Ecosystem dynamics under "top-down" and "bottom-up" control situations generated by intensive harvesting rates

Dinámica de ecosistemas bajo situaciones de control de "arriba hacia abajo" y de "abajo hacia arriba" generadas por tasas de pesca intensivas

Francisco Arreguín-Sánchez

Centro Interdisciplinario de Ciencias Marinas del IPN. Apartado Postal 592, La Paz, Baja California Sur, 23000. México.
e-mail: farregui@ipn.mx

Arreguín-Sánchez F. 2011. Ecosystem dynamics under "top-down" and "bottom-up" control situations generated by intensive harvesting rates. *Hidrobiológica* 21(3): 323-332.

ABSTRACT

"Top-down" and "bottom-up" control processes in exploited ecosystems have been characterised using their impacts on the mean trophic level of catches, changes in biomass, and certain ecosystem attributes. Most scientific contributions have been based on case studies of particular ecosystems. So, the aim of this study is to identify and understand ecosystem processes governing their response to fishing in a more global sense. Simulations were developed using different ecosystems models using the Ecopath with Ecosim suite of programs. Two cases were examined by selecting target species to be exploited during simulations experiments. A high trophic level group (sharks) and a low trophic level group (shrimp) were chosen to represent potential "top-down" and "bottom-up" control situations, respectively. For both cases, a gradient of exploitation was simulated, and ecosystem attributes were estimated. Harvest rates (HR) varied along a gradient of HR = 0.4 to HR = 0.7 for sharks and HR = 0.3 to HR = 0.8 for shrimp. For each simulation, only the target group was modified. Principal Components Analysis was applied, and outputs were obtained using ecosystems as variables and attributes as factors, and vice versa. For sharks, outputs indicate that under a low HR, group attributes govern the response to exploitation. However, when a high HR was applied (higher than the maximum sustainable yield), ecosystem attributes emerged as relevant instead of stock attributes. For sharks, representing "top-down" control, a graphical arrangement of the first two components clearly shows a gradual pattern of response reflecting the transition from stock-level to ecosystem-level processes as HR increases. For shrimp, representing "bottom-up" control, no clear patterns emerged; in this case, the same relevant stock and ecosystem attributes appear across all HRs applied. These results are explained in terms of stock life histories, trophic level, and transfer efficiencies through the food web, suggesting that ecosystem processes behind overfishing are related to the trophic level, and then, fisheries management practice must recognise such particularities.

Key words: Top-down control, bottom-up control, exploitation, ecosystem, trophic-level, sharks, shrimps.

RESUMEN

Los procesos de control de "arriba-hacia-abajo" y de "abajo-hacia-arriba" en ecosistemas explotados se han caracterizado por sus impactos en el nivel trófico medio de las capturas, los cambios en la biomasa, y ciertos atributos del ecosistema. Sin embargo, la mayoría de las contribuciones científicas se han basado en estudios de casos de determinados ecosistemas. El objetivo de este estudio fue identificar y comprender los procesos del ecosistema que definen su respuesta a la pesca en un sentido más global. Las simulaciones se desarrollaron para diferentes ecosistemas modelados usando la plataforma de programas denominada “Ecopath with Ecosim”. Dos casos fueron examinados donde se seleccionaron especies para ser explotadas durante las simulaciones; un grupo de alto nivel trófico (tiburones) y un grupo de bajo nivel trófico (camarón) fueron elegidos para representar las situaciones de control “de arriba hacia abajo” y “de abajo hacia arriba”. En ambos casos, un gradiente de explotación fue simulado, y los atributos del ecosistema estimados. Las tasas de captura (HR) variaron a lo largo de un gradiente de HR = 0.4 a HR = 0.7 para los tiburones y HR = 0.3 a HR = 0.8 para el camarón. Para cada simulación, sólo el grupo objetivo fue modificado. Se aplicó un Análisis de Componentes Principales y las salidas fueron obtenidas utilizando los ecosistemas como variables y atributos como factores, y viceversa. Para los tiburones, los resultados indican que para una HR baja, los atributos del grupo son los que regulan la respuesta a la explotación. Sin embargo, cuando HR es alto (mayor que el correspondiente al rendimiento máximo sostenible), los atributos del ecosistema emergen como relevantes en lugar de los atributos del grupo. Para los tiburones, que representan el control de “arriba-hacia-abajo”, se observa un patrón gradual de respuesta que refleja la transición de stock hacia los procesos a nivel de ecosistema, a medida que aumenta HR. Para el camarón, que representa el tipo de control de “abajo-hacia-arriba”, no surgió patrón alguno, siendo los mismos atributos relevantes los que aparecen como respuesta del stock y del ecosistema, independientemente del nivel de HR. Estos resultados se explican en términos de historias de vida, el nivel trófico, y la eficiencia de la transferencia en la cadena alimentaria; y sugieren que los procesos del ecosistema tras la sobrepesca están relacionados con el nivel trófico, y como consecuencia la práctica de la ordenación pesquera debe reconocer estas particularidades para el éxito del manejo.

Palabras clave: Control de arriba-hacia-abajo, control de abajo-hacia-arriba, explotación, ecosistema, nivel-trófico, tiburones, camarones.

INTRODUCTION

The concept of “fishing down the food web” (FDFW) was introduced by Pauly *et al.* (1998) to express the impact on ecosystems when high trophic levels are overexploited in aquatic ecosystems. The measure of this effect was initially based on the computation of the mean trophic level of catches (MTLC) and later on the marine trophic index (MTI), which considers the MTLC for trophic levels higher than 3.25 (Pauly & Watson, 2005). Pauly *et al.* (2000) also suggested the use of the Fishery-in-Balance (FIB) index as a method for measuring trophic level used by fisheries (Fig. 1). Under sustained or increased fishing intensity, the decline of these indices over time represents FDFW scenarios, which have consequences for the ecosystem and fishing sector. Moreover, if management strategies were developed to reduce such declines, then they could help prevent ecosystem deterioration (e.g., Christensen, 1998; Jackson *et al.*, 2001). Due to decline in world fish catches, FDFW is an increasing concern (Pauly, 1999; Watson & Pauly, 2001).

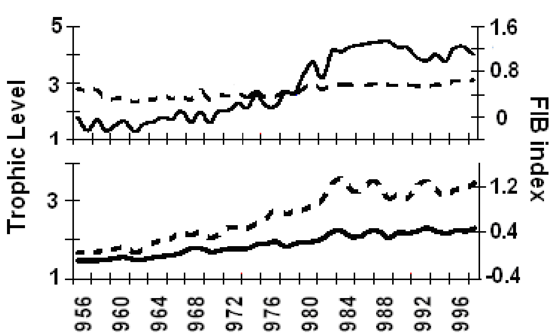

Figure 1. The mean trophic level of catches (TL, dashed line) and Fishery-in-balance index (FIB, solid line) for the Gulf of California (top) and the southern Gulf of Mexico.

A “fishing up the food web” (FUFW) situation was reported by Arreguín-Sánchez *et al.* (2004) related to the pink shrimp (*Farfantepenaeus duorarum*, Burkenroad 1939) stock (a relatively low trophic level species), whose fishery and stock experienced a severe depletion in the southern Gulf of Mexico ecosystem. In this case, MTLC shows an increasing trend over time as shrimp stock abundance decreases (Fig. 1). Because low trophic level species are characterised as being short-lived and fast-growing stock, with relatively high reproduction rates, a FUFW scenario is not common.

“Top-down” and “bottom-up” controls are defined by vulnerability to predation and are dependent on either the predator or the prey. Fishing down the food web is recognised as a decrease in the abundance of the top predators in the trophic web and is characterised by a loss of “top-down” control. In contrast, FUFW results in food availability limitation characterised as an expression of “bottom-up” control.

This study focuses on the ecosystem attributes that play a key role in ecosystem dynamics when selected stocks, from high and low trophic levels, are impacted by top-down or bottom-up effects from fishing.

MATERIALS AND METHODS

A number of ecosystem models constructed with the “Ecopath with Ecosim” (EwE) software have been described in the literature (Christensen & Pauly, 1992; Walters *et al.*, 1997; Pauly *et al.*, 2000).

We selected sharks, as representatives of the high trophic level, to simulate the effects under FDFW and because of the characteristics of their life cycle that make them vulnerable to overexploitation (Hoenig & Gruber, 1990; Pratt & Casey, 1990). Conversely, shrimp were selected as representatives of the low trophic level, because this species is economically important, commonly exploited and presents high recovery rates (Arreguín-Sánchez *et al.*, 1997, 2004). The ecosystems selected in both cases are listed in Table 1, and their location is shown in Figure 2.

For the FDFW experiments, resilient properties of sharks within their own ecosystems were evaluated using the Ecosim model (Walters *et al.*, 1997). The current state of exploitation for sharks was modified to reflect specific harvesting rate (HR) values representing the proportion of the biomass removed by fishing with respect to the stock biomass. Harvesting rate values ranging between 0.3 and 0.7 (using increments of 0.1) were used during simulations. Starting with an unexploited (HR = 0) ecosystem state, HR was applied for a period of three years (starting

Table 1. List of ecosystem models used for simulations. Upper panel for FDFW and bottom panel for FUFW analyses. Sharks and shrimps groups were used to represent high and low trophic levels, respectively.

Ecosystem type	Location	Group File	Name	Source
FDFW-Sharks as target group				
Upwelling	California Monterey Bay	Necton: (Sharks + 2 groups)	Monterey	Olivieri *et al.* (1993)
Continental shelf	Gulf of Mexico Florida shelf	Sharks	Gomexico	Browder (1993)
	Gulf of Mexico Campeche	Sharks	Sondacam	Manickchand-Heileman *et al.* (1998)
	Venezuela shelf	Small sharks	Venezuela	Mendoza (1993)
	Ascension Bay Sharks Mexican Caribbean		Ascenci	Vidal and Basurto (1993)
	Yucatan Shelf	Sharks	Yucatán	Arreguín-Sánchez *et al.* (1993a)
Coral reefs	Barrier reef, Mexican Caribbean	Sharks	Arrecife	Alvárez-Hernández (2003)
	Coral reef, Virgin Islands	Large sharks/rays	Virgin21	Opitz (1993)
Coastal areas	SW Gulf of Mexico	Sharks	Wgmexico	Arreguín-Sánchez *et al.* (1993b)
	Gulf of Nicoya, Costa Rica	Sharks	Nicoya	N. Van Dam (unpublish, Univ. of Costa Rica)
	Los Cabos, Southern Peninsula of Baja California Sharks		Cabos	M. Torres-Alfaro (unpublish, Centro Interdsciplinario de Ciencias Marinas, del IPN, Mexico
FUFW-Shrimp as target group				
Continental shelf	Gulf of Mexico, Yucatan	Penaeid shrimps	Yucatán	Opitz (1993)
	Gulf of Mexico, Campeche	Penaeid shrimps	Campeche	Vega-Cendejas *et al.* (1993)
	Gulf of Mexico, Veracruz	Penaeid shrimps	Wgmexico	Arreguín-Sánchez *et al.* (1993b)
	Central-eastern Gulf of California	Penaeid shrimps	GCalifornia	Arreguín-Sánchez *et al.* (2002)

Figure 2. Location of ecosystems used for simulations. Black stars refers to fishing down the food web, and shite stars for fishing up the food web experiments. For more details about ecosystems see Table 1. Gomexico= Gulf of Mexico Florida shelf. Sondacam = Gulf of Mexico Campeche. Ascenci = Ascension Bay Sharks Mexican Caribbean. Virgin21 = Coral reef, Virgin Islands. Wgmexico = Gulf of Mexico, Veracruz. GCalifornia=Central-eastern Gulf of California.

in year 1). Some resilient properties were measured in the same manner as defined by other authors (Vasconcelos *et al.*, 1997; Pérez-España & Arreguín-Sánchez, 1999a, b; Arreguín-Sánchez & Manichkand-Heileman, 1998) like persistence, magnitude of change, and recovery time. In each simulation, only parameters no auto-correlated were selected for comparison for the target group and its ecosystem (Table 2).

For FUFW, an analogous experiment was developed using shrimp stocks and HRs that ranged between 0.3 and 0.8 (using increments of 0.1). An HR was also applied for a period of three years, and the same resilient properties were computed.

In both experiments, HRs ranged from the state of developing fishery (low rates of exploitation) to overexploitation and encompassed intermediate states of exploitation. We included the maximum sustainable yield level, defined as 50% of the pristine biomass (Clark, 1985) is extracted.

To simulate an unexploited state for the target stocks (i.e., in those cases where the stock in the original ecosystem model was exploited), landing was added to the living biomass, and fishing mortality was removed from the production to biomass (P/B) ratio, thereby reflecting natural mortality. In this state, the best possible model was obtained through the application of the Ecoranger routine included in the Ecopath with Ecosim software. Residuals minimization with a minimum of 3000 iterations was used as the operating criterion. For a detailed description of the Ecoranger routine, see Pauly *et al.* (2000) and Christensen & Walters (2004). The harvest rate was computed as follows (Gulland, 1983):

$$HR = \frac{F}{M + F}\left[1 - e^{M+F}\right]$$

where F = the instantaneous rate of fishing mortality and M = the instantaneous rate of natural mortality, both in years^{-1}.

Because the HR values were predefined and M (natural mortality) was known from Ecopath for each particular state of the target stock, the F value was numerically computed using a simple Newton algorithm. The amount of catch (Y) for a specific HR was then calculated as Y=FB, where B = biomass. For each simulation, the new state of exploitation of the target stock was incorporated into the ecosystem model by reducing the biomass caught from the living biomass (explicit catch), and the corresponding fishing mortality was added to the P/B ratio.

Principal Component Analysis (PCA) was applied to the ecosystem and target group parameters estimated after simulations

Table 2. Ecosystems attributes used to explore response to harvesting rates on sharks and FDFW processes.

	Attributes	Arrecife	Ascenci	Cabos	Gomexico	Monterey	Nicoya	Sondacam	Venezuel	VRGN21	Wgmexico	Yucatan
1	Trophic level	3.62	3.45	3.72	3.78	4.08	4.00	4.25	3.83	3.86	4.77	4.93
2	Biomass	0.42	0.03	0.10	0.08	4.51	0.09	0.08	0.09	0.98	0.17	0.03
3	Ecotrophic efficiency	0.65	0.31	0.70	0.85	0.89	0.47	0.64	0.76	0.71	0.94	0.50
4	Omnivory Index	0.19	0.60	0.30	0.34	0.11	0.22	0.26	0.28	0.45	0.15	0.34
5	Respiration/ Biomass	5.06	7.44	2.37	5.64	4.49	4.51	4.99	3.12	4.00	5.58	7.16
6	Total number of pathways (10^{-4})	0.21	3.37	0.00	0.01	0.01	0.00	0.44	0.04	11.86	0.21	0.41
7	Primary production/ Biomass	5.21	21.75	27.87	27.29	49.5	26.56	50.66	26.33	5.47	5.82	7.27
8	Connectance	0.35	0.45	0.36	0.21	0.23	0.19	0.36	0.32	0.35	0.24	0.28
9	System Omnivory Index	10.80	3.90	7.40	6.20	12.00	4.50	9.90	2.90	15.30	12.70	12.20
10	Finn cycling Index	10.80	3.90	7.40	6.20	12.00	4.50	9.90	2.90	15.30	12.70	12.20
11	Path Length	3.59	18.37	2.70	2.70	4.82	3.77	6.66	4.07	4.06	3.79	3.41
12	Fishery trophic Level	2.66	3.04	0.00	2.60	3.28	3.01	3.54	2.81	0.00	3.44	4.11
13	Net system production (10^{-2})	62.06	17.02	31.06	4.04	50.54	2.10	37.97	16.56	10.77	4.94	1.25
14	Magnitude of Change*	0.58	0.59	0.068	0.00	0.55	0.12	0.00	0.39	0.67	0.00	0.52
15	Time recovery*	75	20.50	50.00	0.00	12.50	1.33	3.71	10.83	38.33	0.00	11.16

for each HR level to identify those attributes with a significant response to changes in HR. Within each of the first two components, relevant attributes were selected by excluding those values whose magnitude was less than 70% of the highest absolute value corresponding to each variable. Next, the analysis of the variables selected was used as a relevant indicator of the ecosystem processes driving the response to fishing.

For FUFW, we used ecosystem models in which the size of the shrimp stocks was clearly different. The Campeche and Gulf of California models represent the most productive fishing grounds in Mexico, with yields ranging from 10 to more than 40 thousands metric tonnes (mt) per year; while Veracruz yields hundreds of metric tonnes, the Yucatan is only a small-scale incipient shrimp fishery (Arreguín-Sánchez & Arcos-Huitrón, 2007). These magnitudes reflect differences in stock size, expressed as biomass, with the influence of specific ecosystem attributes. For this reason, data for PCA analyses were standardised.

RESULTS

In the case of sharks, the ecosystem parameters computed after the simulations are shown in Table 2. For all of the scenarios (given by different HR values), in the PCA analysis, the first two components explained more than 50% of the total variation in the parameters, and the first three components accounted for 67% of the variation. For each component, higher weighted factors indicate those parameters that contribute more to the explained variance (Table 3). These parameters can be separated into two categories: (1) those related to sharks as a functional group such as trophic behaviour, energetic cost, and how sharks as a group within the ecosystem responded to exploitation, (2) those related to ecosystem attributes (e.g., ecosystem production and trophic structure).

Two main aspects emerged from the analysis of the relevant weighting factors on higher trophic level groups like sharks (Table 3). First, under low levels or optimum exploitation conditions, HR <= 0.5 (which indicates a biomass extraction of 50% or less), variables with higher contribution to the explained variance in the first component were related to the target group (sharks). These variables included trophic level and resilient properties such as the magnitude of change and the recovery time and suggested that single-group attributes become relevant in response to fishing pressure. Additionally, two variables related to ecosystem structure attributes (connectance and omnivory index) were

Table 3. Weighting factors of ecosystem and functional group attributes (sharks) when submitted to different harvesting rates (columns) after principal component analysis during FDFW analysis. Numbers in parenthesis represent higher values. *numbers indicate the explained variance by each component.

	0.3	0.4	0.5	0.6	0.7
Component 1 *	29.34	28.53	27.73	26.78	25.71
Connectance	–0.396	–0.406	–0.411	–0.411	–0.405
Omnivory index	–0.319	–0.361	–0.397	–0.442	–0.473
Magnitude of Change	–0.388	–0.366	–0.326		
Trophic Level		(–0.320)	(–0.318)		
Path Length				–0.348	–0.384
Ecotrophic Efficiency				(–0.351)	(–0.383)
Recovery Time	–0.337				
Component 2 *	22.63	22.02	21.60	21.03	21.33
Respiraton/ Biomass ratio	–0.369	–0.381	–0.386	–0.387	–0.388
Total System Production		–0.365	–0.38	–0.393	–0.377
Biomass	–0.355	–0.357	–0.345		
Fishery TrophicLevel			–0.303	–0.365	–0.415
Ecotrophic Efficiency	–0.369	–0.329			
Recovery Time				–0.337	–0.354
Omnivory Index	(–0.346)				

important in explaining variance in the first component. Second, at HR higher than the maximum sustainable yield level (>0.5), characterising overexploitation, ecosystem attributes emerged as relevant, while group attributes become less important (Table 3). Shark harvest scenarios yield a linear array for ecosystems when the two first components were plotted as shown in Figure 3, where an increase in the slope can be observed as the HR increases. This finding suggests that PC2, which is mainly associated with ecosystem functioning, explains more variation as the harvest increases.

For FUFW, the response to an increasing HR in the Campeche and Central Gulf of California ecosystems results in a positive slope in the PCA diagram, and a negative slope for the Veracruz and Yucatan ecosystems (Fig. 4). Even though the purpose was not to estimate the magnitude of the slopes, they appear to be of similar magnitude but of opposite signs. In this case, the main difference between ecosystems is that those with positive slopes sustain larger fisheries than those with negative slopes. Table 4 shows the relevant weighting factors for the first two components

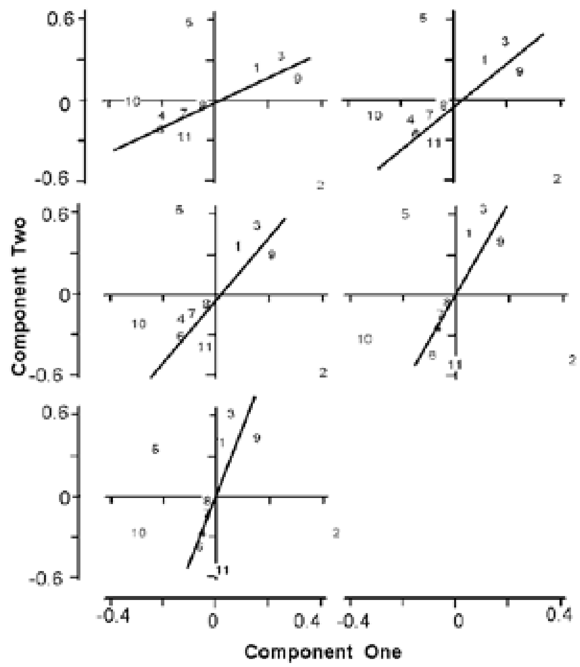

Figure 3. The changes in ecosystems during the simulation of a FDFW with an increasing harvest rate on sharks as revealed by the principal component analysis. The slope is gradually affected by changes in the HR which increased from top-left to down; the numbers indicate the ecosystem: 1.- Arrecife; 2.- Ascenci; 3.- Cabos; 4.- GoMexico; 5.- Monterey; 6.- Nicoya; 7.- Sondacam; 8.- Venezuel; 9.- Virgn21; 10.- WGMexico; 11.- Yucatan.

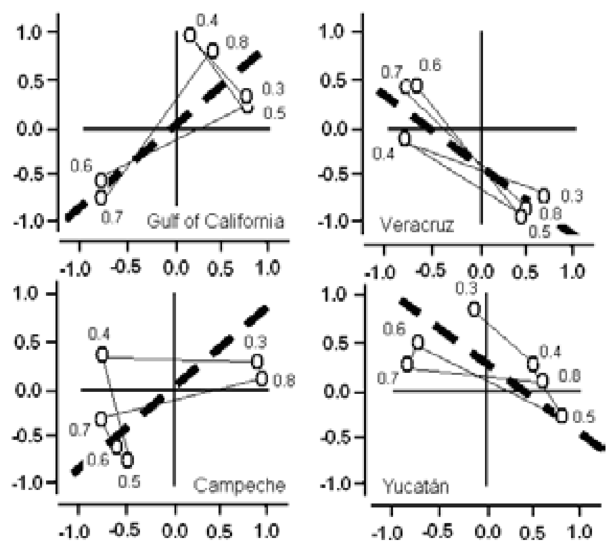

Figure 4. The changes in the relative position of the ecosystem used to simulate FUFW using shrimp as the target species in the first two components of the PCA. Note the tendencies similarity to changes in the harvesting rates in the four ecosystems (thin lines) and the opposite trends (dashed lines) between the Gulf of California and Campeche ecosystems (left) with respect to the Veracruz and Yucatan ecosystems (right).

Table 4. Ecosystem and functional group attributes (shrimps) emerging as relevant when submitted to different harvesting rates (columns) after principal component analysis during FUFW analysis.

0.30	0.40	0.50	0.60	0.70	0.80
TL	TL	TL- *	TL-	TL *	TL *
B	B	B	B	B	B-
OI-	OI	OI-	OI-	OI-	OI- *
C	C	C	C	C-	C
FCI	FCI	FCI	FCI	FCI	FCI
P-	P-	P-	P *	P *	P *
PL	PL	PL *	PL-	PL-	PL
		TNP	TNP	TNP	TNP
TNP- *	TNP- *	TNP- *	TNP *	TNP *	TNP *
	NSP-	NSP-	NSP	NSP	NSP-
	SOI	SOI- *	SOI- *	SOI- *	SOI *
RT-			RT-	RT-	RT-
EE- *	EE- *	EE		EE	
PP/B *		PP/B *	PP/B-	PP/B- *	
R/B *	R/B *				R/B- *
			MC-	MC-	MC-
explained variance					
32.94*	32.85*	34.18*	29.87*	31.26*	32.41*
23.65	22.40	21.08	28.72	23.61	21.93

TL = trophic level; B = biomass, OI = omnivory index; C = Connectance; FCI = Finn's cycling index; P = persistence; PL = path length; TNP = total number of paths; NSP = net system production; SOI = system omnivory index; RT = recovery time; EE = ecotrophic efficency; PP/B = primary production/biomass ratio; R/B = respiration/biomass ratio; MC=Magnitude of change. * Component 2, others Component 1.

where the significant variables involved in the responses to fishing are the same, independent of the HR level, but have variable effects on the ecosystem dynamics. Moreover, the magnitude of the weighting factors for the ecosystems resulted in similar values for the different HRs (Table 5).

Table 5. Ecosystem's weighting factors indicating their relative contribution when submitted to a range of harvesting rates (columns), after PCA. Note similarities in their magnitude.

	0.3	0.4	0.5	0.6	0.7	0.8
Campeche	0.882	–0.766		–0.707	–0.820	0.918
CGoC	0.792		0.787	–0.752	–0.725	
Veracruz		–0.871		–0.725	–0.812	
Yucatán			0.828	–0.732	–0.856	

CGoC = Central. Gulf of California.

DISCUSSION

Fishing down the food web is an important concept highlighting the effect of severe exploitation of higher trophic levels in aquatic ecosystems. In fact, Pauly *et al*. (1998) and Pauly (1999) argue that FDFW can be viewed as an index of ecosystem degradation. Caddy *et al*. (1998) suggest that such indices are not necessarily associated with high fishing pressure but that rather, in some cases, the observed patterns could be a reflection of changes in ecosystem production originated by other causes. In our experiments, we simulated direct changes caused by harvesting rates, though other effects could be analysed in analogous experiments. If we could recreate similar responses, then the implications for successful fisheries management are obvious; we would know the processes behind the ecosystem responses.

The Fishery-in-Balance index (Pauly *et al*., 2000) is probably a better indicator of how a fishery is affecting an ecosystem. Independently of the cause, this index expresses how the trophic levels of fish stock are being modified over time with respect to the whole ecosystem. An important similarity between both indices is that they express changes in the ecosystem structure associated with the trophic level of the target fish species.

The simulations developed here attempt to illustrate some non-obvious ecosystem processes behind FDFW and FUFW. We raised the question: what is occurring within the ecosystem when a high-trophic-level-species or a low-trophic-level-species is gradually exploited from a low to a high HR (ultimately, reflecting overexploitation)? The objective here was to understand which ecosystem processes are more active in these circumstances.

After the application of PCA, important properties emerged in both cases. For FDFW under low HRs, the mechanisms governing recovery are basically properties reflecting the shark stock growing capacity. This is expressed by the magnitude of change and time of recovery as resilient properties. Other significant stock attributes at low HRs include the following: respiration/biomass (as a measure of the energetic cost), biomass, ecotrophic efficiency, and the omnivory index. As the HR increases, ecosystem attributes emerge, and stock attributes become less relevant. The net system production, as an expression of the carrying capacity, and the fishery trophic level and path length, as structural properties, become relevant. The connectance index (a structural property) appears in all of the cases as a relevant variable associated with the first component, even under higher HRs (Fig. 3).

Under low exploitation, the relative contribution of each variable suggests that the first component is associated with the stock ability to recover losses, meanwhile within the second component, variables are more closely associated with survival, energetic cost, and stock size. Under intensive exploitation, the survival and structural attributes of the ecosystem increase within component one. In the second component the greatest contributors, at the stock level, were the time of recovery and energetic cost and, at the ecosystem level, the total system production and fishery trophic level.

Figure 3 suggests that variables in component one become less important as exploitation increases (i.e., importance of the stock-level variables decreased under overexploitation and ecosystem attributes emerged as more relevant). In particular, path length emerges as a new relevant variable, which expresses a structural and complexity property of the ecosystem because it is computed as the total number of trophic links divided by the number of pathways. The emergence of structural attributes as significant variables in ecosystem dynamics during intensive exploitation of high trophic levels suggest a negative impact risk on the ecosystem structure, which is consistent with the FDFW concept recognised by Pauly *et al.* (1998) and Pauly (1999).

The omnivory index at the stock level and connectance index at the ecosystem level appear to be relevant variables. In both cases, relative weights tend to increase with increasing HRs. This trend probably represents the importance of the ability of the stock and the ecosystem to gain or obtain energy to maintain their mass balance.

Even when the second component maintains its global weight with increased exploitation, the relative weight of variables changes; energetic cost at the stock level, expressed by R/B ratio, maintains significant weight, although stock size becomes irrelevant and the time of recovery becomes relevant. This finding suggests that resilient properties emerge when the stock is strongly depleted by exploitation, causing an imbalance of biomass. In this component, the total system production appears to be a relevant variable at almost all exploitation rates (with the exception of the lowest, HR = 0.3).

The trends described above suggest two clear responses: (1) when a high trophic level stock is subjected to a low HR, the stock attributes influence the recovery process. (2) When the stock is subject to a high HR and the stock alone is not sufficient to recover losses (overexploitation), ecosystem mechanisms associated with structural and functional properties emerged as the primary stock and ecosystem responses. Under these high-levels of exploitation, the resilient properties of the target group become more relevant.

The FDFW concept is associated with the Fishery trophic level (Table 2), appears to be relevant at HRs $\geq$ 0.5, and could represent a limiting biological reference point. Once a high-trophic level stock is greatly or fully overexploited, its impact is strongly reflected in the fishery trophic level indicator and in the MTLC and FIB indices.

Regarding FUFW, less contrast was observed with respect to the relevant variables influencing mechanisms for stock and ecosystem recovery after exploitation. In fact, from Table 4, we may suggest that the same variables are relevant over the range of simulated HRs that attempted to reflect low and high exploitation. Biomass, omnivory index, trophic level, and resilience properties appear relevant at the stock level. Connectance, Finn cycling index, path length, number of paths, and the system omnivory index are ecosystem structure properties. Net system production, respiration/biomass ratio, and primary production/biomass ratio appear to be relevant ecosystem functional attributes. The only characteristic that appears to be relevant exclusively for high HRs was the magnitude of change.

Evidently, there is a contrast between ecosystem and exploited stock (within that ecosystem) processes under FDFW and FUFW. In FDFW, there is a clear contrast between relevant attributes concerning under- and overfishing. Under FUFW, however, the same stock and ecosystem attributes participate in the response over the entire exploitation range. Clearly, the trophic level of the target species makes the difference among these situations. More importantly, the processes behind the impact of fishing at the base of the trophic pyramid are the same along a wide range of exploitation. Processes at the top of the trophic pyramid that govern the response to exploitation are different for both under- and overexploitation.

ACKNOWLEDGMENTS

The author would like to thank the following sources of support: GEF-UNIDO-Gulf of Mexico LME, SEP-CONACyT 104974, WWF-KH88, ANR-CONACyT 111465, and Incofish (EC-003739). The author would also like to thank the National Polytechnic Institute through project SPI-IPN-20110785, 20121444; COFAA and EDI. Author thanks comments and suggestions to the manuscript by Dr. Rodrigo Moncayo Estrada and Dr. Hugo Arancibia. Also thanks M.C. Gerardo García who processed PCA for sharks.

REFERENCES

Alvarez-Hernández, J. H. 2003. Trophic model of a fringing coral reef in the southern Mexican Caribbean. *In*: Zeller D., Booth, S., Mohammed E. & Pauly D. (Eds.). *From Mexico to Brazil: Central Atlantic fisheries catch trends and ecosystem models. Fisheries Centre Research Reports* 11(6): 1- 264.

Arreguín-Sánchez, F. 2002. Flows of biomass and structure in an exploited benthic ecosystem in the gulf of California, México. *Ecological Modelling* 156: 167-183.

Arreguín-Sánchez, F. & Arcos-Huitrón, E. 2007. Fisheries catch statistics for Mexico. p. 81-103 *In*: Zeller, D. & D. Pauly (Eds.) Reconstruction of marine fisheries catches for key countries and regions (1950-2005). Fisheries Centre Research Reports 15(2). Fisheries Centre, University of British Columbia, Canada. 163 p.

Arreguín-Sánchez, F. & S. Manickchand-Heileman. 1998. The trophic role of lutjanid fish and impacts of their fisheries in two ecosystems in the Gulf of Mexico. *Journal of Fish Biology* 53 (Supplement A): 143-153

Arreguín-Sánchez, F., J. C. Seijo & E. Valero. 1993a. An application of the ECOPATH II to the North continental shelf ecosystem of Yucatan, Mexico. *In*: Christensen, V. & D. Pauly. *Trophic box models of Aquatic Ecosystems*. ICLARM Conference Proceedings 26. Philippines, pp. 269-278.

Arreguín-Sánchez, F., E. Valero & E. A. Chávez. 1993b. A trophic box model of the coastal fish communities of the Southwestern Gulf of Mexico. *In*: Christensen, V. & D. Pauly. *Trophic models of Aquatic Ecosystems*. ICLARM Conference Proceedings 26. Philippines, pp. 197-205.

Arreguín-Sánchez, F., L. E. Schultz-Ruiz, A. Gracia-Gasca, J. A. Sánchez & T. Alarcón. 1997. Las Pesquerías de camarón de altamar: explotación, dinámica y evaluación. *In*: Flores-Hernández, D., P. Sánchez-Gil, J.C. Seijo & F. Arreguín-Sánchez (Eds.). *Análisis y diagnóstico de los recursos pesqueros críticos del Golfo de México*. Universidad Autónoma de Campeche, *EPOMEX Serie Científica* 7: 145-172.

Arreguín-Sánchez, F., M. Zetina-Rejón, S. Manickand-Heileman, M. Ramírez-Rodríguez & L. Vidal. 2004. Simulated response to harvesting strategies in an exploited ecosystem in the southern Gulf of México. *Ecologica Modelling* 172: 421-432.

Browder, J. 1993. A pilot model of the Gulf of Mexico continental shelf. *In*: Christensen, V. & D. Pauly (Eds.). *Trophic models of Aquatic Ecosystems*. ICLARM Conference Proceedings 26. Philippines, pp. 279-284

Caddy J. F., J. Csirke, S. M. Garcia & R. J. R. Grainger. 1998. How Pervasive Is "Fishing Down Marine Food Webs"?. Technical Comments. *Science* 282: 1-1383.

Christensen, V. 1998. Fishery-induced changes in a marine ecosystem: insights from models of the Gulf of Thailand. *Journal of Fish Biology* 53(Suppl. A): 128-142.

Christensen, V. & D. Pauly. 1992. Ecopath II– a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61: 169–185.

Christensen, V. & C. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172:109-140.

Clark, C. W. 1985. Bioeconomic modelling and fisheries management. A Wiley-Interscience Publication, New York, New York, USA. 291 p.

Gulland, J. A. 1983. *Fish stock Assessment, a manual of basic methods*. London, FAO/John Wiley and Sons. 223 p.

Hoenig, J. & S. Gruber. 1990. Life history patterns in the elasmobranches: implications for fisheries management. *In*: Pratt, J., S. Gruber & T. Taniuchi (Eds.). *Elasmobranchs as living resources: Advances in the biology, ecology, systematics and the status of the fisheries*. U.S. Dep. Commerce NOAA *Technical Report*. NMFS 90:1-16

Jackson J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, & R. R. Warner. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* 293: 629-638.

Manikchand-Haileman, S., L. A. Soto, & E. Escobar. 1998. A preliminary trophic model of the continental shelf, South-western Gulf of Mexico. *Estuarine Coastal and Shelf Science* 46: 885–899.

Mendoza, J. J. 1993. A preliminary biomass budget for the northern Venezuela. *In*: Christensen, V. & D. Pauly (Eds.). *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings 26: 285-297.

Olivieri, R. A., A. Cohen & F. P. Chavez. 1993. An ecosystem model of Monterrey Bay, California. *In*: Christensen, V. & D. Pauly (Eds.). *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings. 26: 315-322.

Opitz, S. 1993. A quantitative model of the trophic interactions in a Caribbean Coral Reef Ecosystem. *In*: Christensen, V. & D. Pauly (Eds.). *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings 26: 259-267.

Pauly, D. 1999. Fishing down marine food webs as an integrative concept. *In*: D. Pauly, V. Christensen & L. Coelho (Eds.). *Proc. "98 EXPO Conference on OceanFood Webs and Economic Productivity*, Lisbon, Portugal, 1-3 July 1998. ACP-EU Fisheries Research Report 5. pp. 4-6.

Pauly, D. & R. Watson. 2005. Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. *Philosophical Transactions of the Royal Society B* 360 (1454): 415-423.

Pauly, D., V. Christensen & C. Walters. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* 57: 697-706.

Pauly, D., V. Christensen, J. Dalsgraad, R. Froese & F. Torres Jr. 1998. Fishing Down Food Webs. *Science* 279: 860-863.

Pérez-España, H. & F. Arreguín-Sánchez. 1999a. A measure of ecosystem maturity. *Ecological modelling* 2: 129-135.

Pérez-España, H. & F. Arreguín-Sánchez. 1999b. Complexity related to behavior of stability in modeled coastal zone ecosystems. *Aquatic Ecosystem Health and Management* 119: 79-85.

Pratt, J. & J. Casey. 1990. Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. *In*: Pratt, J., S. Gruber & T. Taniuchi (Eds). *Elasmobranchs as living resources: Advances in the biology, ecology, systematics and the status of the fisheries*. U.S. Dep. Commerce NOAA Technical Report NMFS 90: 97-109.

Vasconcellos, M., S. Mackinson, K. Sloman & D. Pauly. 1997. The stability of trophic mass-balance models of Marine ecosystems: a comparative analysis. *Ecological Modelling* 100: 125-134.

Vega.Cendejas, M. E., F. Arreguín-Sánchez & M. Hernández. 1993. Trophic fluxes on the Campeche Bank, Mexico. *In*: Christensen, V. & D. Pauly (Eds.). *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings 26: 206-213.

Vidal, L. & M. Basurto. 2003. A preliminary trophic model of Bahía de la Ascensión, Quintana Roo, Mexico. *In*: Zeller D., Booth, S., Mohammed E. & D. Pauly (Eds.). *From Mexico to Brazil: Central Atlantic fisheries catch trends and ecosystem models*. Fisheries Centre Research Reports 11 (6): 1-264.

Walters, C., Christensen V., & D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 7: 1-34.

Watson, R. & D. Pauly. 2001. Systematic deteriorations in world fisheries catch trends. *Nature* 414: 534-536.

Recibido: 27 de junio de 2011.

Aceptado: 16 de noviembre de 2011.