 - False whales | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 6 - Hakes | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 7 - Whales | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 8 - Creakers | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 9 - Guitarfish | 0 |     |     |     |     |     |     |     |     |     |     |     | 0.001 |
| 10 - Groupers | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 11 - Squillas | 0.007 |     |     |     |     |     |     |     |     |     |     |     | 0.018 |
| 12 - Crabs | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 13 - Rays | 0.012 |     |     |     |     |     |     |     |     |     |     |     | 0.005 |
| 14 - Rocky shrimp | 0.001 | 0 |     |     |     |     |     |     |     |     |     |     | 0.001 |
| 15 - Flat fishes| 0.012 | 0.023 |     |     |     |     |     |     |     |     |     |     | 0.002 |
| 16 - Other fishes| 0.059 | 0.012 | 0.037 |     |     |     |     |     |     |     |     |     | 0.029 |
| 17 - Lantern fish| 0.001 | 0.117 |     |     |     |     |     |     |     |     |     |     |     |
| 18 - Brown shrimp | 0 |     |     |     |     |     |     |     |     |     |     |     |     |
| 19 - Blue shrimp | 0.005 | 0.012 |     |     |     |     |     |     |     |     |     |     | 0.006 |

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niche overlap. High overlap corresponds to detritus consumers and some planktivorous groups, such as small pelagic and linter fish. Direct and indirect impacts between groups in the ecosystem were computed and are shown in Fig. 4 for selected groups, i.e., those targeted for conservation, such as totoaba, vaquita, and sea lion, and important fisheries resources, such as shrimp. In general terms, mammals impacted negatively on other mammals, probably because they share similar prey. Species targeted for conservation were slightly impacted negatively by fishing fleets, with the exception of sea lions and shrimp fleets. Although totoaba were impacted most, vaquita were affected negatively, probably because of its very small population or lack of information. Detritus in the system affected almost all groups positively, as happens in the coastal lagoons where discrete trophic levels, mostly in the 3.0–4.0 range, and were attributed to dependence of the food web on detritus and to the abundance of juvenile fish using lagoons as nursery areas (Yáñez-Arancibia et al., 1988; Manikchand-Haileman et al., 1998a). In contrast, some authors reported high fractional trophic levels for continental shelf ecosystems (Arreguín-Sánchez et al., 1993b; Manikchand-Haileman et al., 1998b), where adult fish were expected to be more abundant. In this work, we found neither was dominant. However, we observed a distribution proportional to the number of groups in the 2.5–3.6 range, including almost all invertebrates and many fish groups, most of them primary or secondary consumers. Accordingly, we hypothesized that, since there are many detritovores in lagoons, the Northern Gulf of California is used as a nursery and a maturing area where many groups reach adult age.

4. Discussion

Comparing this model with five models of marine ecosystems used around Mexico, we observed that ratios of total consumption and total respiration to total system throughput suggest higher energy use in

Table 4 (Continued)

<table>
<thead>
<tr>
<th>Prey</th>
<th>Predator</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cephalopods</td>
<td></td>
<td>0.049</td>
<td>0.117</td>
<td>0.112</td>
<td>0.002</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polychaetes</td>
<td></td>
<td>0.241</td>
<td>0.154</td>
<td>0.097</td>
<td>0.298</td>
<td>0.156</td>
<td>0.16</td>
<td>0.212</td>
<td>0.276</td>
<td>0.087</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grunts</td>
<td></td>
<td>0.087</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molluscs</td>
<td></td>
<td>0.041</td>
<td>0.016</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small pelagics</td>
<td></td>
<td>0.347</td>
<td>0.342</td>
<td>0.095</td>
<td>0.224</td>
<td>0.333</td>
<td>0.101</td>
<td>0.175</td>
<td>0.139</td>
<td>0.053</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthic macro-invertebrates</td>
<td></td>
<td>0.121</td>
<td>0.228</td>
<td>0.352</td>
<td>0.022</td>
<td>0.199</td>
<td>0.49</td>
<td>0.283</td>
<td>0.009</td>
<td>0.501</td>
<td>0.177</td>
<td>0.300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zooplankton</td>
<td></td>
<td>0.051</td>
<td>0.122</td>
<td>0.377</td>
<td>0.084</td>
<td>0.119</td>
<td>0.361</td>
<td>0.155</td>
<td>0.461</td>
<td>0.24</td>
<td>0.700</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phytoplankton</td>
<td></td>
<td>0.023</td>
<td>0.017</td>
<td>0.034</td>
<td>0.047</td>
<td>0.324</td>
<td>0.188</td>
<td>0.038</td>
<td>0.127</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Algae</td>
<td></td>
<td>0.216</td>
<td>0.364</td>
<td>0.078</td>
<td>0.286</td>
<td>0.24</td>
<td>0.037</td>
<td>0.255</td>
<td>0.199</td>
<td>0.576</td>
<td>0.317</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Quantities are percentages of each prey in the diet of each predator.
Fig. 2. Flowchart of biomass showing trophic interactions in the Northern Gulf of California system. All flows are expressed in tonnes/km² per year. Boxes are placed on the Y-axis according to trophic level; the size of each is proportional to biomass for each group. B: biomass, P: production, and Q: consumption.
Table 6

<table>
<thead>
<tr>
<th>Source</th>
<th>Ascendency</th>
<th>Overhead</th>
<th>Capacity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flow bits</td>
<td>Percent</td>
<td>Flow bits</td>
</tr>
<tr>
<td>Import</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Internal flow</td>
<td>2822.9</td>
<td>10.9</td>
<td>15138.8</td>
</tr>
<tr>
<td>Export</td>
<td>2072.1</td>
<td>8.5</td>
<td>540.8</td>
</tr>
<tr>
<td>Respiration</td>
<td>1292.8</td>
<td>5.5</td>
<td>4057.6</td>
</tr>
<tr>
<td>Total</td>
<td>6187.8</td>
<td>23.9</td>
<td>19737.1</td>
</tr>
</tbody>
</table>

The Northern Gulf of California ecosystem; in fact the two indices are about 68 and 27%, respectively, higher than the average of the ecosystems that were compared. The connectance index and system omnivory are 16 and 95% higher than the averages, suggesting that the Northern Gulf of California is highly dynamic, more complex, and probably a more mature ecosystem among those compared (Table 7).

One of the main challenges in ecosystem theory is to define ecosystem reference point (ERP), which can be...
Fig. 4. Selected mixed trophic impact groups of the Northern Gulf of California model. Positive and negative effects on biomass of each group are represented above and below the line.
Table 7
Comparison of ecosystem statistics

<table>
<thead>
<tr>
<th>Index</th>
<th>Veracruz</th>
<th>Yucatán</th>
<th>Campeche</th>
<th>Central GC</th>
<th>Northern GC</th>
<th>Average</th>
<th>Maximum/average (%)</th>
<th>Minimum/average (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC/TST</td>
<td>0.456</td>
<td>0.327</td>
<td>0.622</td>
<td>0.707</td>
<td><strong>1.068</strong></td>
<td>0.636</td>
<td>167.89</td>
<td>51.39</td>
</tr>
<tr>
<td>SR/TST</td>
<td>0.266</td>
<td>0.187</td>
<td>0.376</td>
<td>0.391</td>
<td><strong>0.414</strong></td>
<td>0.327</td>
<td>126.65</td>
<td>57.37</td>
</tr>
<tr>
<td>SFD/TST</td>
<td>0.278</td>
<td>0.123</td>
<td>1.439</td>
<td>0.216</td>
<td><strong>1.068</strong></td>
<td>0.636</td>
<td>167.89</td>
<td>51.39</td>
</tr>
<tr>
<td>SAP/TST</td>
<td>0.186</td>
<td>0.215</td>
<td>1.574</td>
<td>0.715</td>
<td><strong>2.159</strong></td>
<td>0.759</td>
<td>195.40</td>
<td>55.68</td>
</tr>
<tr>
<td>TP TR</td>
<td>0.389</td>
<td>0.754</td>
<td>3.063</td>
<td>1.385</td>
<td><strong>1.068</strong></td>
<td>0.636</td>
<td>167.89</td>
<td>51.39</td>
</tr>
<tr>
<td>TB/TST</td>
<td>0.199</td>
<td>0.032</td>
<td>0.010</td>
<td>0.015</td>
<td><strong>0.019</strong></td>
<td>0.019</td>
<td>168.42</td>
<td>52.63</td>
</tr>
<tr>
<td>CI</td>
<td>0.244</td>
<td>0.278</td>
<td>0.281</td>
<td>0.245</td>
<td><strong>0.318</strong></td>
<td>0.273</td>
<td>116.40</td>
<td>89.31</td>
</tr>
<tr>
<td>SO</td>
<td>0.155</td>
<td>0.195</td>
<td>0.173</td>
<td>0.327</td>
<td><strong>0.544</strong></td>
<td>0.278</td>
<td>195.40</td>
<td>55.68</td>
</tr>
<tr>
<td>CMTL</td>
<td>3.440</td>
<td>4.110</td>
<td>2.620</td>
<td>2.990</td>
<td><strong>3.026</strong></td>
<td>2.930</td>
<td>126.15</td>
<td>86.56</td>
</tr>
</tbody>
</table>

Bold numbers are maximum values, and italic numbers are minimum values.

SC: sum of consumption; TST: total system throughput; SR: sum of respiration; SFD: sum of flows to detritus; SAP: sum of production; TR: total respiration; TPP: total primary production; TB: total biomass; CI: connectance index; SO: system omnivory; CMTL: catch mean trophic level.

used for management purposes in the same way as biological reference point (BRP), for exploited fish stocks (Hilborn and Walters, 1992). Even when no ERPs have been defined, some ecosystem attributes can be used to prevent negative influences of exploitation on ecosystem health. Pauly et al. (1998) explained that “fishing down the food web” is a symptom of ecosystem deterioration when high trophic levels are being overexploited. In a similar way, Arreguín-Sánchez et al. (2003a) describe “fishing up the food web” when a low trophic level is overexploited. In both cases, ecosystem structure and function change. Arreguín-Sánchez et al. (2003a) suggest that the balance of production and losses through trophic levels can be used to measure how the ecosystem is being exploited. However, the lower limits of production that are needed to maintain or recover an ecosystem remain unknown. One approach to measure this balance is through biomass and trophic catch pyramid analysis. A pyramid apex angle is an index of ecosystem structure (Pauly and Christensen, 1993). If the angles for biomass and catch pyramids are not significantly different, one interpretation is that use of the ecosystem is balanced. In the case of the upper Gulf of California, the difference between biomass decrease rate (1.07) and catch rate (0.97) with trophic level is less than 10%. Additionally, mixed trophic impact analysis shows that the most affected groups were impacted more by predation and competition than by fishing pressure (Fig. 4).

We suggest that the last point must be examined in future works to increase and improve the foundations that allow more precise evaluations of the health of the system, and for obtaining more specific tools to make better decisions about ecological regulation of the system.

Acknowledgements

F.A.S. thanks the Consejo Nacional de Ciencia y Tecnología (CONACYT) project 34865-B, Instituto Politécnico Nacional (IPN) CGPI project 20010287, COFAA, EDI, and INCO-DC project “Putting fisheries in the ecosystem context.” JLM and SLC received support from CIBNOR project EP3.1. MVMZ holds CONACYT scholarship No. 144436. Thanks to the CIBNOR editing staff.

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