



# Meta-analysis of Ecopath models reveals secondary productivity patterns across the Gulf of Mexico



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## ABSTRACT

The Gulf of Mexico large marine ecosystem (LME) is ecologically and economically important, yet faces numerous anthropogenic stressors. Common metrics driving ecosystem assessment and management, particularly at the LME scale, include fisheries harvest and primary productivity. However, neither is adequate in revealing a complete picture of ecosystem health. Secondary production is an important functional component of marine ecosystems. Yet, inherent difficulties in measuring higher productivity limit its use as an ecosystem indicator. The goals of this study were to: 1) use existing ecosystem models to estimate secondary production within the Gulf of Mexico, 2) identify productivity hotspots based on spatial patterns of secondary productivity across the Gulf LME, 3) compare trophic structure, function, efficiency, and productivity among ecosystem types within the Gulf, and 4) determine effectiveness of primary productivity as an indicator of secondary productivity. A meta-analysis of 18 Ecopath models describing Gulf of Mexico subsystems was conducted. Representative systems included temperate estuaries, tropical lagoons, continental shelves, and coral reefs. Annual secondary production ranged from 128 tonnes (t) wet weight (ww) km<sup>-2</sup> in Tampamachoco Lagoon to 15 466 t ww km<sup>-2</sup> in the Florida Keys. Spatial patterns of secondary productivity across the Gulf of Mexico LME demonstrate higher values in coastal regions, especially coral reefs. Secondary production is largely supported by benthic food webs across all ecosystems. Benthic food webs are also more efficient with regards to transfer of production than pelagic food webs. No significant relationships between primary and secondary production were observed via linear regression for any ecosystem type, indicating that primary production is not a strong indicator of secondary production. Comparative analyses of ecosystems across the Gulf of Mexico, such as the one presented here, identify critical areas at the LME scale, and support ecosystem-based management initiatives.

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## 1. Introduction

Large marine ecosystems (LMEs) are expanses of ocean >200 000 km<sup>2</sup> that are defined by distinct features including bathymetry, hydrography, trophic dynamic relationships, and ecosystem productivity (Sherman and Hempel, 2009). LMEs are typically associated with coasts and continental shelves, encompassing the most ecologically and economically productive areas of the ocean. The shift toward ecosystem-based management has

emphasized the need to examine ecosystem dynamics and ecological health at the LME scale (Crowder and Norse, 2008; Sherman and Hempel, 2009).

Assessing ecosystem health requires an examination of the structure and function of the system. While it is relatively easy to directly measure structural components of ecosystems, it is difficult to analyze functional components, such as energy flows or rates of processes. An important functional component of ecosystems is productivity. The majority of primary production occurs via photosynthesis by plants and algae. Secondary production is the conversion of energy from primary producers by consumers to produce new biomass. Tertiary production is the conversion of energy from prey by higher-trophic level predators. It is common to simultaneously examine secondary and tertiary productivity, with no distinction made between these two trophic levels, and this approach is taken throughout this analysis. Thus, all productivity

*Abbreviations:* ZOP, zooplankton; BEN, macro-, meio-, and micro-benthos; CMB, crustaceans, molluscs, and other mega-benthos; DEM, demersal fishes; PEL, pelagic fishes; SKR, sharks and rays; MAM, marine mammals; BRD, seabirds; PPD, primary producers; SPD, total secondary production (i.e., sum of all groups, excluding PPD).

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occurring higher than at the primary level will be referred to as secondary productivity.

Common metrics driving management decisions within LMEs include fisheries harvest and primary productivity (Sherman and Hempel, 2009). However, neither is adequate in revealing a complete picture of the health or integrity of an ecosystem. Fisheries harvest is often referred to as productivity, and while it is true that economic productivity occurs when resources are harvested, this is not equivalent to ecological productivity (Pauly and Christensen, 1995; Ryther, 1969). Fisheries harvest is ultimately driven by economic and regulatory factors. Primary productivity alone is useful and relatively easy to measure directly, but it is also important to examine productivity at higher trophic levels (i.e., secondary production). Unfortunately, obtaining direct measurements of higher productivity in the field is difficult (Rigler and Downing, 1984).

Models are an important tool because of difficulties inherent with large scale studies (Li et al., 2009; Vidal and Pauly, 2004). Models essentially represent sets of hypotheses about how systems work. Ecosystem models, by definition, include more than one trophic component of a system and incorporate external influences such as chemical, climatological or physical factors (Fulton, 2010). Model construction is typically driven by the need to understand ecosystem processes (e.g., productivity, diversity, connectivity, and resilience) and the factors that influence these processes (Morissette, 2007; Plaganyi, 2007). Ecosystem models are an aggregation of the best available data and knowledge of a system, and the science necessary for developing ecosystem-based management initiatives can be derived from such models (Li et al., 2009; Murawski et al., 2010; Plaganyi, 2007).

The goals of the current study were to: 1) use existing ecosystem models to estimate secondary production within the Gulf of Mexico, 2) identify productivity hotspots based on spatial patterns of secondary productivity across the Gulf LME, 3) compare trophic structure, function, efficiency, and productivity among ecosystem types within the Gulf, and 4) determine effectiveness of primary productivity as an indicator of secondary productivity. The Ecopath software suite is one of the most widely-used whole ecosystem modeling domains. Here we compare results from Ecopath models from different subsystems within the Gulf of Mexico.

## 2. Study area

The Gulf of Mexico is one of 64 defined LMEs world-wide (Sherman and Hempel, 2009). Often referred to as America's fish market and gas station, the Gulf faces severe anthropogenic stressors. Fishing in the Gulf is a multi-billion dollar industry, supporting a large number of coastal residents. The Gulf of Mexico accounts for a large percentage of the total United States (U.S.) landings of shrimp (72%), oysters (66%), and domestic fish (18%). Mexico's shrimp (45%), oyster (90%), and domestic fish (50%) fisheries are also largely supported by the Gulf (Yanez-Arancibia and Day, 2004). The Gulf of Mexico is an important resource for oil and gas exploration and drilling activities, contributing to more than half of the U.S. crude oil (54%) and natural gas (52%) production (NOAA, 2011), and nearly all of Mexico's oil (80%) and gas (90%) production (Yanez-Arancibia and Day, 2004).

The coastal zone experiences the most direct and severe anthropogenic disturbances, including coastal development, land-use change, freshwater diversion, increased pollutant and nutrient loading, and direct extraction from, and use of, estuaries and coasts (Bricker et al., 2008; Lotze et al., 2006; Montagna et al., 2002). Growing coastal populations are particularly influential on coastal development and land-use change. In 2000, populations within Gulf States exceeded 48 and 14 million in the U.S. and Mexico, respectively (Adams et al., 2004). Expansive drainage

basins contribute to pollution and eutrophication of the Gulf, particularly in the Mississippi River Delta region. The drainage basin of the Gulf covers more than 60% of the continental U.S. and 40% of Mexico (Yanez-Arancibia and Day, 2004). Nutrient loading can trigger hypoxic events that result in mass mortalities of fish and other marine life. The annual hypoxia event off the Louisiana coast, often referred to in the media as the "dead zone," can occupy an area greater than 20 000 km<sup>2</sup> (Rabalais et al., 2002). These anthropogenic stressors have led to significant degradation of estuarine and marine ecosystems over the past century.

## 3. Methods

### 3.1. Ecopath modeling approach

Ecopath models were used for this analysis because many exist for Gulf of Mexico subsystems, and the model framework presents a consistent approach for comparison across marine ecosystems (Pauly et al., 1999; Vidal and Pauly, 2004). The Ecopath software suite is designed to construct and analyze mass-balance trophic models of entire ecosystems (i.e., from primary producers to apex predators). Each model is constructed of numerous ecosystem groups each composed of a single species or several functionally similar species (Christensen et al., 2008). The model framework incorporates two approaches that: 1) estimate biomass and food consumption for each model group (Polovina, 1984), and 2) analyze flows between groups and calculate various ecosystem indices (Ulanowicz, 1986). Two master equations, representing production and consumption, form the foundation of Ecopath models (Christensen et al., 2008). They are linked via the predation mortality term, where the consumption of a predator equals the predation mortality of its prey:

$$\begin{aligned} \text{Production} = & \text{Catches} + \text{Predation Mortality} + \text{Net Migration} \\ & + \text{Biomass Accumulation} + \text{Other Mortality} \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Consumption} = & \text{Production} + \text{Respiration} \\ & + \text{Unassimilated Food} \end{aligned} \quad (2)$$

Thus, the production of each group (Equation (1)) is linked to the consumption of all applicable predator groups (Equation (2)). Model construction is based on field-observed data, and missing parameters are estimated based on the mass-balance assumption (Christensen et al., 2008). All models go through model-fitting and parameterization steps, in which the model structure and input values are evaluated. Adjustments are made as needed based on expert knowledge.

### 3.2. Estimating secondary productivity from Gulf of Mexico Ecopath models

A literature search was conducted to find published Ecopath models of Gulf ecosystems. Only models that examined entire subsystems of the Gulf of Mexico were included, thus excluding models that only examined specific habitat types within a subsystem. For example, a model of an entire estuary would be included, while a model of a seagrass bed within an estuary would be excluded from this analysis. Additionally, only models for which data were freely available at the time of this analysis were included. Eighteen Ecopath models were found that satisfy these criteria (Table 1), two of which were developed at the Gulf-scale to represent coastal (Walters et al., 2008) and continental shelf (Browder, 1993) systems.

**Table 1**  
Characteristics of Ecopath models included in this analysis.

Model <sup>a</sup>	Study area	Country	Approximate area (km <sup>2</sup> )	Number of functional groups	Ecosystem type <sup>b</sup>	Reference
1	Florida Keys	U.S.	30	20	C	Venier and Pauly, 1997
2	West Florida Shelf	U.S.	170 000	59	B	Okey et al., 2004
3	Weeks Bay	U.S.	7	14	A	Althausen, 2003
4	Breton Sound	U.S.	1 100	39	A	de Mutsert et al., 2012
5	Gulf of Mexico (shelf)	U.S., Mexico	Gulf-scale	15	B	Browder, 1993
6	Gulf of Mexico (coast)	U.S., Mexico	Gulf-scale	63	B	Walters et al., 2008
7	Tamiahua Lagoon	Mexico	800	13	A	Abarca-Arenas and Valero-Pacheco, 1993
8	Tampamachoco Lagoon	Mexico	15	23	A	Rosado-Solorzano and Guzman del Proo, 1998
9	SW Gulf of Mexico	Mexico	55 000	24	B	Arreguin-Sanchez et al., 1993a
10	Mandinga Lagoon	Mexico	33	20	A	de la Cruz-Aguero, 1993
11	Laguna Alvarado	Mexico	62	30	A	Cruz-Escalona et al., 2007
12	Bay of Campeche	Mexico	65 000	19	B	Manickchand-Heileman et al., 1998a
13	Terminos Lagoon	Mexico	2 500	20	A	Manickchand-Heileman et al., 1998b
14	Campeche Bank	Mexico	250	19	B	Vega-Cendejas et al., 1993
15	Celestun Lagoon	Mexico	28	16	A	Chavez et al., 1993
16	Yucatan Shelf	Mexico	100 000	21	B	Arreguin-Sanchez et al., 1993b
17	Yucatan Peninsula	Mexico	1 500	18	C	Alvarez-Hernandez, 2003
18	Bahia de la Ascension	Mexico	260	19	A	Vidal and Basurto, 2003

<sup>a</sup> Corresponds to labels in Fig. 1 and Table 2.

<sup>b</sup> Ecosystem abbreviations: A = estuary or lagoon, B = continental shelf or coast, C = coral reef.

Biomass values reported in dry weight were converted to wet weight (ww) using a 1:5 ratio (Christensen and Pauly, 1993a; Parsons et al., 1977). Biomass and production:biomass ratios provided in each model were used to calculate annual production for modeled groups. All values were standardized to tonnes (t) km<sup>-2</sup> year<sup>-1</sup> to enable spatial comparison across models.

Original models were composed of 13–63 functional groups (Table 1). To enable comparison between models, groups in each model were aggregated into 9 common groups, based on trophic function: zooplankton (ZOP), macro-, meio-, and micro-benthos (BEN), crustaceans, molluscs and other mega-benthos (CMB), demersal fish (DEM), pelagic fish (PEL), sharks and rays (SKR), marine mammals (MAM), seabirds (BRD), and primary producers (PPD) (Table 2). If the original model did not include a group, it was left out; parameters were not estimated for any missing functional groups. Annual production was calculated for each aggregate functional group by summing production from each contributing group. For example, if the original model included several crabs and molluscs, production from each group was summed to obtain a

total production value for the CMB aggregate group. For each model, all functional groups (excluding PPD) were summed to obtain an estimate of total secondary production (SPD) of the modeled ecosystem (Table 2).

### 3.3. Spatial patterns of secondary productivity across the Gulf of Mexico LME

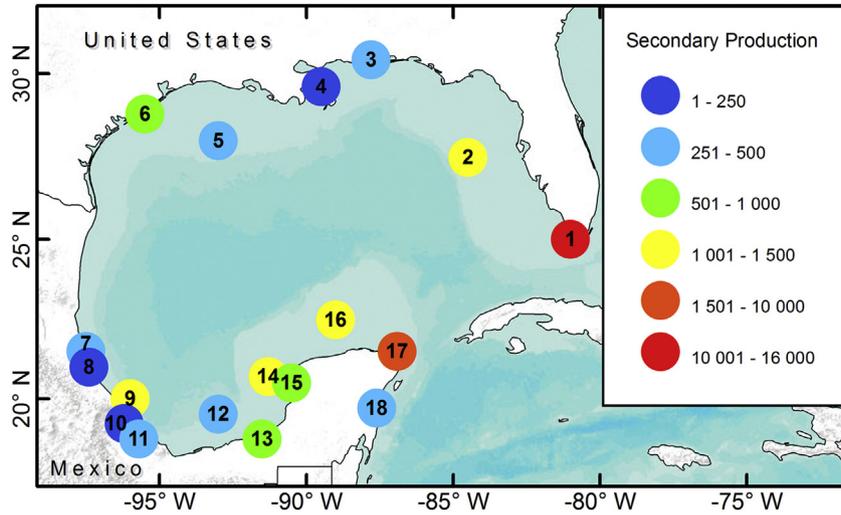
Annual secondary production (t ww km<sup>-2</sup>) of each modeled system was mapped to examine spatial distribution of models and relative productivity (Fig. 1). A Voronoi map was generated with the ArcGIS (version 10) Geostatistical Analyst extension to examine spatial trends in secondary production across the Gulf of Mexico LME (Fig. 2). Sample points were haphazardly designated along the coastline to capture small-scale estuarine and coastal models (approximately 0.5° latitude by 0.5° longitude). A grid of sample points (1° latitude by 1° longitude) was created to cover the remainder of the Gulf. Each point was assigned a secondary productivity value based on which modeled area the point was located.

**Table 2**  
Productivity estimates obtained from Ecopath models of Gulf of Mexico subsystems.

Model <sup>a</sup>	Study area	Productivity (t ww km <sup>-2</sup> year <sup>-1</sup> ) by functional group <sup>b</sup>									
		SPD	BEN	CMB	DEM	ZOP	PEL	SKR	MAM	BRD	PPD
1	Florida Keys	15 466	10 421	1 321	712	2 600	412	0.32	–	–	30 124
2	West Florida Shelf	1 078	514	92	15	450	8	0.13	0.004	<0.001	6 987
3	Weeks Bay	256	130	19	4	98	5	–	0.214	–	1 239
4	Breton Sound	243	72	11	50	88	22	–	–	–	3 956
5	Gulf of Mexico (shelf)	282	110	15	8	143	7	0.04	0.002	–	1 221
6	Gulf of Mexico (coast)	764	183	13	15	511	39	2.16	–	–	6 881
7	Tamiahua Lagoon	297	216	40	12	28	2	–	–	–	1 283
8	Tampamachoco Lagoon	128	58	41	10	16	3	–	–	–	1 710
9	SW Gulf of Mexico	1 337	873	146	44	230	44	0.51	–	–	1 661
10	Mandinga Lagoon	198	18	2	2	176	1	0.00	–	–	590
11	Laguna Alvarado	283	65	40	25	149	4	0.09	0.001	–	1 290
12	Bay of Campeche	361	187	27	4	124	19	0.08	–	–	4 668
13	Terminos Lagoon	692	462	116	5	107	2	–	–	–	12 937
14	Campeche Bank	1 109	556	232	75	234	12	–	–	–	2 369
15	Celestun Lagoon	553	332	52	8	162	–	–	–	–	1 890
16	Yucatan Shelf	1 189	846	177	8	150	7	0.05	–	–	2 271
17	Yucatan Peninsula	5 441	2 716	1 152	304	1 267	2	0.05	–	0.214	25 033
18	Bahia de la Ascension	271	48	2	1	219	1	0.12	0.004	0.054	3 417

<sup>a</sup> Corresponds to labels in Fig. 1 and Table 1.

<sup>b</sup> Functional group abbreviations: SPD = total secondary production (excluding PPD), BEN = macro-, meio-, and mirco-benthos, CMB = crustaceans, molluscs, and other mega-benthos, DEM = demersal fishes, ZOP = zooplankton, PEL = pelagic fishes, SKR = sharks and rays, MAM = marine mammals, BRD = seabirds, PPD = primary producers.



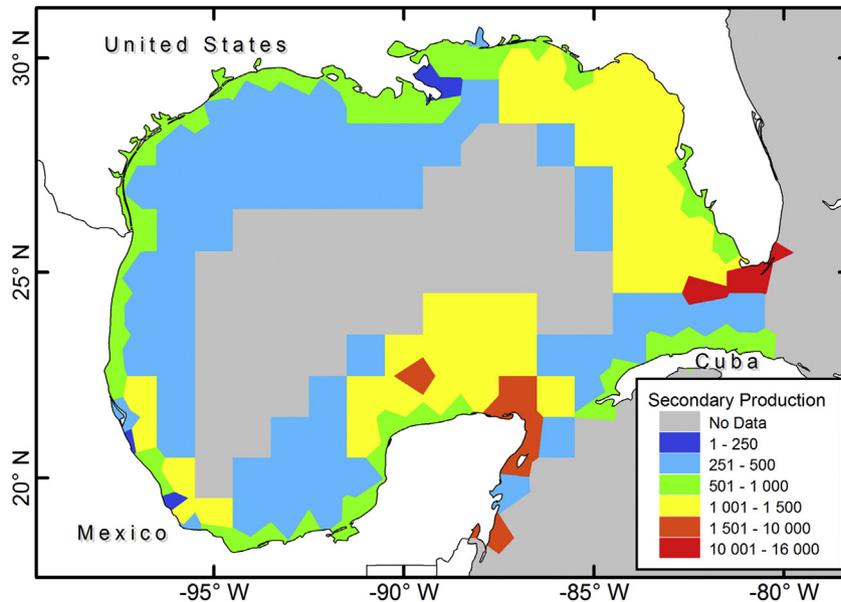
**Fig. 1.** Distribution of Ecopath models and annual secondary production ( $t\ ww\ km^{-2}$ ) associated with each model. Models identified by numbers listed in Tables 1 and 2. Models 5 and 6 represent Gulf-scale estimates for the continental shelf and coast, respectively.

Productivity values resulting from the Gulf-scale continental shelf (Browder, 1993) and coast (Walters et al., 2008) models were used when a specific model did not exist for a point located along the shelf or coast, respectively. Points located beyond the shelf (i.e., open ocean) were assigned no data because no relevant models were available. The Voronoi method generates polygons around sample points so that any location in the polygon is closer to the enclosed sample point than any other point. Values assigned to each polygon can be calculated by a variety of statistics based on the polygon and its neighbors. The “simple” method was used here, where the value of each cell is determined by the value of the enclosed sample point. This method is most appropriate for examining local influence (Prabaharan et al., 2011).

**3.4. Trophic function, productivity and efficiency by ecosystem type**

Models were aggregated into three common ecosystem types to enable comparison of attributes among various subsystems

within the Gulf LME: estuaries and lagoons (A), coastal waters and continental shelves (B), and coral reefs (C, Table 1). For each ecosystem type, annual production of each functional group was averaged across all relevant models. Functional groups were assigned to either pelagic (ZOP → PEL → SKR + MAM) or benthic (BEN → CMB → DEM) food chains, and ecological pyramids of production were constructed for both the pelagic and benthic components of each ecosystem type (Fig. 3). Primary production (PPD) was divided into pelagic (i.e., phytoplankton) and benthic (i.e., submerged aquatic vegetation) components when possible. We chose to assign the SKR group to the pelagic food chain for simplicity of pyramid construction, though some models included benthic-feeding sharks and rays. Marine mammals often represented top predators within their systems. Thus, we added the SKR and MAM groups to compose the top level of pelagic pyramids. Birds (BRD) were not included in our trophic pyramids because this group was absent from the majority of models.



**Fig. 2.** Annual secondary production ( $t\ ww\ km^{-2}$ ) estimates across the Gulf of Mexico LME, as obtained from Ecopath models.

Transfer efficiencies (TE, %) of production were calculated for each pyramid level.

$$TE = \frac{P_n}{P_{n-1}} * 100 \quad (3)$$

where  $P_n$  is the production at one trophic level, and  $P_{n-1}$  is the production at the preceding trophic level. For each ecosystem type, we also calculated the TE of average total primary production to total secondary production to examine general trends in efficiency of transferring primary production to higher production among different types of ecosystems (Fig. 3).

3.5. Correlation between primary and secondary production

Primary and secondary production data for each ecosystem type were analyzed via linear regression (R version 3.0.1) to determine if

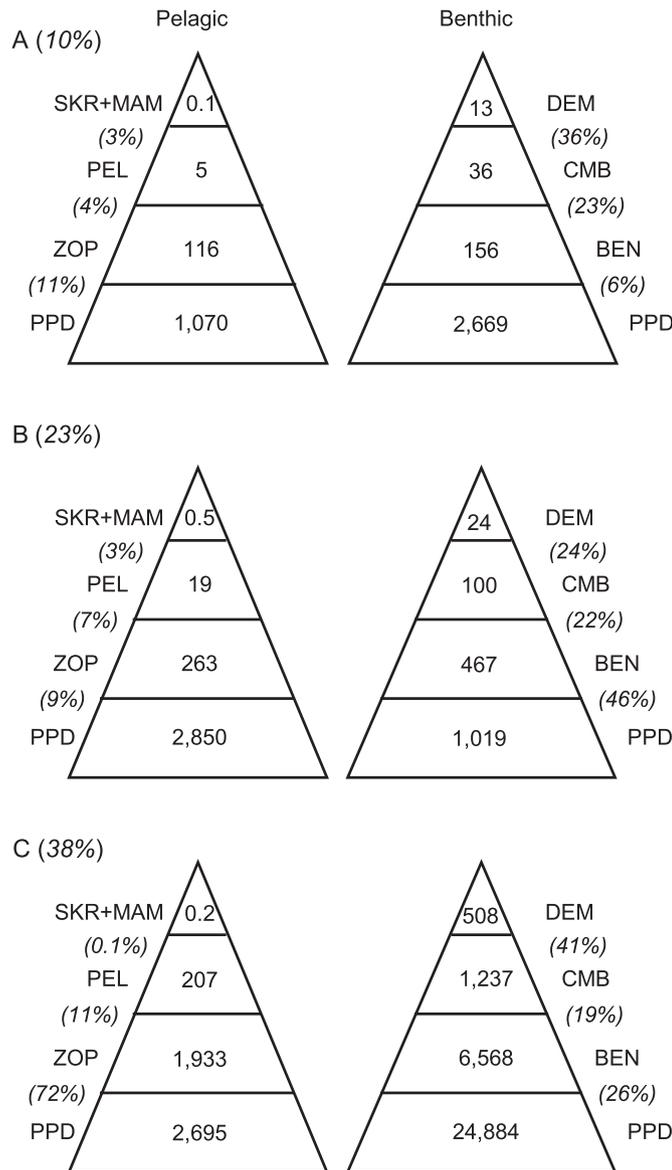


Fig. 3. Ecological pyramids of average annual production (t ww km<sup>-2</sup>) of pelagic (left) and benthic (right) food chains of Gulf of Mexico Ecopath models by system type: (A) estuaries and lagoons, (B) continental shelves and coasts, and (C) coral reefs. Trophic transfer efficiencies (%) of production are shown (italicized) between each trophic level (trophic group abbreviations are defined in Table 2). Transfer efficiencies of total primary production to total secondary production for each system type are shown (% italicized) with ecosystem labels in top left.

primary productivity is an accurate indicator of secondary productivity. Data were log-transformed (log<sub>10</sub>x) prior to analysis. Regression analyses were conducted for estuaries and lagoons (quantity (n) = 9) and coastal waters and continental shelves (n = 7, Fig. 4). Linear regression was not performed for coral reef models because of the small sample size (n = 2).

4. Results

4.1. Ecopath models in the Gulf of Mexico

Two-thirds of the models included in this analysis were developed for Mexican systems in the southern half of the Gulf of Mexico (Table 1, Fig. 1). Four models describe U.S. systems. Two models were developed at the Gulf-scale to represent continental shelf (Browder, 1993) and coastal (Walters et al., 2008) systems. No models specific to Cuba were found.

Not all models had all trophic groups for comparison (Table 2). The majority of models were missing data for marine mammals (72%) and birds (83%). Data for sharks and rays were also sparse (missing in 39% of models). Missing data for these groups is not

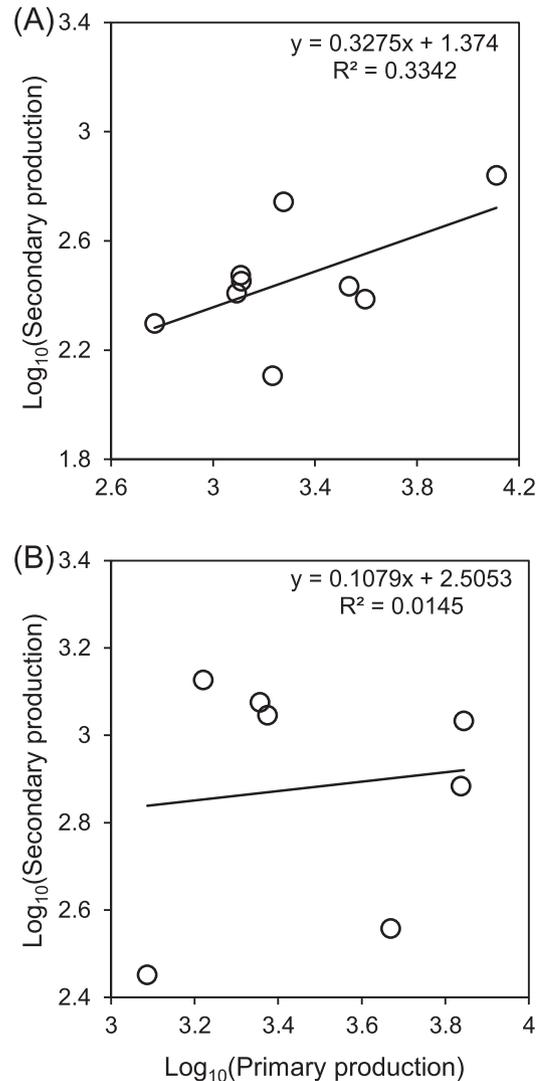


Fig. 4. Linear correlation of log-transformed primary and secondary production data (originally measured in t ww km<sup>-2</sup> year<sup>-1</sup>) for (A) estuaries and lagoons, and (B) continental shelves and coasts.

likely to inhibit overall system comparison because the relative contribution of production was minor in models for which these groups were included (<0.3% of total secondary productivity).

#### 4.2. Spatial patterns of secondary productivity across the Gulf of Mexico LME

Annual secondary production in the Gulf of Mexico ranged from 128 t ww km<sup>-2</sup> in Tampamachoco Lagoon to 15 466 t km<sup>-2</sup> in the Florida Keys (Table 2). Secondary productivity was highest for coral reef ecosystems (average 10 455 t km<sup>-2</sup> year<sup>-1</sup>). Coastal and shelf systems had the next highest secondary productivity (average 874 t km<sup>-2</sup> year<sup>-1</sup>). The Gulf-scale continental shelf model (Browder, 1993) had a lower annual secondary production (282 t km<sup>-2</sup>) than all other models for this ecosystem group (361–1 337 t km<sup>-2</sup>), while the Gulf-scale coastal model (Walters et al., 2008) had an annual secondary production close to the group average (764 t km<sup>-2</sup>). Half of the models included in this analysis examined inshore estuarine areas, with an average secondary production of 325 t km<sup>-2</sup> annually. Two temperate estuary models were included in this analysis (average 249 t km<sup>-2</sup> year<sup>-1</sup>). Tropical lagoon systems in the southern Gulf of Mexico showed a wide range in productivity, from Tampamachoco Lagoon (128 t km<sup>-2</sup> year<sup>-1</sup>) to Terminos Lagoon (692 t km<sup>-2</sup> year<sup>-1</sup>).

Productivity hotspots are evident in the eastern and southeastern Gulf of Mexico (Fig. 2). Relatively high productivity in these areas is associated with coral reef systems and the shallow carbonate shelves of the Florida and Yucatan Peninsulas. Areas of relatively low productivity are evident in the northern and southwestern Gulf, associated with estuarine systems (Fig. 2).

#### 4.3. Trophic function, productivity and efficiency by ecosystem type

Average productivity values for each ecosystem type indicate that 63–80% of total secondary production of each system is supported by the benthic food chain. Benthic secondary productivity is approximately twice as high as pelagic secondary productivity in estuarine (1.7:1) and continental shelf (2.1:1) systems. In coral reef systems, benthic secondary productivity is nearly four times as high as pelagic secondary productivity (3.9:1). The largest contribution of secondary production in all system types is from the benthos functional group (BEN). The Florida Keys model has the highest BEN productivity (10 421 t ww km<sup>-2</sup> year<sup>-1</sup>). This high productivity results from abundant corals and associated benthos in the region (Venier and Pauly, 1997).

Benthic food webs are not only more productive than pelagic food webs, but also more efficient with regards to energy transfer (Fig. 3). Since Lindeman (1942), trophic transfer efficiencies (TEs) have been assumed to fall within an approximate range of 10–20% (Burns, 1989; Christensen and Pauly, 1993b). About half of all TEs calculated in this analysis were between 5 and 25% (Fig. 3). Overall, the highest and lowest TEs occur within the pelagic pyramid for coral reef systems (Fig. 3c). The highest TE (72%) occurs between primary producers (i.e., phytoplankton) and zooplankton; the lowest TE (0.1%) occurs between the third and fourth trophic levels (PEL → SKR + MAM). All remaining TEs for pelagic pyramids were between 3 and 11 percent. Transfer efficiencies for benthic pyramids ranged from 6 to 46 percent. The most efficient (46%) occurs in continental shelf and coastal systems between the primary producer and benthos groups (PPD → BEN, Fig. 3b). System transfer efficiencies of total primary to secondary production were: 10% for estuarine systems, 23% for continental shelves, and 38% for coral reefs (Fig. 3).

#### 4.4. Correlation between primary and secondary production

Linear regression analyses indicate weak positive correlations between primary and secondary production data for each ecosystem type examined. A relatively stronger correlation was evident for estuarine systems (Fig. 4a,  $R^2 = 0.334$ ,  $p = 0.1$ ) compared to continental shelf systems (Fig. 4b,  $R^2 = 0.015$ ,  $p = 0.8$ ), though neither were highly significant. These analyses indicate that primary production is not a strong indicator of secondary production, and this relationship may be highly variable for different ecosystem types.

### 5. Discussion

This meta-analysis of Ecopath models serves to integrate available ecological data across the Gulf of Mexico LME into a coherent and visual framework. Eighteen Ecopath models developed for subsystems of the Gulf of Mexico were included. Models were constructed by a variety of research groups for various purposes. Methodological differences in model construction are inherent, and were most evident in the level of detail used to define model groups. Aggregation of original model groups into common functional groups reduced the importance of such individual details and allowed a comparative view of structure and energy flow within and among modeled systems.

Some ecological groups were not included in original models, and this has the potential to bias our comparative analysis. Some models were developed to examine general ecological structure and function, and thus attempt to include all major ecosystem components. Others have been developed with more specific goals, often relating to fisheries management. Such models focus more heavily on commercially important fisheries species. Some of the differences evident in model groups could also be attributed to the various ecosystem types and finer scale habitats present.

The fact that models examined different types of systems was not an issue for the purposes of this analysis; a broad comparison of system types was desirable. Aggregation of models into common system types enabled a comparison of structure and energy flow within and among ecosystem types. We did, however, exclude models from our analysis that examined only specific habitat types within an ecosystem. While habitat differences are an important consideration, such a fine-scale habitat analysis would not enhance our understanding of productivity at the LME-scale.

Different temporal and spatial scales were evident among models. Issues of temporal scale have the potential to bias our analysis. Production was standardized to annual values to eliminate within-year variations, and models that examined only specific seasons were not included in our analysis. Models were constructed of data from varying time periods, ranging from the 1950s to early-2000s. The majority of models encompassed data over a span of about 2 decades, while some models only examined data from 1 to 3 years. Fundamental changes can occur that alter energy flow and production of systems over time.

Spatial scale problems were eliminated by comparing production on a per-unit-area (t km<sup>-2</sup>) basis. The challenge associated with spatial uncertainty centers on major data gaps, the most significant of which is the disparity in data availability and model development. Several important ecosystems have not been modeled (e.g., open ocean, Flower Garden Banks). Some habitats are especially difficult to sample (e.g., deep sea), and thus widespread data are not available for model construction. Overall, there is a predominance of models in the southern Gulf of Mexico, with a lack of models in the northern Gulf (Fig. 1).

It is nearly impossible to validate secondary productivity estimates across the Gulf. We can examine the results in the context of

what is known about these ecosystems. For example, it is well known that coral reef ecosystems are highly productive, and this is depicted rather well in our analysis. Productivity hotspots are evident near the Florida Keys and Yucatan Peninsula where corals are abundant (Fig. 2).

In addition, areas of the West Florida Shelf and Yucatan Shelf have relatively higher productivity than the rest of the continental shelf of the Gulf of Mexico. The relatively shallow carbonate shelves of the Florida and Yucatan peninsulas support more productive bottom habitats (e.g., coral reefs) compared to the terrigenous shelves of the remainder of the Gulf of Mexico. The Yucatan and West Florida shelves also occupy areas in the path of the Loop Current, and are known to experience coastal upwelling (Darnell and Defenbaugh, 1990). Increased nutrients in surface waters of these areas are known to support high ecosystem productivity.

Unfortunately, no Ecopath models have been developed for the Flower Garden Banks reef system, located approximately 100 miles offshore of the Texas–Louisiana border. However, we could expect secondary productivity to be relatively high in this region. The Flower Garden Banks reef system is relatively pristine with exceptional coral cover (approximately 50%) compared to reef systems of Mexico, Florida, and the greater Caribbean (Aronson et al., 2005).

Coastal and continental shelf models exhibit a wide range in productivity. The Gulf-scale continental shelf model (Browder, 1993) had the lowest annual secondary production of the group, and the Gulf-scale coastal model (Walters et al., 2008) fell just below the group average. Overall, it appears that the Gulf-scale models estimate lower secondary productivity compared to location-specific models of coastal and shelf systems. Development of both Gulf-scale models was based in the U.S. Therefore, focus (and available data) may have been biased toward temperate systems, without taking into account the potential higher productivity of tropical systems in Mexico. The only location-specific models for continental shelves exist on the carbonate shelves of Yucatan (Arreguin-Sanchez et al., 1993b) and West Florida (Okey et al., 2004). No location-specific models of terrigenous shelves were available at the time of this analysis. Muddy and relatively narrow terrigenous shelves characteristic of the northern and western Gulf can support highly productive fisheries, but do not support the productive bottom habitats like the carbonate shelves of the southeastern Gulf (Darnell and Defenbaugh, 1990). These factors may contribute to the seemingly large difference between the general and specific shelf models.

An unexpected result of our analysis is the relatively low productivity associated with most estuarine models. Such systems have long been thought to be some of the most productive systems in the world. A significant proportion of estuarine productivity may stem from shoreline habitats (e.g., marshes) that serve as important nursery habitats, but are often not included in these models. The majority of coastal marine organisms have complex life-history patterns that involve movement among various environments throughout multiple life phases, resulting in a certain degree of connectivity across an estuarine-ocean continuum (Gillanders et al., 2003). During development, organisms may migrate to different environments as their foraging and refuge requirements change (Beck et al., 2001). Habitat shifts during different phases of an organism's life cycle represent the transport of secondary production, and productivity of a local region depends on large-scale exchanges and connectivity. Thus, when examining annual averages, the productivity that originates in estuarine habitats may be more pronounced in coastal and shelf areas utilized by adults once they migrate from their estuarine nursery areas (Beck et al., 2001; Gillanders et al., 2003). In addition, estuarine systems are more heavily impacted by anthropogenic influences (Lotze et al., 2006).

Low relative productivity may indicate ecosystem stress and degradation by such influences.

Ecological pyramids highlight key differences between pelagic and benthic food chains and productivity among ecosystem types (Fig. 3). Transfer efficiencies can vary greatly due to system-specific and model-specific reasons. Some estimates may be skewed by the fact that trophic groups are assumed to be linked as a chain, rather than in a more realistic food web (Burns, 1989). This is the case in our analysis, as our trophic groups are highly aggregated and simplified. Though highly variable, the estimates of TE remain remarkably close to the long-assumed 10% rule. Generally, it is assumed that TE will decrease at higher trophic levels because of increased respiration (Burns, 1989; Christensen and Pauly, 1993b). This trend is apparent in pelagic pyramids of all system types. However, the relative efficiency between trophic levels in benthic pyramids varies by ecosystem type.

Trophic transfer efficiencies in benthic pyramids are generally higher than those in pelagic pyramids (Fig. 3). Recent studies of freshwater lakes indicate benthic food chains may be more efficient in their transfer of energy compared to pelagic pathways (Vander Zanden et al., 2006). Such differences could be partly attributed to differences in the physical structure of benthic and pelagic habitats, with prey more concentrated and more easily detected in benthic environments. Difference in prey body size, or food quality may also contribute to the efficiency of energy transfer (Vander Zanden et al., 2006). The benthic food web can also be supported by water column productivity in addition to benthic productivity. There is often a shunt of production from pelagic to benthic pathways via detritus. The benthic environment is also supported by falls of large dead marine mammals and fishes, which likely die of old age and are generally protected from predation by their large size. Fishery discards can also contribute to bottom productivity (Vidal and Pauly, 2004).

In estuarine systems, the majority of primary productivity is from benthic producers (84.8%, Fig. 3a). The reverse is true for coastal and shelf systems, with the majority of primary productivity occurring pelagically (76.6%, Fig. 3b). In coral reef systems, over 90% of primary productivity occurs in the benthic food chain (Fig. 3c). The reason for high benthic primary productivity in estuarine and reef systems is the shallower depth which allows for the presence and growth of relatively large primary producer species (e.g., submerged aquatic vegetation), as opposed to deeper continental shelf environments where primary productivity stems predominately from small primary producers (e.g., phytoplankton).

Primary production is often used as a proxy for examining ecosystem productivity. Linear regression analyses do not indicate strong relationships between primary and secondary production (Fig. 4). This implies that primary productivity may not be a reliable indicator of secondary productivity. When we focus on primary production as a means for indicating system productivity, we are not able to capture differences in transfer efficiencies and secondary productivity. Even if primary production is similar between areas, other effects (e.g., fishing) differ, and thus could cause significant differences in secondary production between the systems. Therefore, it is best to use a suite of indicators that include secondary productivity.

## 6. Conclusions

There is a pressing need to study and manage systems at a larger scale (e.g., LMEs). The relatively recent growth in ecological modeling efforts demonstrates that we are beginning to understand quite a bit about the structure and function of marine habitats and ecosystems. However, it is no longer sufficient to examine

ecosystems on the scale we have previously. In essence, we know a lot about the pieces, but we need to manage the whole.

Our capabilities are limited when it comes to examining ecosystem dynamics at a large scale. We cannot conduct controlled experiments at the LME-scale, and consistent sampling across an LME (and often across international borders) is difficult. For these reasons, we often use metrics that are relatively easy to measure as indicators of ecosystem health. Currently, the most common metrics include primary productivity and fisheries landings. This analysis has shown that these metrics may not be suitable as sole indicators of ecosystem productivity and health.

Models and comparative ecosystem analyses may be the most promising approaches for understanding the role of key ecosystem processes at larger scales and the subsequent development of decision-support tools necessary for effective management (Crowder and Norse, 2008; Murawski et al., 2010). Models are a representation of our best available knowledge about entire ecosystems and the dynamics and interactions occurring within and among them. Even with the inherent limitations of modeling studies, the results of such efforts can provide useful information.

We have presented a methodology for using models beyond the original purposes. Our analysis provides a framework in which strong, ecologically-based decision-support tools could be developed with available data and knowledge. Comparative analyses of systems across the Gulf will strengthen understanding of ecological processes at the LME scale, and support ecosystem-based management initiatives.

#### Author contributions

Conceived and designed the analyses: BNB PAM. Performed the analyses: BNB. Contributed analysis tools: PAM. Wrote the paper: BNB. Extensive editorial comments, insight into results: PAM. All authors have approved the final article.

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