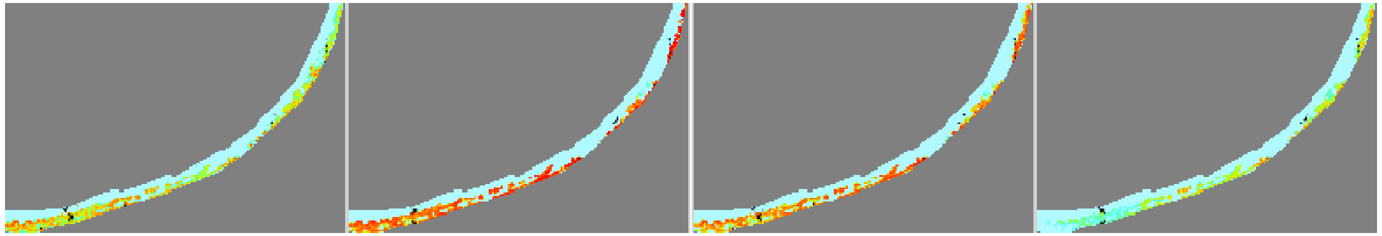
Marine Biodiversity Observation Network (MBON): Monitoring Ecosystem Structure and Function in the Florida Keys



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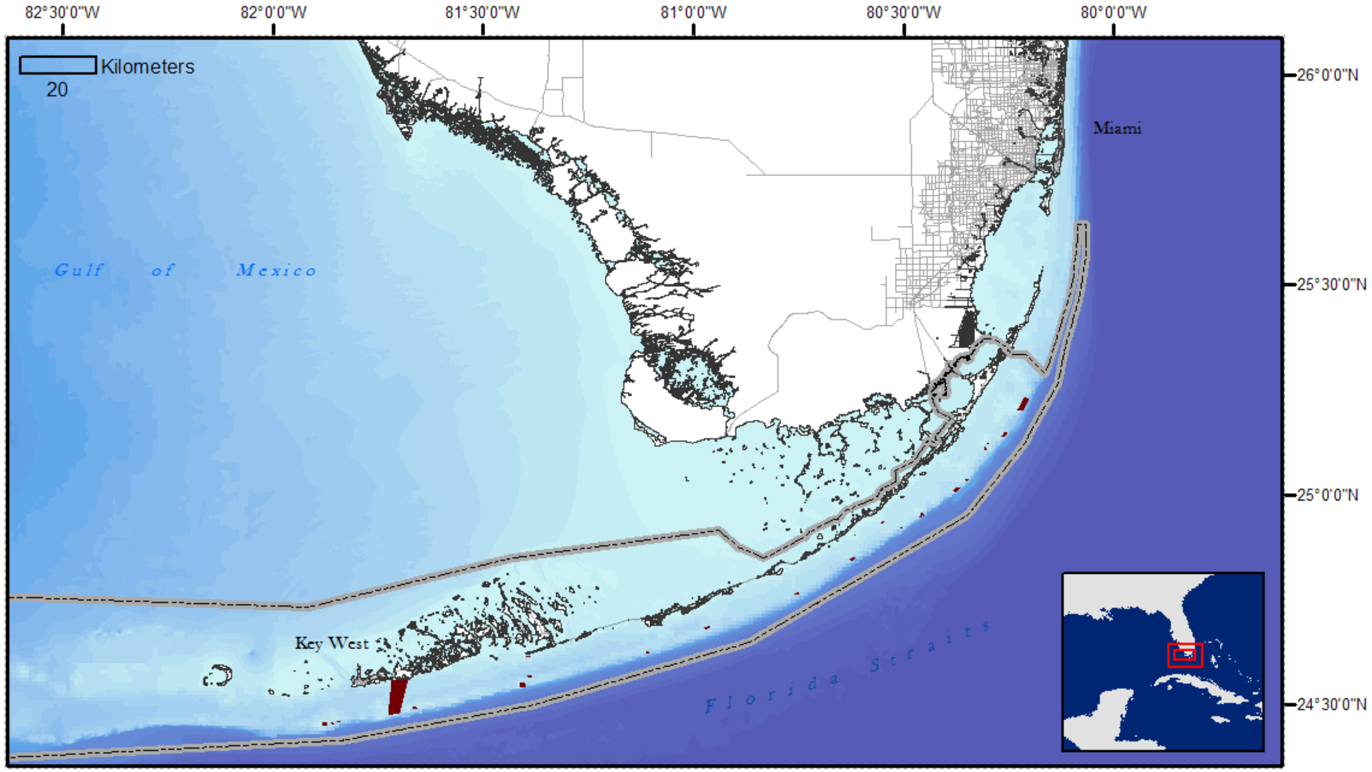
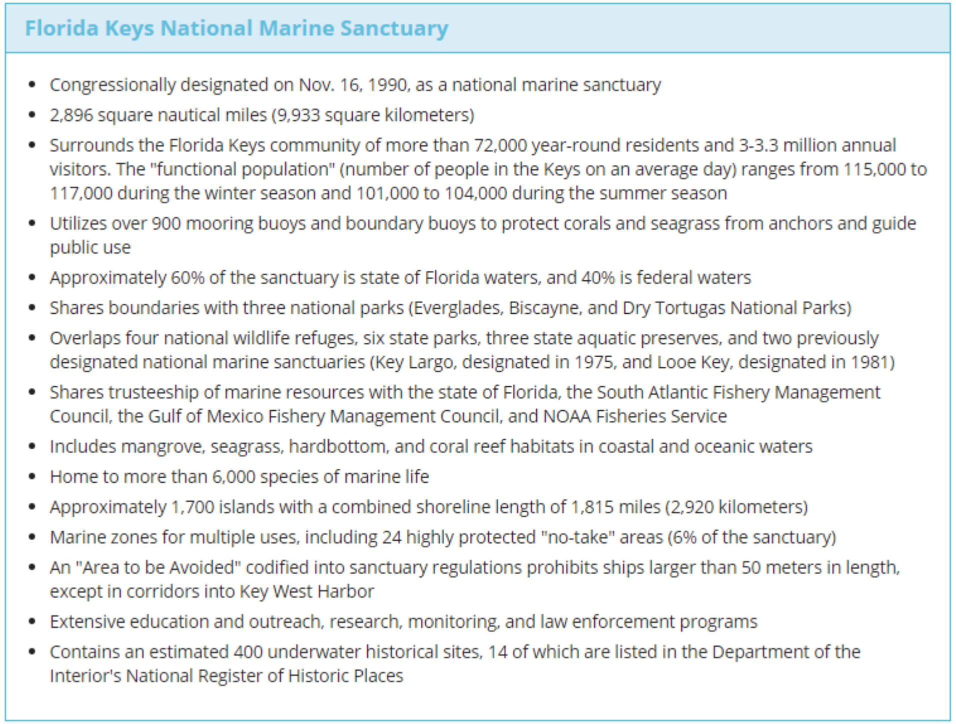
The Florida Keys



Florida Keys National Marine Sanctuary

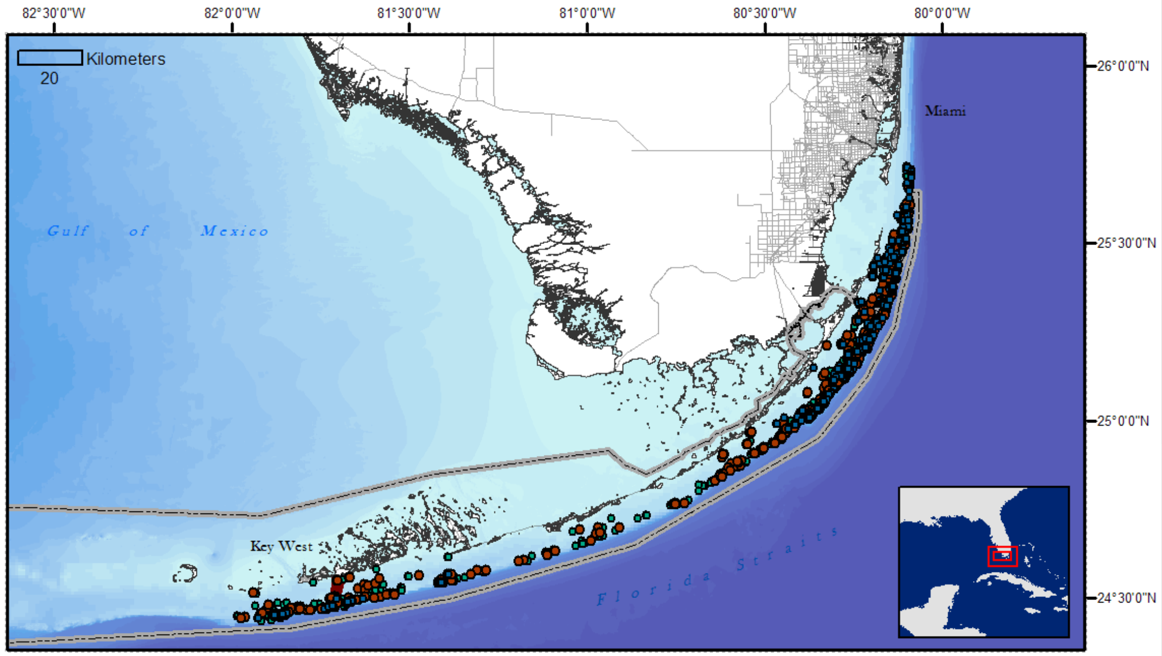


Florida Keys National Marine Sanctuary

- Congressionally designated on Nov. 16, 1990, as a national marine sanctuary
- 2,896 square nautical miles (9,933 square kilometers)
- Surrounds the Florida Keys community of more than 72,000 year-round residents and 3-3.3 million annual visitors. The "functional population" (number of people in the Keys on an average day) ranges from 115,000 to 117,000 during the winter season and 101,000 to 104,000 during the summer season
- Utilizes over 900 mooring buoys and boundary buoys to protect corals and seagrass from anchors and guide public use
- Approximately 60% of the sanctuary is state of Florida waters, and 40% is federal waters
- Shares boundaries with three national parks (Everglades, Biscayne, and Dry Tortugas National Parks)
- Overlaps four national wildlife refuges, six state parks, three state aquatic preserves, and two previously designated national marine sanctuaries (Key Largo, designated in 1975, and Looe Key, designated in 1981)
- Shares trusteeship of marine resources with the state of Florida, the South Atlantic Fishery Management Council, the Gulf of Mexico Fishery Management Council, and NOAA Fisheries Service
- Includes mangrove, seagrass, hardbottom, and coral reef habitats in coastal and oceanic waters
- Home to more than 6,000 species of marine life
- Approximately 1,700 islands with a combined shoreline length of 1,815 miles (2,920 kilometers)
- Marine zones for multiple uses, including 24 highly protected "no-take" areas (6% of the sanctuary)
- An "Area to be Avoided" codified into sanctuary regulations prohibits ships larger than 50 meters in length, except in corridors into Key West Harbor
- Extensive education and outreach, research, monitoring, and law enforcement programs
- Contains an estimated 400 underwater historical sites, 14 of which are listed in the Department of the Interior's National Register of Historic Places

Existing Monitoring Programs

- Extensive Benthic Habitat Mapping
- Coral Reef Evaluation and Monitoring Project (CREMP)
- Florida Reef Resilience Program (FRRP)
- EPA Water Quality Protection Program
- NOAA/FIU/DEP Seagrass Monitoring Program
- NOAA/FWC/UM Reef Fish Visual Census Program



Florida Keys National Marine Sanctuary

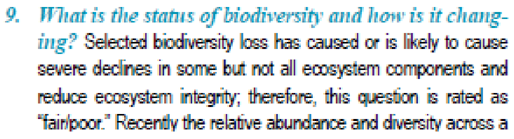
Sanctuary Management Questions

- Sanctuary Condition Reports

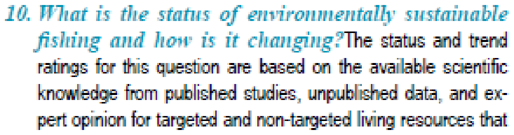
Site History and Resources 10
- Geology 10
- Water Circulation 11
- Early Exploration and Settlement 12
- Development of the Florida Keys 12
- Commerce 13
- Designation of the Sanctuary 14
- Habitats 16
- Living Resources 18
- Maritime Archaeological Resources 19

Pressures on the Sanctuary 20
- Pressures on Water Quality 20
- Commercial and Recreational Fishing 23
- Bleaching Events and Climate Change 24
- Weather Disturbances 26
- Diseases of Marine Organisms 26
- Vessel Use 28
- Coastal Development 29
- Non-Indigenous Species 30
- Wildlife Disturbance 30
- Artificial Reefs 31
- Marine Debris 31
- Military Use 32
- Pressures to Maritime Archaeological Resources 33

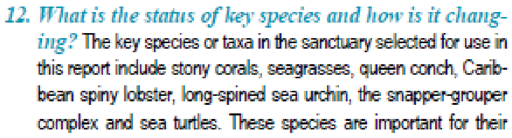
State of Sanctuary Resources 34
- Water 35
- Habitat 40
- Living Resources 46
- Maritime Archaeological Resources 60



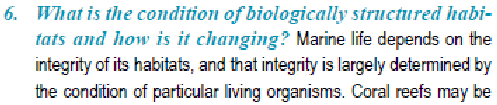
9. What is the status of biodiversity and how is it changing? Selected biodiversity loss has caused or is likely to cause severe declines in some but not all ecosystem components and reduce ecosystem integrity; therefore, this question is rated as "fair/poor." Recently the relative abundance and diversity across a



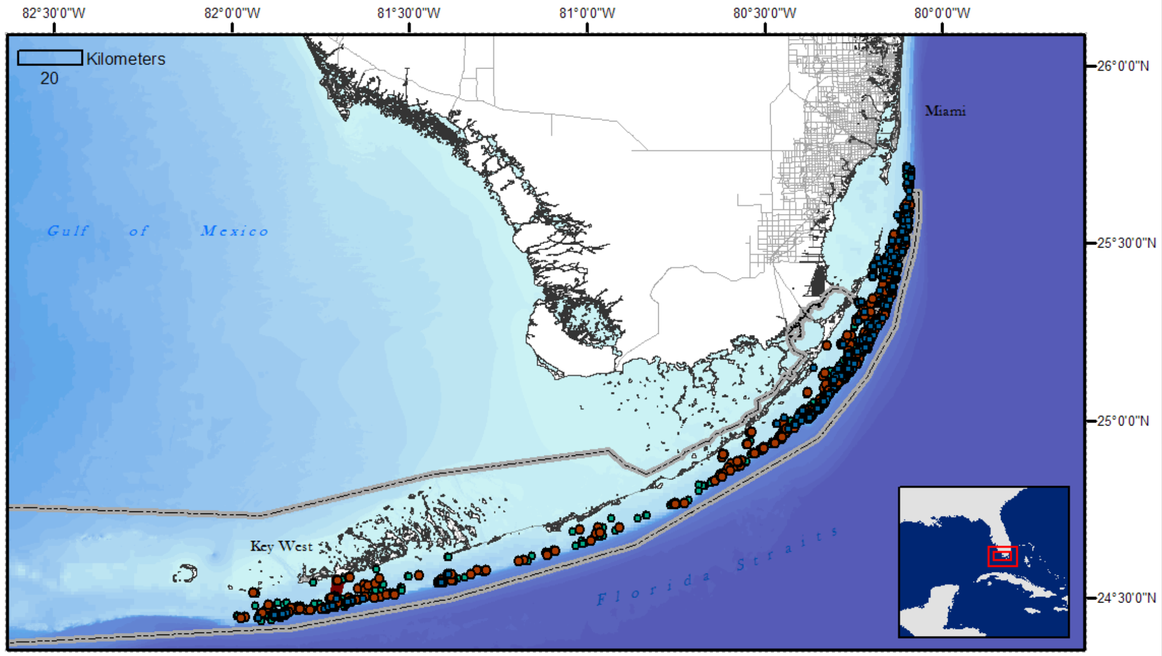
10. What is the status of environmentally sustainable fishing and how is it changing? The status and trend ratings for this question are based on the available scientific knowledge from published studies, unpublished data, and expert opinion for targeted and non-targeted living resources that



12. What is the status of key species and how is it changing? The key species or taxa in the sanctuary selected for use in this report include stony corals, seagrasses, queen conch, Caribbean spiny lobster, long-spined sea urchin, the snapper-grouper complex and sea turtles. These species are important for their



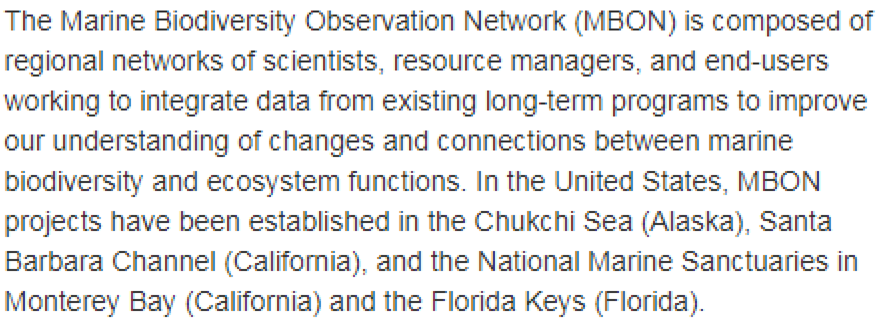
6. What is the condition of biologically structured habitats and how is it changing? Marine life depends on the integrity of its habitats, and that integrity is largely determined by the condition of particular living organisms. Coral reefs may be



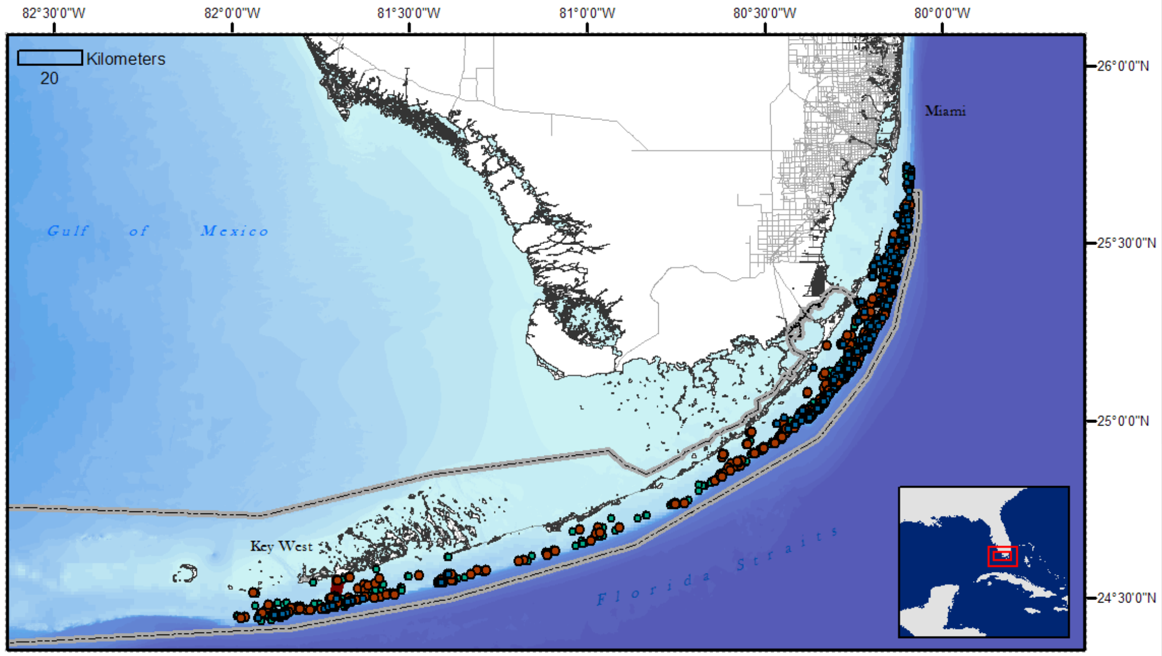
Florida Keys National Marine Sanctuary

Additional Needs

- Marine Biodiversity Observation Network



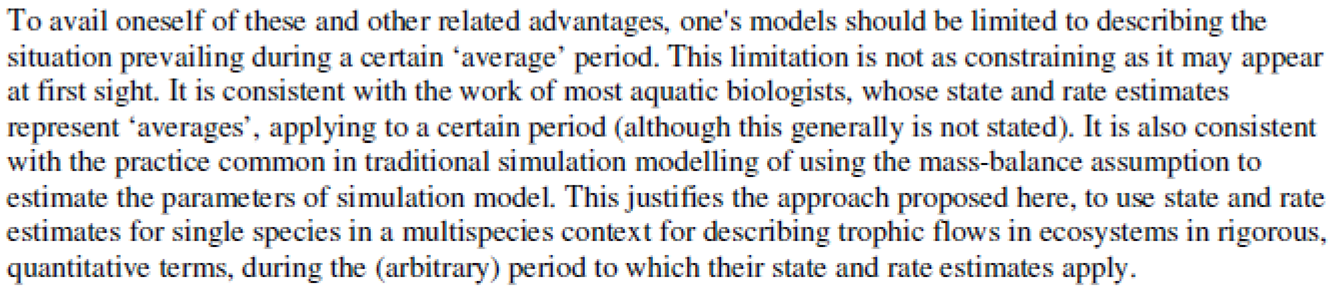
The Marine Biodiversity Observation Network (MBON) is composed of regional networks of scientists, resource managers, and end-users working to integrate data from existing long-term programs to improve our understanding of changes and connections between marine biodiversity and ecosystem functions. In the United States, MBON projects have been established in the Chukchi Sea (Alaska), Santa Barbara Channel (California), and the National Marine Sanctuaries in Monterey Bay (California) and the Florida Keys (Florida).



Florida Keys National Marine Sanctuary

- NOAA Integrated Ocean Observing System (IOOS) Essential Biological Variables
  - Diet, mortality rates, etc.

The Ecosystem Modeling Perspective



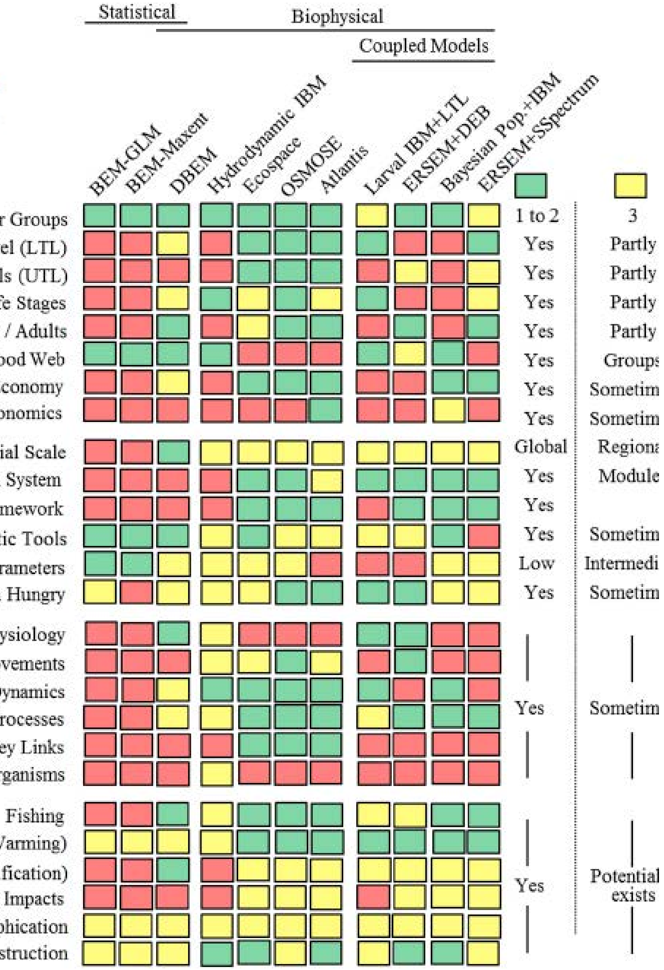
To avail oneself of these and other related advantages, one's models should be limited to describing the situation prevailing during a certain ‘average’ period. This limitation is not as constraining as it may appear at first sight. It is consistent with the work of most aquatic biologists, whose state and rate estimates represent ‘averages’, applying to a certain period (although this generally is not stated). It is also consistent with the practice common in traditional simulation modelling of using the mass-balance assumption to estimate the parameters of simulation model. This justifies the approach proposed here, to use state and rate estimates for single species in a multispecies context for describing trophic flows in ecosystems in rigorous, quantitative terms, during the (arbitrary) period to which their state and rate estimates apply.

Ecopath with Ecosim   Christensen, Walters, Pauly, and Forrest

Existing Ecosystem Models and Applications

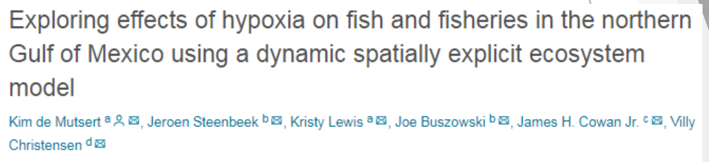
Projecting changes in the distribution and productivity of living marine resources: A critical review of the suite of modelling approaches used in the large European project VECTORS

Myron A. Peck [a], Christos Arvanitidis [b], Momme Butenschön [c], Donata Melaku Canu [d], Eva Chatzinikolaou [b], Andrea Cucco [e], Paolo Domenici [e], Jose A. Fernandes [c], Loic Gasche [f], Klaus B. Huebert [a, 1], Marc Hufnagl [a], Miranda C. Jones [g, 2], Alexander Kempf [h], Friedemann Keyl [h], Marie Maar [i], Stéphanie Mahévas [f], Paul Marchal [j], Delphine Nicolas [k] … Karen E. van de Wolfshaar [n]



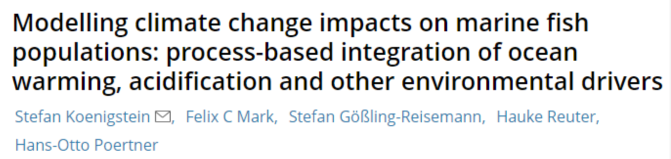
		BEM-GLM	BEM-Maxent	DBEM	Hydrodynamic IBM	Ecospace	OSMOSE	Atlantis	Larval IBM+LTL	ERSEM+DEB	Bayesian Pop+IBM	ERSEM+SSpectrum	🟩	🟨
		Statistical		Biophysical										
									Coupled Models					
Modelled Ecosystem Components	Species or Groups	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟨	🟩	🟩	🟨	1 to 2	3
	Lower Trophic Level (LTL)	🟥	🟥	🟨	🟥	🟩	🟩	🟩	🟩	🟥	🟥	🟩	Yes	Partly
	Upper Trophic Levels (UTL)	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟥	🟨	🟥	🟨	Yes	Partly
	UTL Early Life Stages	🟥	🟥	🟨	🟩	🟨	🟩	🟨	🟩	🟥	🟥	🟨	Yes	Partly
	UTL Juvenile / Adults	🟥	🟥	🟩	🟥	🟨	🟩	🟩	🟥	🟩	🟥	🟩	Yes	Partly
	Whole Food Web	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟩	🟨	🟩	🟥	Yes	Groups
	Single Human Sector / Economy	🟥	🟥	🟨	🟥	🟩	🟩	🟩	🟥	🟥	🟩	🟩	Yes	Sometim
	Multiple Human Sectors / Economics	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟥	🟥	🟨	🟥	Yes	Sometim
Model Class Attributes	Spatial Scale	🟥	🟥	🟩	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	Global	Regiona
	Coupled Model System	🟥	🟥	🟥	🟥	🟩	🟩	🟨	🟩	🟩	🟩	🟩	Yes	Module
	Common Structural Framework	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟥	🟩	🟩	🟩	Yes	
	Well Accepted Diagnostic Tools	🟩	🟩	🟩	🟨	🟩	🟨	🟨	🟨	🟨	🟩	🟥	Yes	Sometim
	Number of Parameters	🟩	🟩	🟨	🟨	🟨	🟨	🟥	🟥	🟥	🟨	🟨	Low	Intermedi
	Data Hungry	🟨	🟥	🟨	🟨	🟨	🟩	🟩	🟩	🟩	🟨	🟨	Yes	Sometim
Mechanisms	Physiology	🟥	🟥	🟩	🟨	🟥	🟥	🟥	🟩	🟩	🟥	🟥	Yes	Sometim
	Behaviorally-Mediated Movements	🟥	🟥	🟥	🟨	🟨	🟩	🟨	🟥	🟩	🟥	🟥		
	Physical Transport Dynamics	🟥	🟥	🟨	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟥		
	Density-dependent Processes	🟥	🟥	🟨	🟨	🟩	🟩	🟩	🟨	🟩	🟩	🟩		
	Dynamic Predator-Prey Links	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟥	🟥	🟥	🟥		
	Adaptive Capacity of Organisms	🟥	🟥	🟥	🟨	🟥	🟥	🟥	🟥	🟥	🟥	🟥		
Interacting Pressures/Drivers	Fishing	🟥	🟥	🟩	🟨	🟩	🟩	🟩	🟨	🟨	🟩	🟩	Yes	Potential exists
	Climate Change (Warming)	🟨	🟨	🟨	🟨	🟩	🟩	🟩	🟩	🟩	🟩	🟩		
	Climate Change (Acidification)	🟥	🟥	🟩	🟥	🟨	🟨	🟨	🟨	🟨	🟨	🟨		
	Alien Invasive Species Impacts	🟥	🟥	🟥	🟥	🟨	🟨	🟨	🟥	🟨	🟨	🟨		
	Eutrophication	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨		
	Direct Habitat Loss / Destruction	🟨	🟨	🟨	🟩	🟩	🟨	🟩	🟨	🟩	🟩	🟨		

Applications



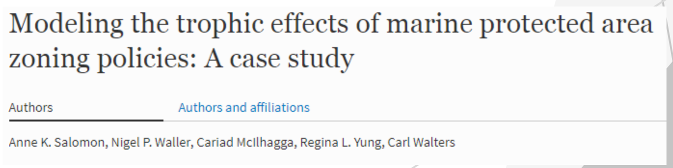
Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model

Kim de Mutsert [a], Jeroen Steenbeek [b], Kristy Lewis [a], Joe Buszowski [b], James H. Cowan Jr. [c], Villy Christensen [d]



Modelling climate change impacts on marine fish populations: process-based integration of ocean warming, acidification and other environmental drivers

Stefan Koenigstein, Felix C Mark, Stefan Gößling-Reisemann, Hauke Reuter, Hans-Otto Poertner

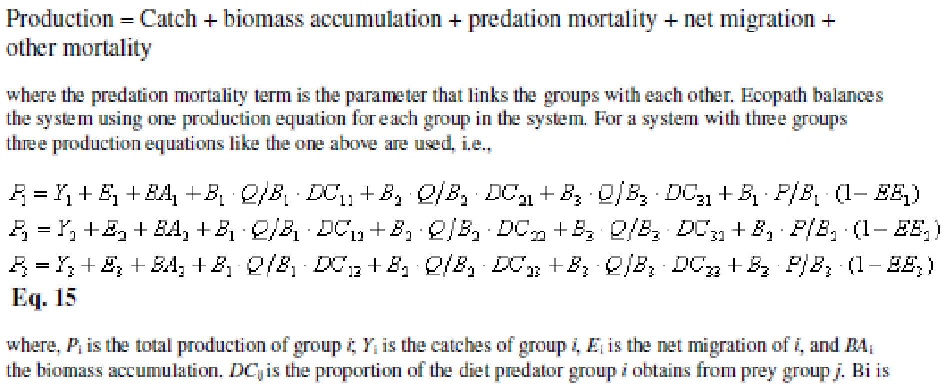


Modeling the trophic effects of marine protected area zoning policies: A case study

Anne K. Salomon, Nigel P. Waller, Cariad McIlhagga, Regina L. Yung, Carl Walters

Ecopath with Ecosim and Ecospace (EwE)

- Mass Balance of a Box



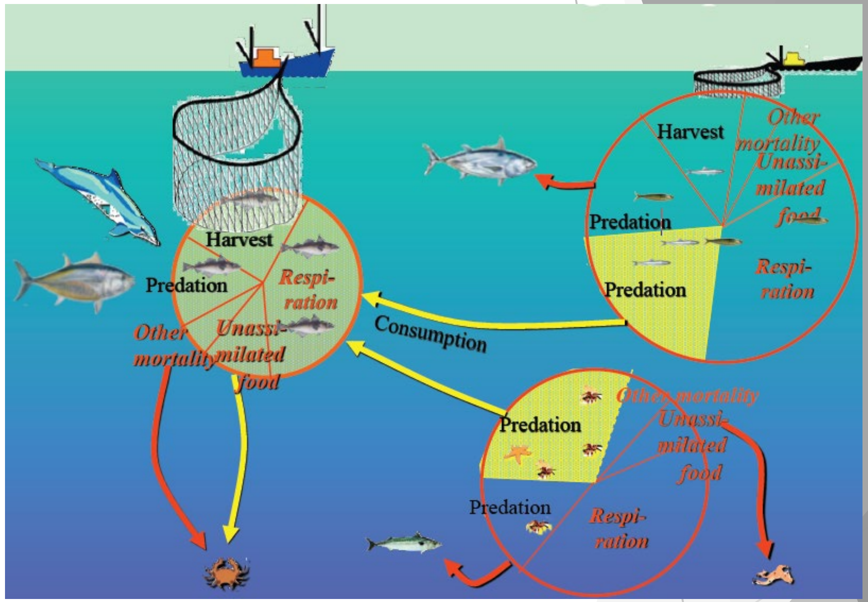
Production = Catch + biomass accumulation + predation mortality + net migration + other mortality

where the predation mortality term is the parameter that links the groups with each other. Ecopath balances the system using one production equation for each group in the system. For a system with three groups three production equations like the one above are used, i.e.,

$$P_1 = Y_1 + E_1 + BA_1 + B_1 \cdot Q/B_1 \cdot DC_{11} + B_2 \cdot Q/B_2 \cdot DC_{21} + B_3 \cdot Q/B_3 \cdot DC_{31} + B_1 \cdot P/B_1 \cdot (1 - EE_1)$$
$$P_2 = Y_2 + E_2 + BA_2 + B_1 \cdot Q/B_1 \cdot DC_{12} + B_2 \cdot Q/B_2 \cdot DC_{22} + B_3 \cdot Q/B_3 \cdot DC_{32} + B_2 \cdot P/B_2 \cdot (1 - EE_2)$$
$$P_3 = Y_3 + E_3 + BA_3 + B_1 \cdot Q/B_1 \cdot DC_{13} + B_2 \cdot Q/B_2 \cdot DC_{23} + B_3 \cdot Q/B_3 \cdot DC_{33} + B_3 \cdot P/B_3 \cdot (1 - EE_3)$$

Eq. 15

where, P_i is the total production of group i; Y_i is the catches of group i, E_i is the net migration of i, and BA_i the biomass accumulation. DC_{ij} is the proportion of the diet predator group i obtains from prey group j. Bi is



- Requirements per trophic group
  - Biomass (t/km^2)- Visual Census (Count and Length)
  - Production (Z; Literature, empirical equations)
  - Consumption (Literature, Q/B = Longevity)
  - Diet (Literature, Stomach Contents)
  - Catch (Trip ticket program, Creel surveys)

Ecopath → Ecosim → Ecospace

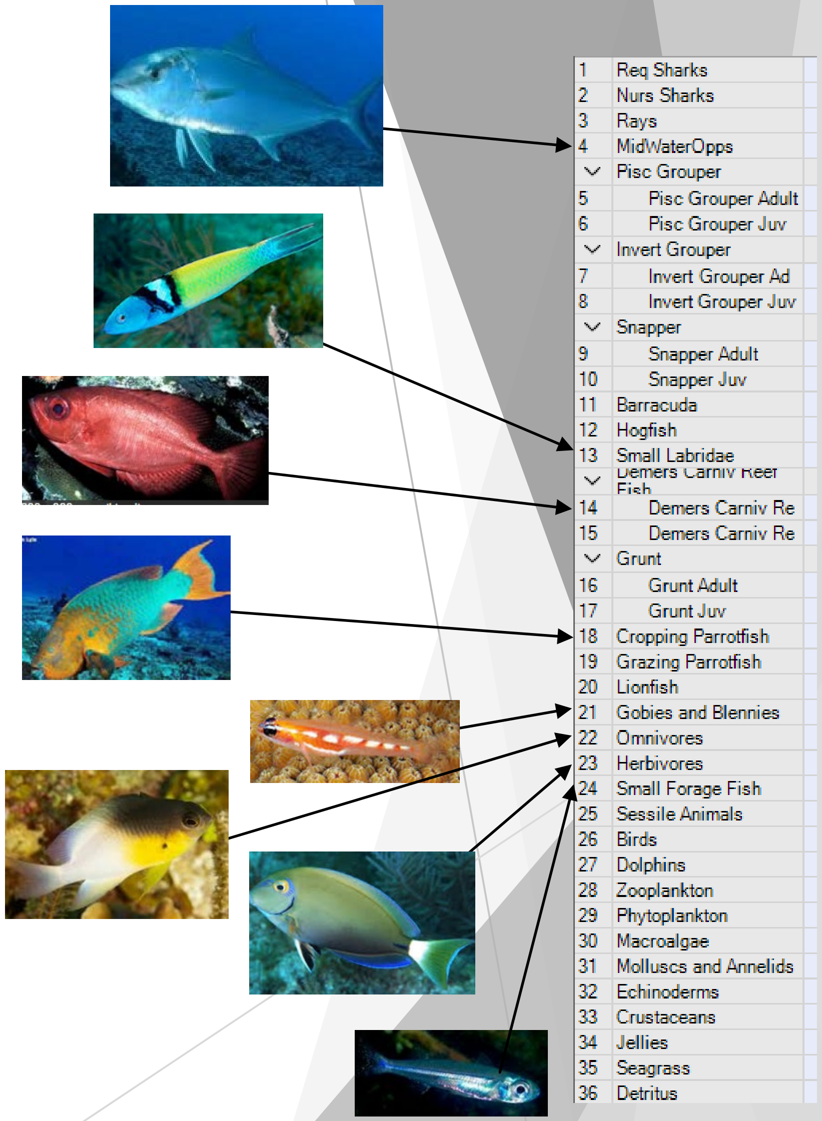
Base Trophic Relationships →
Change over Time →
Change over Space and Time

EwE Ecosystem Metrics

- Structural
    - What are the general characteristics of the ecosystem in terms of energy efficiency?
    - How is the system influenced by fishing?
    - Are these characteristics changing over time?
    - Are these metrics within an acceptable range?
- Functional
    - Which groups are the most influential trophic groups in the system?
    - Are these groups consistently influential?

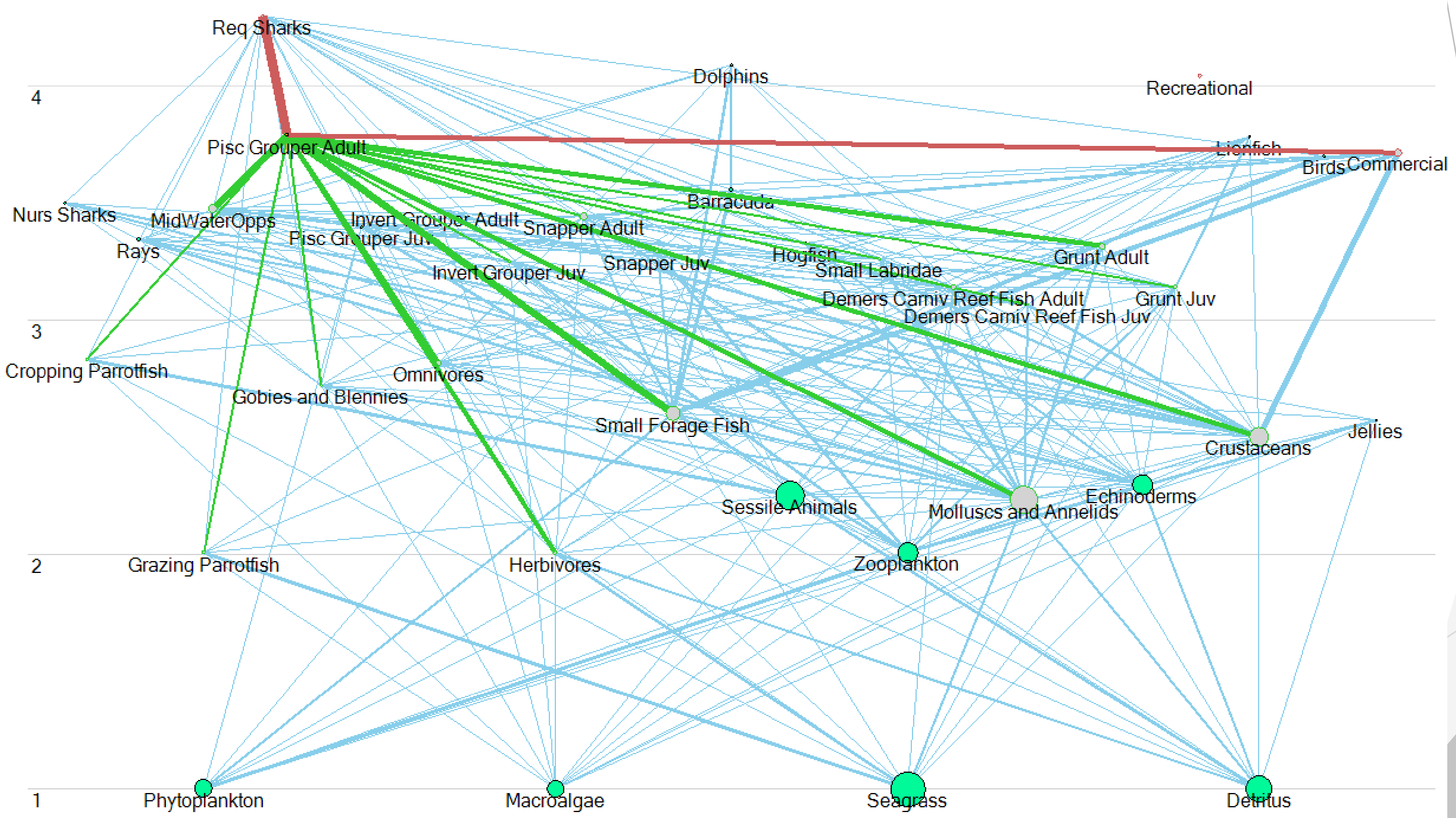
FKNMS EwE Model

- We constructed a 36-box FKNMS model that:
  - Aggregates 224 reef fish species into 19 trophic groups
  - Divides fishing mortality into recreational and commercial fleets
  - Fits to timeseries from 1994 to 2012
  - Parameterizes spatial relationships between biomass, chlorophyll-A (Chl-A), sea surface temperature (SST), distance to reefs, and depth

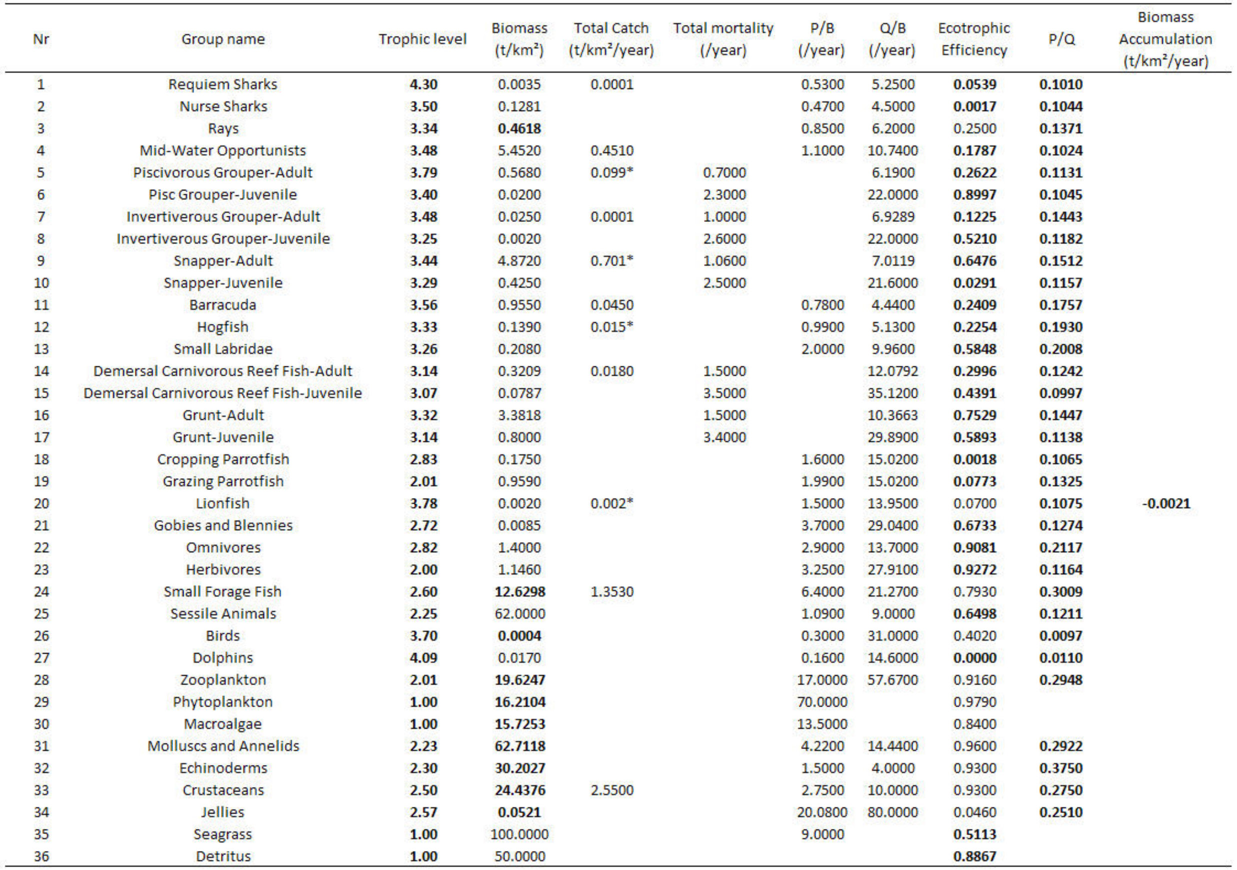


1	Req Sharks
2	Nurs Sharks
3	Rays
4	MidWaterOpps
	Pisc Grouper
5	Pisc Grouper Adult
6	Pisc Grouper Juv
	Invert Grouper
7	Invert Grouper Ad
8	Invert Grouper Juv
	Snapper
9	Snapper Adult
10	Snapper Juv
11	Barracuda
12	Hogfish
13	Small Labridae
	Demers Carniv Reef Fish
14	Demers Carniv Re
15	Demers Carniv Re
	Grunt
16	Grunt Adult
17	Grunt Juv
18	Cropping Parrotfish
19	Grazing Parrotfish
20	Lionfish
21	Gobies and Blennies
22	Omnivores
23	Herbivores
24	Small Forage Fish
25	Sessile Animals
26	Birds
27	Dolphins
28	Zooplankton
29	Phytoplankton
30	Macroalgae
31	Molluscs and Annelids
32	Echinoderms
33	Crustaceans
34	Jellies
35	Seagrass
36	Detritus

FKNMS EwE Model

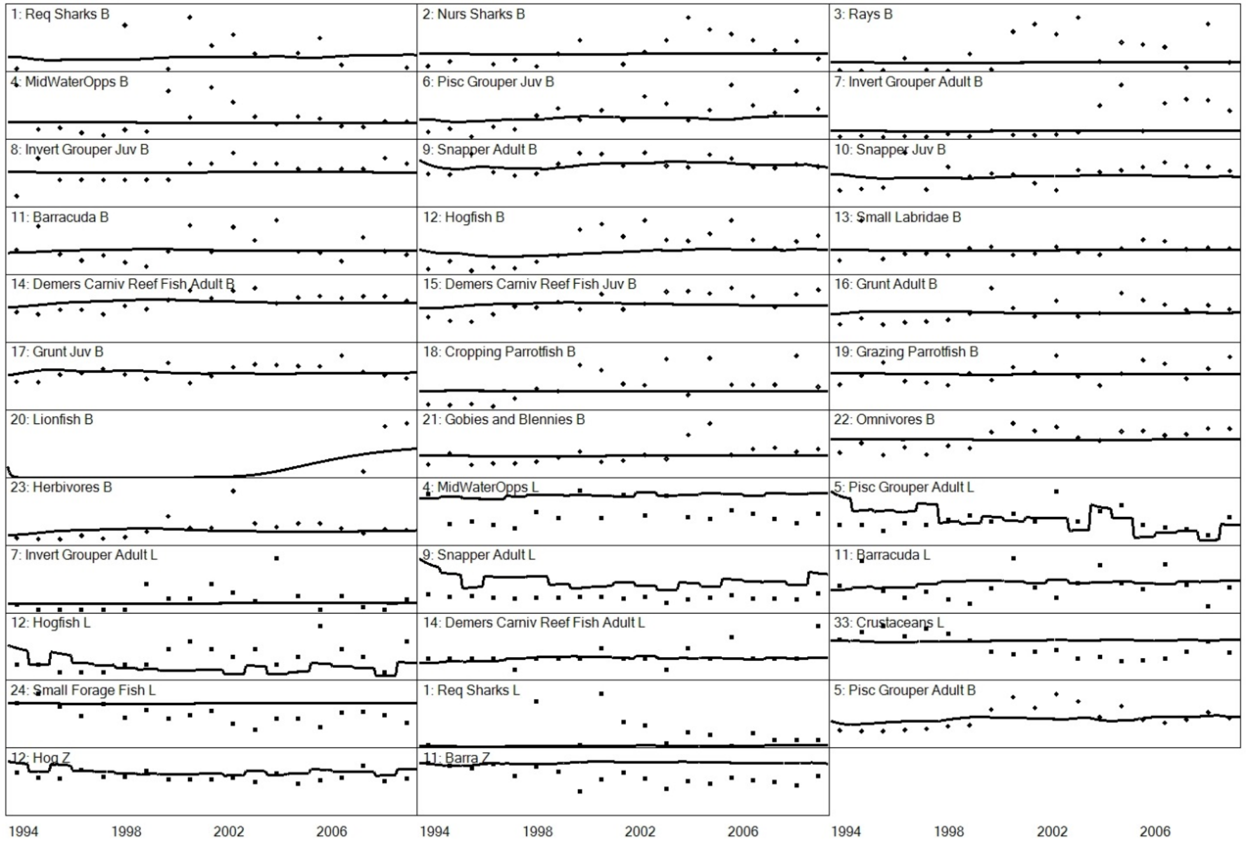


FKNMS Ecopath Model



Nr	Group name	Trophic level	Biomass (t/km^2)	Total Catch (t/km^2/year)	Total mortality (/year)	P/B (/year)	Q/B (/year)	Ecotrophic Efficiency	P/Q	Biomass Accumulation (t/km^2/year)
1	Requiem Sharks	**4.30**	0.0035	0.0001		0.5300	5.2500	**0.0539**	**0.1010**	
2	Nurse Sharks	**3.50**	0.1281			0.4700	4.5000	**0.0017**	**0.1044**	
3	Rays	**3.34**	**0.4618**			0.8500	6.2000	0.2500	**0.1371**	
4	Mid-Water Opportunists	**3.48**	5.4520	0.4510		1.1000	10.7400	**0.1787**	**0.1024**	
5	Piscivorous Grouper-Adult	**3.79**	0.5680	0.099*	0.7000		6.1900	**0.2622**	**0.1131**	
6	Pisc Grouper-Juvenile	**3.40**	0.0200		2.3000		22.0000	**0.8997**	**0.1045**	
7	Invertiverous Grouper-Adult	**3.48**	0.0250	0.0001	1.0000		6.9289	**0.1225**	**0.1443**	
8	Invertiverous Grouper-Juvenile	**3.25**	0.0020		2.6000		22.0000	**0.5210**	**0.1182**	
9	Snapper-Adult	**3.44**	4.8720	0.701*	1.0600		7.0119	**0.6476**	**0.1512**	
10	Snapper-Juvenile	**3.29**	0.4250		2.5000		21.6000	**0.0291**	**0.1157**	
11	Barracuda	**3.56**	0.9550	0.0450		0.7800	4.4400	**0.2409**	**0.1757**	
12	Hogfish	**3.33**	0.1390	0.015*		0.9900	5.1300	**0.2254**	**0.1930**	
13	Small Labridae	**3.26**	0.2080			2.0000	9.9600	**0.5848**	**0.2008**	
14	Demersal Carnivorous Reef Fish-Adult	**3.14**	0.3209	0.0180	1.5000		12.0792	**0.2996**	**0.1242**	
15	Demersal Carnivorous Reef Fish-Juvenile	**3.07**	0.0787		3.5000		35.1200	**0.4391**	**0.0997**	
16	Grunt-Adult	**3.32**	3.3818		1.5000		10.3663	**0.7529**	**0.1447**	
17	Grunt-Juvenile	**3.14**	0.8000		3.4000		29.8900	**0.5893**	**0.1138**	
18	Cropping Parrotfish	**2.83**	0.1750			1.6000	15.0200	**0.0018**	**0.1065**	
19	Grazing Parrotfish	**2.01**	0.9590			1.9900	15.0200	**0.0773**	**0.1325**	
20	Lionfish	**3.78**	0.0020	0.002*		1.5000	13.9500	0.0700	**0.1075**	**-0.0021**
21	Gobies and Blennies	**2.72**	0.0085			3.7000	29.0400	**0.6733**	**0.1274**	
22	Omnivores	**2.82**	1.4000			2.9000	13.7000	**0.9081**	**0.2117**	
23	Herbivores	**2.00**	1.1460			3.2500	27.9100	**0.9272**	**0.1164**	
24	Small Forage Fish	**2.60**	**12.6298**	1.3530		6.4000	21.2700	0.7930	**0.3009**	
25	Sessile Animals	**2.25**	62.0000			1.0900	9.0000	**0.6498**	**0.1211**	
26	Birds	**3.70**	**0.0004**			0.3000	31.0000	0.4020	**0.0097**	
27	Dolphins	**4.09**	0.0170			0.1600	14.6000	**0.0000**	**0.0110**	
28	Zooplankton	**2.01**	**19.6247**			17.0000	57.6700	0.9160	**0.2948**	
29	Phytoplankton	**1.00**	**16.2104**			70.0000		0.9790		
30	Macroalgae	**1.00**	**15.7253**			13.5000		0.8400		
31	Molluscs and Annelids	**2.23**	**62.7118**			4.2200	14.4400	0.9600	**0.2922**	
32	Echinoderms	**2.30**	**30.2027**			1.5000	4.0000	0.9300	**0.3750**	
33	Crustaceans	**2.50**	**24.4376**	2.5500		2.7500	10.0000	0.9300	**0.2750**	
34	Jellies	**2.57**	**0.0521**			20.0800	80.0000	0.0460	**0.2510**	
35	Seagrass	**1.00**	100.0000			9.0000		**0.5113**		
36	Detritus	**1.00**	50.0000					**0.8867**		

FKNMS Ecosim Model



Structural Metrics

- Total System Throughput (TST)
  - Total trophic flow (P, Q, R, Ex)
  - Indirect indicator of ecosystem size
- Mean Transfer Efficiency (TE)
  - Ratio of production between trophic levels
  - How much is lost between levels due to M, egestion, unassimilated food
  - Important for estimating other metrics
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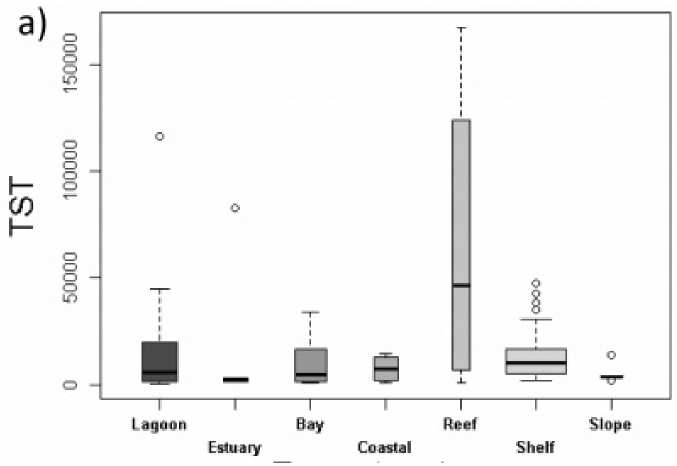
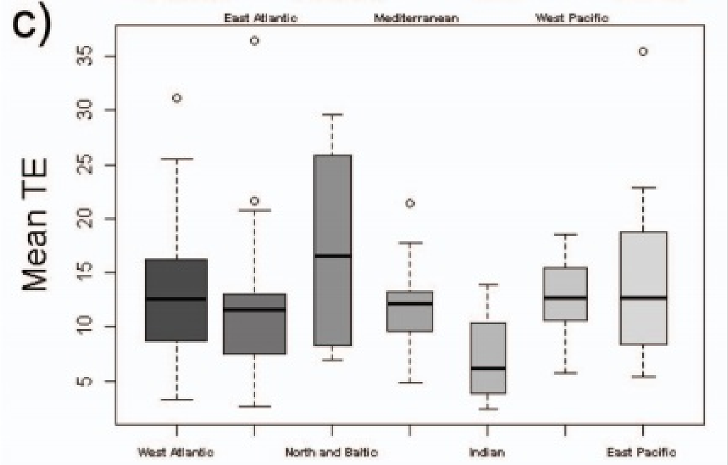
Johanna Jacomina Heymans[1]*, Marta Coll[2,3¤], Simone Libralato[4], Lyne Morissette[5], Villy Christensen[6]





Structural Metrics

- Total System Throughput
- Mean Transfer Efficiency
- Mean Trophic Level of the Catch
  - TL considers the fraction or prey in diet and the TL of prey
  - Potential changes in community structure due to fishing
  - Decreasing value indicates smaller, faster fish (lower trophic levels) are increasingly dominating the system
- Primary Production Required to Sustain the Fishery
  - Given the number of links to a predator and the TE between levels, What percentage of the PP is required to maintain the catch.
  - A measure of human impacts on the lowest trophic level
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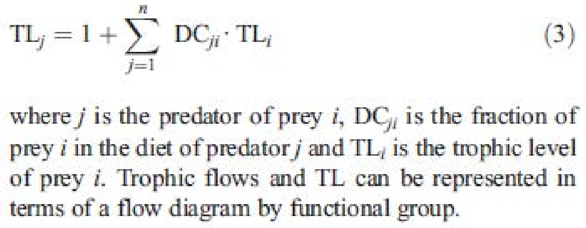
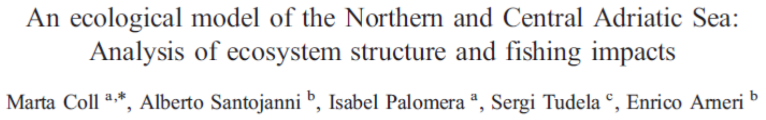


$$\mathrm{TL}_j = 1 + \sum_{j=1}^{n} \mathrm{DC}_{ji} \cdot \mathrm{TL}_i \qquad (3)$$

where j is the predator of prey i, DC_{ji} is the fraction of prey i in the diet of predator j and TL_i is the trophic level of prey i. Trophic flows and TL can be represented in terms of a flow diagram by functional group.



An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts

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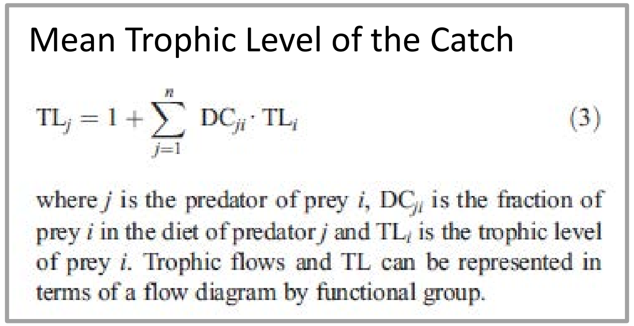

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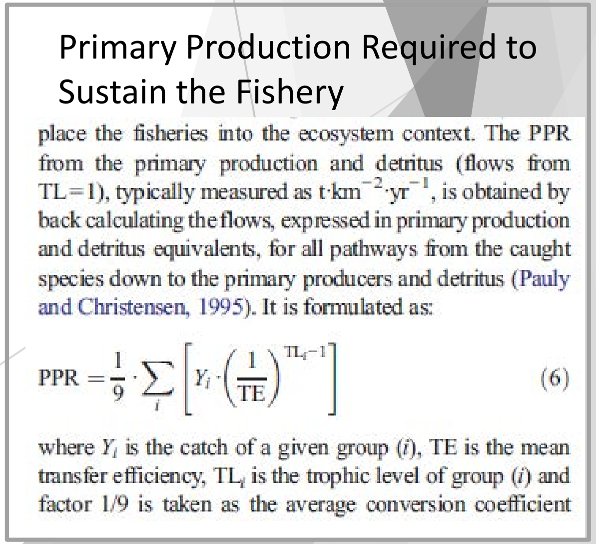
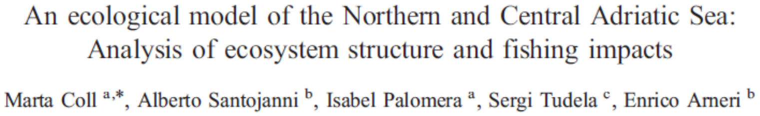


Primary Production Required to Sustain the Fishery

place the fisheries into the ecosystem context. The PPR from the primary production and detritus (flows from TL = 1), typically measured as $\mathrm{t \cdot km^{-2} \cdot yr^{-1}}$, is obtained by back calculating the flows, expressed in primary production and detritus equivalents, for all pathways from the caught species down to the primary producers and detritus (Pauly and Christensen, 1995). It is formulated as:

$$\mathrm{PPR} = \frac{1}{9} \cdot \sum_i \left[Y_i \cdot \left(\frac{1}{\mathrm{TE}} \right)^{\mathrm{TL}_i - 1} \right] \qquad (6)$$

where Y_i is the catch of a given group (i), TE is the mean transfer efficiency, TL_i is the trophic level of group (i) and factor 1/9 is taken as the average conversion coefficient



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Primary production required to sustain global fisheries

D. Pauly* & V. Christensen

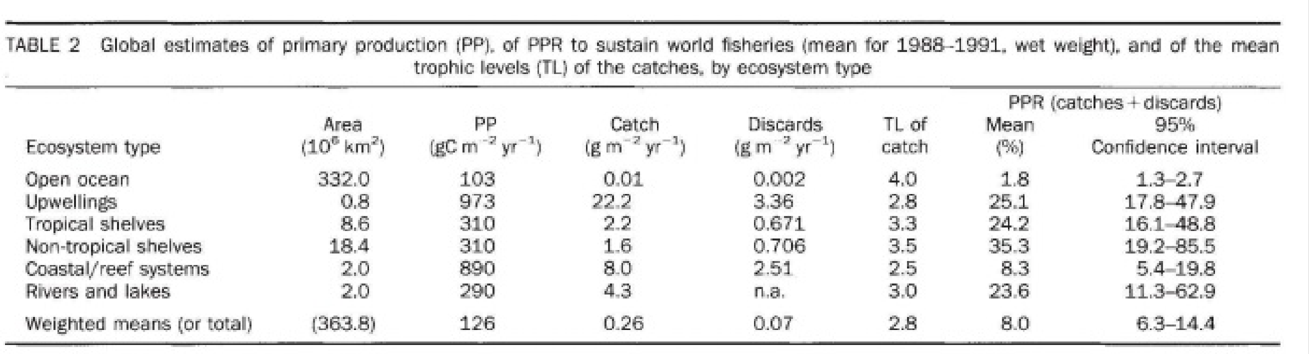
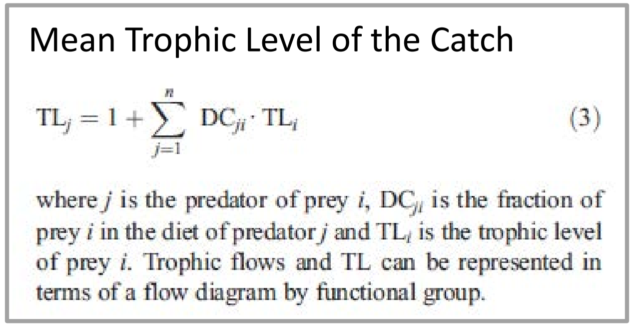


TABLE 2 Global estimates of primary production (PP), of PPR to sustain world fisheries (mean for 1988–1991, wet weight), and of the mean trophic levels (TL) of the catches, by ecosystem type

						PPR (catches + discards)	
Ecosystem type	Area (10^6 km^2)	PP (gC m^{-2} yr^{-1})	Catch (g m^{-2} yr^{-1})	Discards (g m^{-2} yr^{-1})	TL of catch	Mean (%)	95% Confidence interval
Open ocean	332.0	103	0.01	0.002	4.0	1.8	1.3–2.7
Upwellings	0.8	973	22.2	3.36	2.8	25.1	17.8–47.9
Tropical shelves	8.6	310	2.2	0.671	3.3	24.2	16.1–48.8
Non-tropical shelves	18.4	310	1.6	0.706	3.5	35.3	19.2–85.5
Coastal/reef systems	2.0	890	8.0	2.51	2.5	8.3	5.4–19.8
Rivers and lakes	2.0	290	4.3	n.a.	3.0	23.6	11.3–62.9
Weighted means (or total)	(363.8)	126	0.26	0.07	2.8	8.0	6.3–14.4



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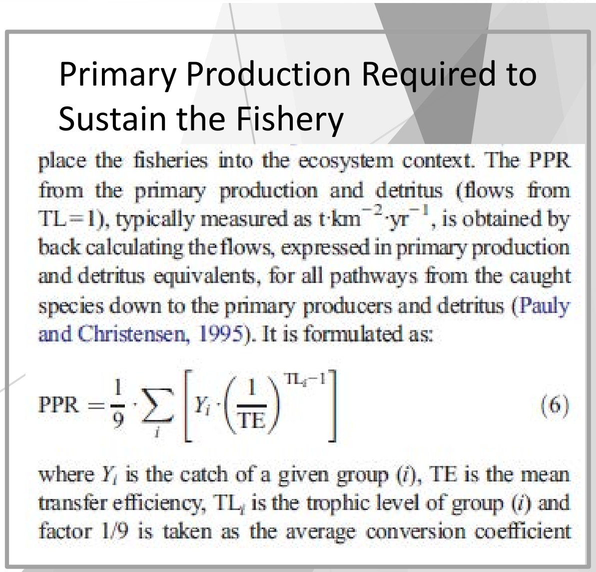

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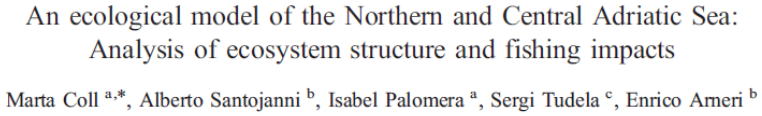

An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts

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FKNMS Structural Trends

Metric	1994	2000	2012
Total System Throughput (tn km/yr)	6802	6746	6764
Mean Trophic Level of the Catch	2.8	2.8	2.9
Primary Production Required to Sustain the Fishery (considering pp)	14%	17%	17%
Mean Transfer Efficiency	15%	15%	15%
Total Biomass (excluding detritus) t/km	365	359	360
Total Catch	5.23	5.5	6


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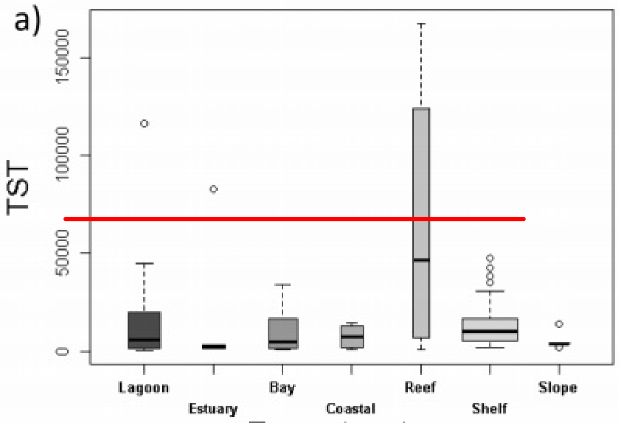
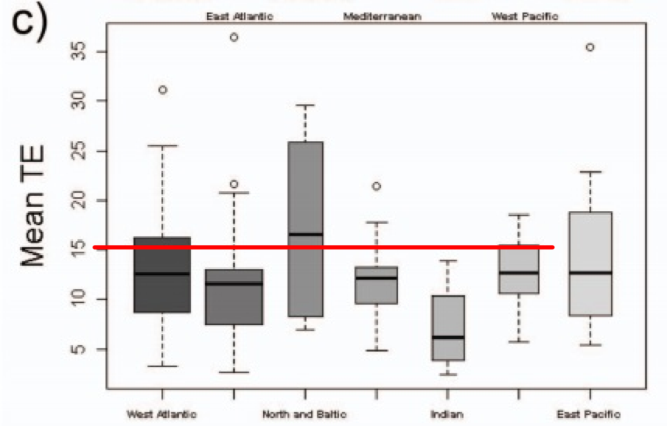
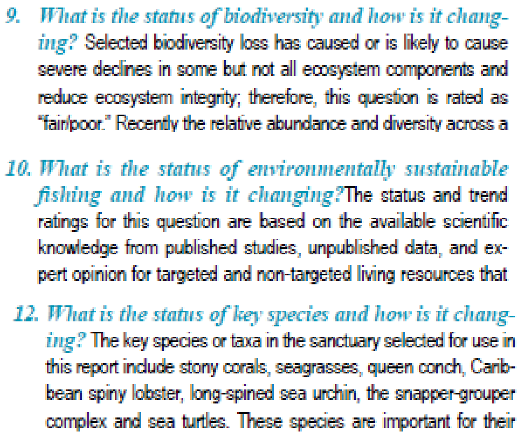




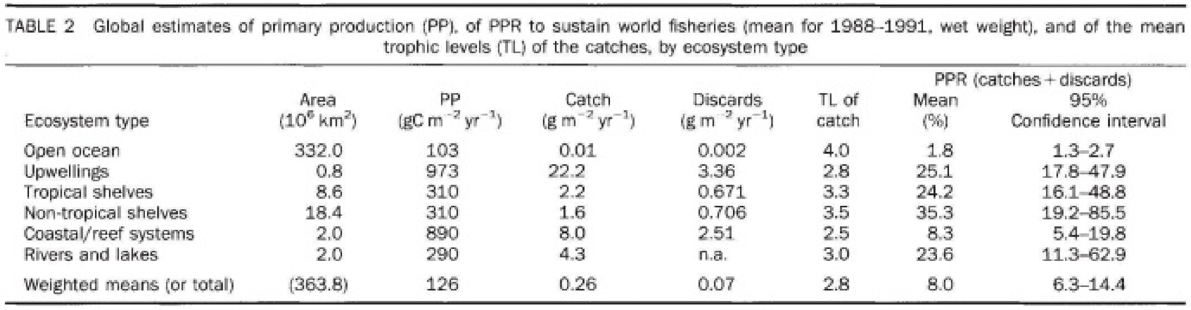

9. *What is the status of biodiversity and how is it changing?* Selected biodiversity loss has caused or is likely to cause severe declines in some but not all ecosystem components and reduce ecosystem integrity; therefore, this question is rated as "fair/poor." Recently the relative abundance and diversity across a

10. *What is the status of environmentally sustainable fishing and how is it changing?*The status and trend ratings for this question are based on the available scientific knowledge from published studies, unpublished data, and expert opinion for targeted and non-targeted living resources that

12. *What is the status of key species and how is it changing?* The key species or taxa in the sanctuary selected for use in this report include stony corals, seagrasses, queen conch, Caribbean spiny lobster, long-spined sea urchin, the snapper-grouper complex and sea turtles. These species are important for their


Primary production required to sustain global fisheries

D. Pauly* & V. Christensen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2.8 17%

Functional Metrics

- Mixed Trophic Impact (MTI)
  - Sensitivity analysis: How much does an increase in biomass affect all other groups?
  - Indirect and direct effects
  - Positive or negative values

- Relative Total Effect
  - The sum of all MTI values across all groups
  - High value = influential group

- Keystoneness
  - The total effect weighted by the contribution of biomass from the group

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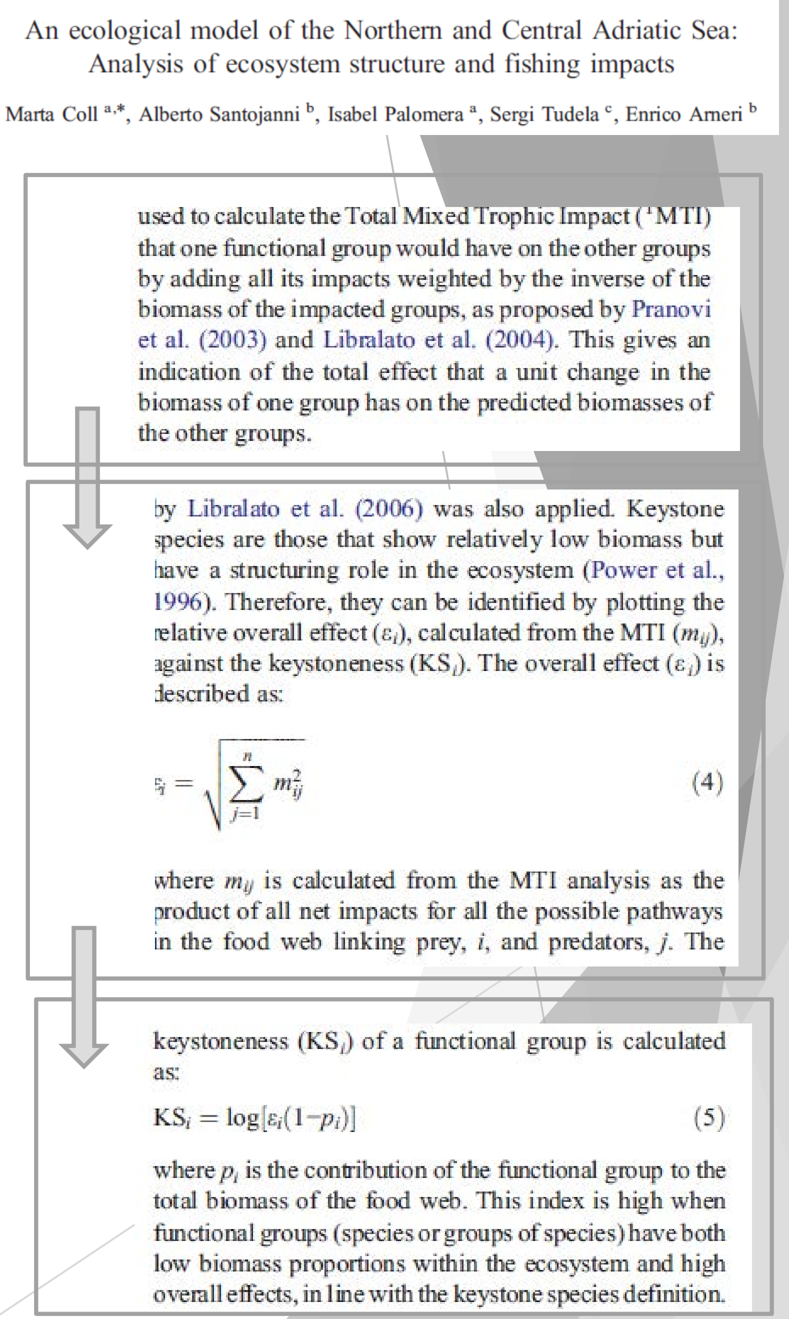

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used to calculate the Total Mixed Trophic Impact ($^{\mathrm{T}}$MTI) that one functional group would have on the other groups by adding all its impacts weighted by the inverse of the biomass of the impacted groups, as proposed by Pranovi et al. (2003) and Libralato et al. (2004). This gives an indication of the total effect that a unit change in the biomass of one group has on the predicted biomasses of the other groups.

by Libralato et al. (2006) was also applied. Keystone species are those that show relatively low biomass but have a structuring role in the ecosystem (Power et al., 1996). Therefore, they can be identified by plotting the relative overall effect (ε_i), calculated from the MTI (m_{ij}), against the keystoneness (KS_i). The overall effect (ε_i) is described as:

$$\varepsilon_i = \sqrt{\sum_{j=1}^{n} m_{ij}^2} \qquad (4)$$

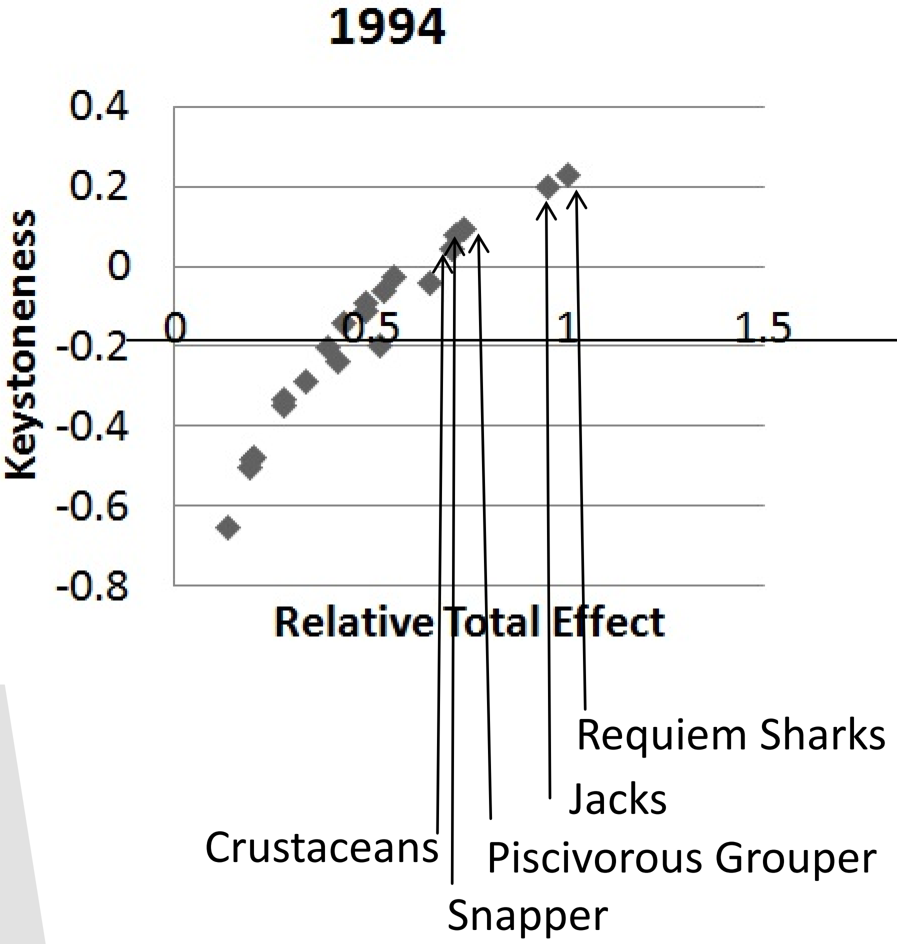
where m_{ij} is calculated from the MTI analysis as the product of all net impacts for all the possible pathways in the food web linking prey, i, and predators, j. The

keystoneness (KS_i) of a functional group is calculated as:

$$\mathrm{KS}_i = \log[\varepsilon_i(1-p_i)] \qquad (5)$$

where p_i is the contribution of the functional group to the total biomass of the food web. This index is high when functional groups (species or groups of species) have both low biomass proportions within the ecosystem and high overall effects, in line with the keystone species definition.

FKNMS Functional Trends



Requiem Sharks

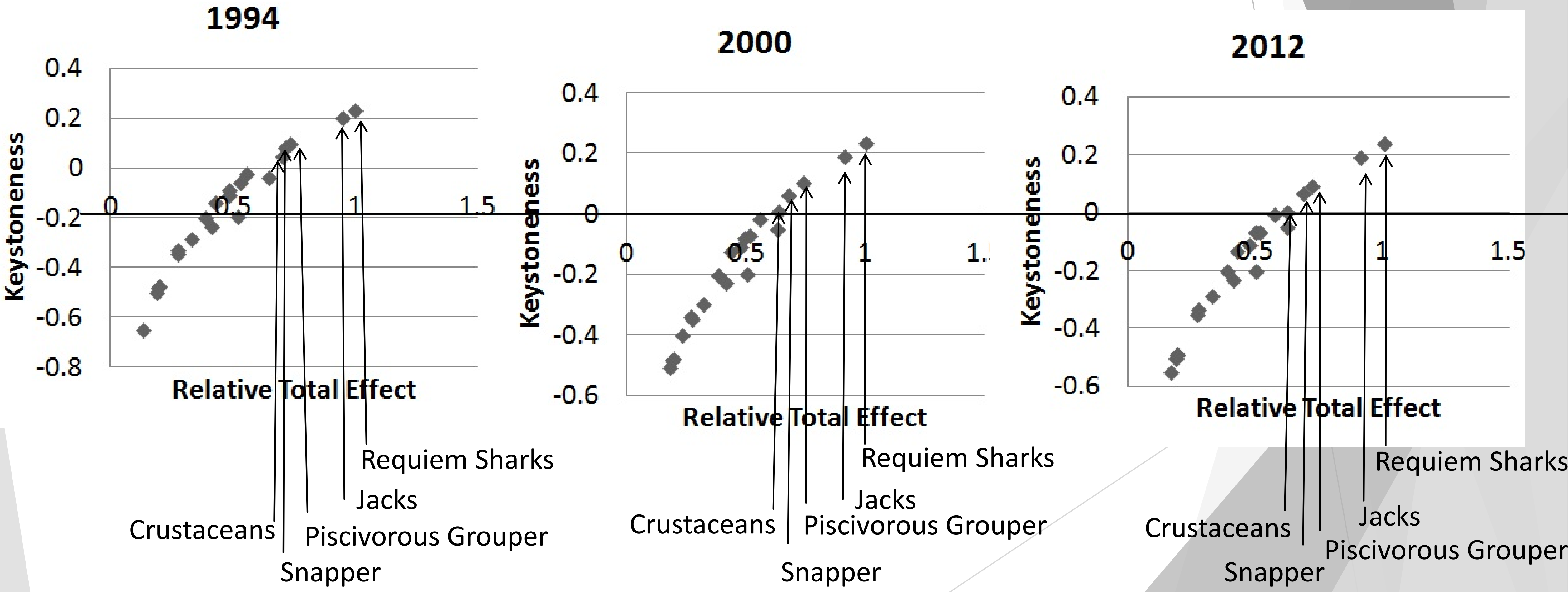
Jacks

Piscivorous Grouper

Crustaceans

Snapper

FKNMS Functional Trends



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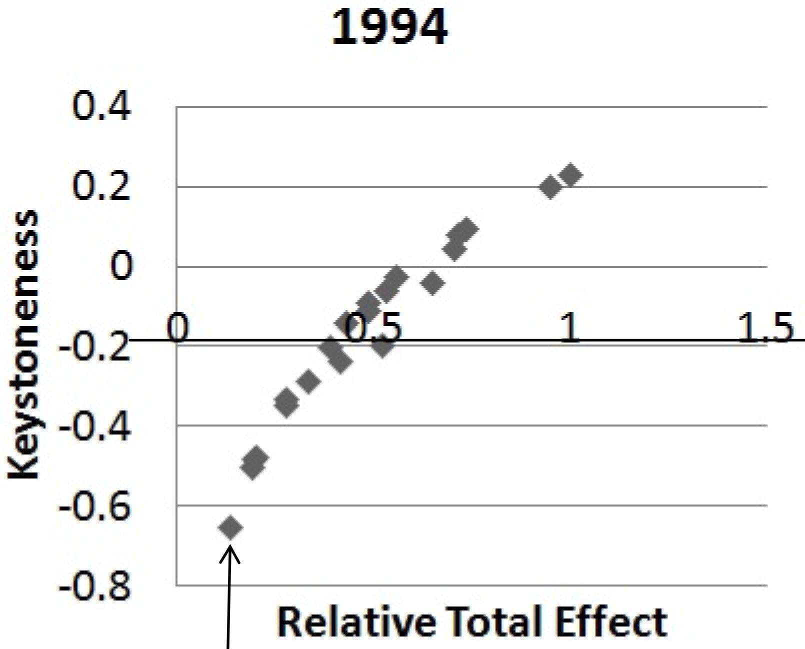
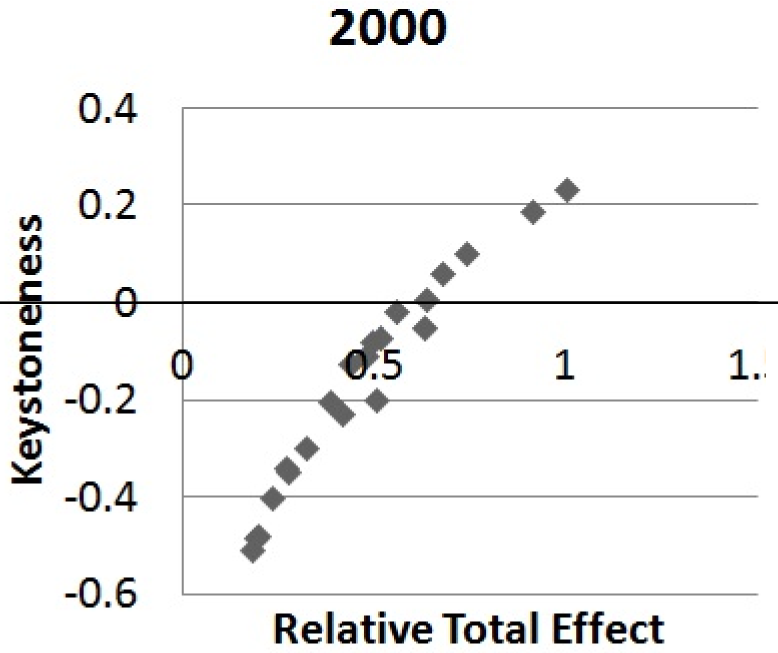
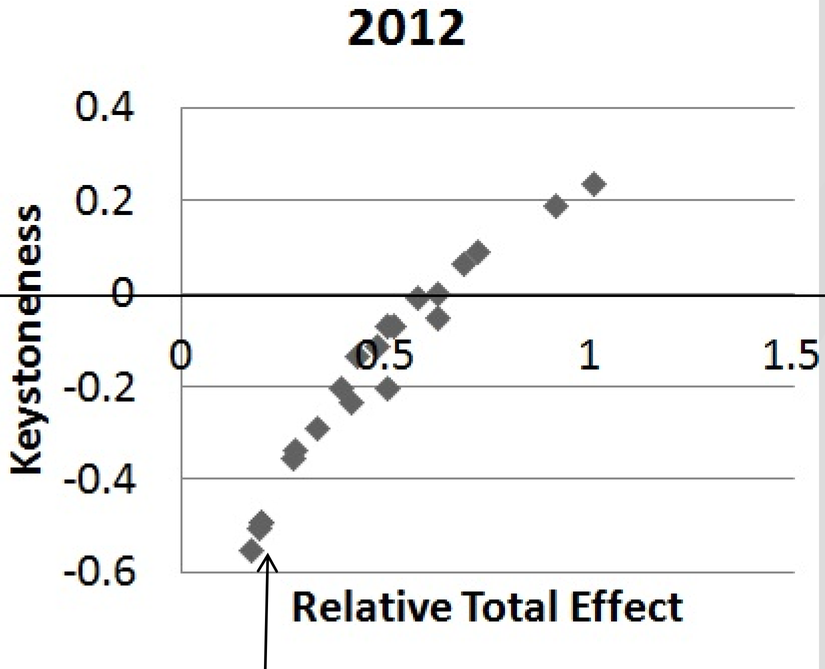






Herbivores

Lionfish

Other Applications

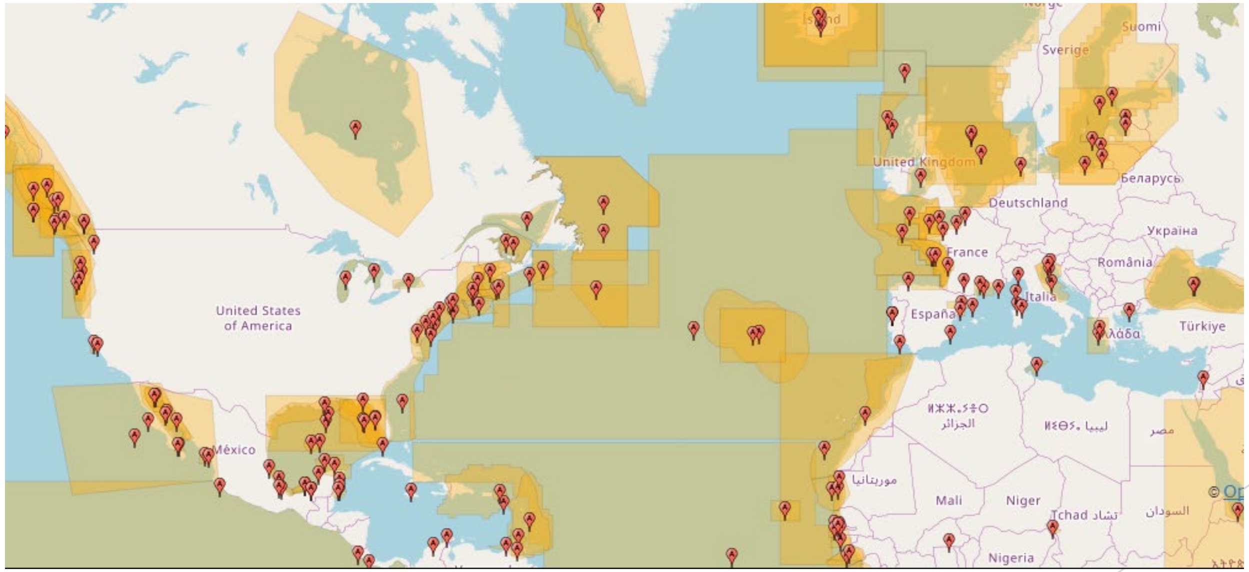
- What do we gain by accounting for biotic relationships in such an explicit way?
- We can examine the effect of alternative MPA scenarios while accounting for responses to environmental variation
- However, are species distribution predictions valid?
  - By Extension, MPA expectations

Ecopath → Ecosim → **Ecospace**

Base Trophic Relationships →
Change over Time →
Change over Space and Time

Moving Forward

- Use Species Distribution Models to refine Ecospace functional responses
- Consider different environmental covariates beyond SST, Depth, Chl-A, Distance
- Run varying MPA scenarios (No MPAs, Existing, Newly Proposed)
- Think about using these models in Ocean Observing Systems



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Bridging the gap between ecosystem modeling tools and geographic information systems: Driving a food web model with external spatial–temporal data

Jeroen Steenbeek[a,b,*], Marta Coll[b,c], Leigh Gurney[d], Frédéric Mélin[d], Nicolas Hoepffner[d], Joe Buszowski[a], Villy Christensen[a,b]

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[b] *Ecopath International Initiative Research Association, Barcelona, Spain*
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ABSTRACT

Research toward the impacts of climate change and human activities on marine ecosystems is challenged by the limitations of present-day ecosystem models to address the interrelated spatial dynamics between climate, ocean chemistry, marine food webs, and human systems. The work presented here, the spatial–temporal data framework, is part of a larger study, the NF-UBC Nereus Program, to develop a new approach to model interoperability for closing the gap between marine ecosystem modeling tools via geographic information systems (GIS) technology. The approach we present simplifies interdisciplinary model interoperability by separating technical and scientific challenges into a flexible and modular software approach. To illustrate capabilities of the new framework, we use a remote-sensing derived spatial and temporal time series to drive the primary production dynamics in an existing food web model of the North-Central Adriatic using the Ecospace module of the Ecopath with Ecosim approach. In general, the predictive capabilities of the food web model to hind-cast ecosystem dynamics are enhanced when applying the new framework by better reflecting observed species population trends and distributions. Results show that changes at the phytoplankton level due to changes in primary production are realistically reproduced and cascade up the pelagic food web. The dynamics of zooplankton and small and large pelagic fish are impacted. Highly exploited demersal species such as European hake do, however, not show clear signs of cascading. This may be due to the high fishing pressure on this species and the resulting strong historical decline in the area. In general, the development of the new framework offers ecosystem modelers with unprecedented capabilities to include spatial–temporal time series into food web analysis with a minimal set of required steps. It is a promising step toward integrating species distribution models and food web dynamics, and future implementations of interdisciplinary model interoperability.

1. Introduction

The effects of climate change and human interactions on global ecosystems are noticeable worldwide, yet the effects on communities and food webs are still poorly understood (Purves et al., 2013). Research to understand marine changes are challenged by the limitations of present-day ecosystem models to address the interrelated spatial dynamics between climate, ocean chemistry, marine food webs, and human systems due to the discrete sciences that these models are derived from. Since all environmental processes are interconnected, and since sustainable terrestrial ecosystems are linked with healthy, productive oceans, there is a real need to advance our understanding on these processes to prevent the environmental health from steadily declining (Butchart et al., 2010).

Marine ecosystem models (MEM) are mathematical tools that help analyze and forecast dynamics within marine ecosystems, and how these ecosystems respond to external stressors such as fishing and changes in environmental factors (Plagányi, 2007; Fulton, 2010; Christensen and Walters, 2011). MEM tools can inform policy makers and scientists about issues such as sustainable fishing,

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marine conservation, and long-term food security. However, the majority of present day MEM tools were originally built as expert tools by and for scientists to address questions of a specific scope, and have limited applicability. Based on largely proprietary data formats and coding platforms, existing MEM tools are often physically unfit to collaborate with other modeling approaches to address matters beyond the scientific discipline that models were written for (Steenbeek, 2012a,b).

To analyze changing climate conditions and the impact on marine communities and food webs, one requires analytical capabilities to address the interrelated dynamics between climate, ocean biochemistry, marine organisms and food webs, and socio-economic systems, crossing traditional scientific disciplines in the process and covering large geographical and temporal scales. For this, MEM tools need to be flexible enough to collaborate with other models in order to put their expert capabilities to use in a large, analytical context.

Coupling the science of discrete MEM tools requires significant interdisciplinary effort. This challenge is exacerbated by lack of communication protocols and common data standards between modeling approaches (Steenbeek, 2012a,b). Geographic Information Systems (GIS) offer essential data formats and operations that provide the foundation for implementing the link between models, while industry-standard software design practices offer the necessary structures to enable models to collaborate (Jolma et al., 2008).

Here, a flexible spatial–temporal framework for bridging the gap between MEM tools using GIS was developed (Steenbeek, 2012a,b). The aim of this framework was to improve the feasibility of MEM tools to interoperate via GIS data standards by (i) examination of marine ecosystem modeling needs, available models and tools, (ii) interoperability criteria, (iii) data standards used in the scientific community, and (iv) scientific issues that arise from current limited model interoperability.

This research was conducted as part of the Nippon Foundation – UBC “Nereus – Predicting the Future Ocean” program, aiming at furthering the development of coupled modeling approaches to assess the dynamics of ecosystems through an interdisciplinary approach. Especially, the concept of end-to-end (E2E) models is receiving significant scientific interest in peer-reviewed literature (e.g., Travers et al., 2007; Libralato and Solidoro, 2009; Rose et al., 2010; Steele and Ruzicka, 2011; Rose, 2012), but definitions of what end-to-end constitutes and how E2E models should be constructed greatly varies. Recent inventories (Plagányi, 2007; Travers et al., 2007; Fulton, 2010) describe the challenges that are faced by E2E models. For example, they need to: (i) include processes that are traditionally contained within discrete scientific disciplines, and implement bi-directional transfer of appropriate information between different sciences to reflect feedback effects between ecosystem components; (ii) join processes that typically operate on spatial and temporal scales that may differ by several orders of magnitude; (iii) consider a potentially open-ended number of species, chemicals, socio-economic aspects, each described in a proprietary manner using different and potentially incompatible units; (iv) assess the impacts and cascading effects of anthropogenic perturbations in every aspect of marine ecosystems; and (v) evaluate and communicate the impacts of uncertainty.

E2E models seek to address these challenges by integrating dedicated functionality of ever increasing scope within their proprietary frameworks and code environment. Such E2E models tend to become inflexible and complex, and they require extensive funding and expertise to parameterize, operate, and maintain. Embedded sub-models share temporal and spatial scales, risking representation of modeled entities at inappropriate resolutions (Fulton et al., 2009). Moreover, the fixed connections within the E2E imply fixed scientific pathways through the modeling complex, limiting the ability to test different hypotheses within the E2E.

More modular modeling frameworks, such as the Multiscale Integrated Model of Ecosystem Services (MIMES), offer an extensible set of modules that collaborate on a common set of data definitions and conventions focused on ecosystem value (Boumans and Costanza, 2007; Nelson and Daily, 2010). Although providing a wide range of advanced capabilities to represent the socio-economic aspects of E2E models, the value-focused view of this model offers limited consideration of marine ecosystems beyond exploited marine species, and is in particular unsuitable to represent ecology and the effects of climate change (Waage et al., 2008; Nelson and Daily, 2010). Therefore, an intermediate modular approach to model integration is required, where individual models inter-communicate without compromise in functionality or scale; where models can be replaced to test different hypothesis, and which can alter its scope to address different aspects of reality (Steenbeek, 2012a,b).

Here we present the spatial–temporal data exchange module of such a model interoperability framework, which we test using a remote-sensing derived time series of spatial and temporal data to drive the primary production of an available food web model. The food web model used for the test was previously developed with the spatial explicit model Ecospace of the Ecopath with Ecosim v6 (EwE6) modeling approach (Christensen and Walters, 2004) and represents the North-Central (NC) Adriatic Sea in the Mediterranean basin (Coll et al., 2007, 2009; Fouzai et al., 2012).

We apply the new spatial–temporal framework at a regional scale, and results (both considering data in monthly time steps and annual time steps) are compared with the original model to evaluate if the results differ, and if so, if the new framework improves the model’s capability to hind-cast past ecosystem dynamics.

2. Methodology

2.1. Ecological model

We use the ecological modeling approach Ecopath with Ecosim version 6 (EwE6) as a test case for spatial–temporal model interoperability (Steenbeek, 2012a,b). EwE is the most widely used modeling approach for assessing aquatic food web dynamics and analyzing the impact of fishing, with more than 6000 users in over 150 countries, and with more than 600 academic publications to date based on the approach (ProQuest, 2012). Despite its perceived simplicity (Plagányi, 2007), EwE is increasingly used in ecosystem-based management assessments (e.g., Christensen and Walters, 2005, 2011; Cisneros-Montemayor et al., 2012).

The EwE software is developed using the Microsoft .NET platform (Christensen and Lai, 2007), which offers a range of technical benefits such as compatibility with a suite of programming languages and the theoretical ability to run on any operation system (ECMA International, 2012). The core model of the EwE approach is the Ecopath model (Christensen and Pauly, 1992), a static model of marine ecosystems, the time-dynamic model Ecosim (Walters et al., 1997, 2000), and the time–space dynamic model Ecospace (Walters et al., 1999, 2010). Annex A provides an overview of EwE.

The spatial and temporal module of EwE, Ecospace, has been widely applied to quantify the spatial impacts of fishing on marine species, and to analyze the outcomes of management options such as the establishment of marine protected areas and its impact in terms of spatial distribution of marine species and fishing effort (e.g., Walters et al., 2000, 2008, 2010). It can also be used for spatial optimization (Christensen et al., 2009) and to assess the impact of climate change by linking the Ecospace model with lower trophic level models (Fulton, 2011).

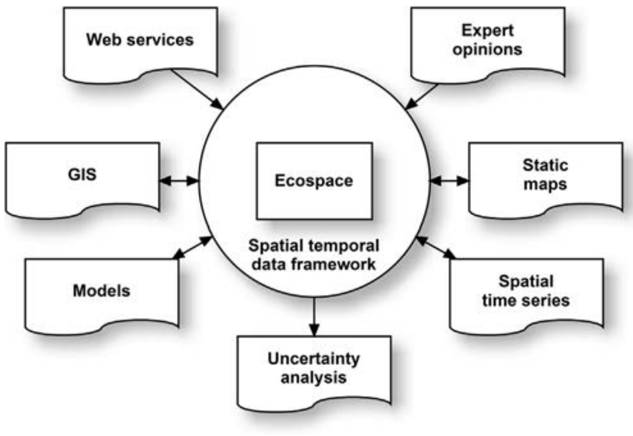

Fig. 1. A spatial–temporal data framework that encapsulated the Ecospace model, and provides access to a wide range of spatially enabled data sources.

Ecospace was built to model biomass interactions within an ecosystem across a two-dimensional grid over time in typically monthly time steps. It distributes biomass values of functional groups across a grid of equally sized cells, and uses the temporal equations to model how biomasses vary within each cell in the grid over time by considering trophic interactions, fishing and species movement (Walters et al., 1999, 2010). Beside a mass-balanced Ecopath model and an Ecosim configuration, the Ecospace model requires a nominal set of input, including a basemap, which identifies the spatial bounds and grid dimensions (Walters et al., 1999) (Annex A).

Spatial variations in driver variables such as the primary productivity map have significant impacts on the Ecospace dynamics (Martell et al., 2002). However, up to the present study, a continued and major shortcoming of the Ecospace routines was its lack of facilities to read and produce true geo-spatial data into driver layers. Migration to the .NET environment facilitated the additions of a plug-in system in EwE to complement the approach with new functionality without changes to the underlying EwE source code (Christensen and Lai, 2007). Through this study, the EwE software was extended via plug-ins to interoperate with external spatial–temporal data and models (Fig. 1). This functionality allows the Ecospace model to interact with a wide range of spatial data sources, handle GIS data, and interact with other spatial ecosystem models.

2.2. Spatial–temporal data framework

There is an increasing demand to use the Ecospace model in conjunction with spatial analytical tools, species distribution models, and planning tools such as Marxan (e.g., Loos, 2011). The .NET-based plug-in system in EwE opens for development of a flexible spatial–temporal data exchange and model interoperability framework (Fig. 1), which solves key connectivity shortcomings of Ecospace whilst advancing end-to-end modeling (Steenbeek, 2012a,b). Here, we present aspects of this spatial–temporal data framework to facilitate the exchange of geospatial and temporal data with the Ecospace model (Walters et al., 1999, 2010).

2.2.1. Design of the framework

From an operational perspective, the framework needs to: (i) provide access to static spatial files of relevant data to generate a basemap; (ii) deliver spatial time series of relevant data during execution to drive the model; (iii) enable delivery of results as spatial time series for consumption by tools and models in the framework; (iv) allow read and write access to geospatial data formats and data delivery media common to the environmental sciences; (v) permit data interoperability for any spatial extent and raster cell size; and (vi) enable seamless extensions to include new data formats and geospatial operations to accommodate future, unforeseen needs.

To serve in an end-to-end model interoperability environment, the framework needs to: (i) support bi-directional exchange of spatial–temporal data with an open-ended range of collaborating models in an end-to-end approach; (ii) sustain scientifically sound translation of data between models; (iii) allow flexible access to sub-models to test different hypotheses; (iv) permit the use and exchange of ecological metadata; (v) store intermediate results to allow assessments of error; and (vi) enable outside control during execution of time steps.

To serve in a GIS interoperability environment the framework needs to: (i) support the use and exchange of spatial metadata; (ii) allow a suite of geospatial operations needed to interpolate geospatial data; (iii) enable a detailed overview of performed data conversions; and (iv) provide access to all intermediate data produced to facilitate uncertainty analysis.

The framework may be operated by ecosystem modelers that have limited GIS experience. Therefore, we must (i) reduce the need for users to interact with the framework, yet not limit framework capabilities, functionality, and data content; (ii) minimize complexity in user interfaces so that modelers can work with GIS data as an extension of more familiar ecological model data, without requiring in-depth knowledge of GIS data formats and transformations; and (iii) support post-run validation of the data transformations performed by the framework to allow in-depth assessments of the geospatial functionality.

The range of requirements and extensibility calls for a modular design of the framework (Fig. 2). Modularity in software technology is a technique that breaks down program functionality in separate, interchangeable components or modules (Baldwin and Clark, 2000) that work together to implement the purpose of a program. Modules can be grouped in similar functionality, where each module of the same type implements similar functionality in a unique manner and can be exchanged to switch functionality without disrupting the flow of a program (e.g., Cook, 1991; Gamma et al., 1994).

The principle of modularity, even though a common software design principle since the introduction of object oriented programming in the early 1970s (Cook, 1991; Gamma et al., 1994) and widely used in GIS systems, is not widely applied in the field of model interoperability (Steenbeek, 2012a,b). The framework developed here is, however, designed so that the complex task of model interoperability becomes feasible if the tasks are logically separated and grouped by functionality, and are then executed via chains of relatively small, configurable, and conceptually comprehensible modules.

The functional design of the framework depicts the pathways for how external data are integrated (Fig. 3). Data integration functionality is divided into the layers ‘data access’, ‘data conversion’, and ‘data integration’. Independent post-run analysis is facilitated by the storage of intermediate results produced by the data access, data conversion, and data integration components of the framework.

The pathway of how incoming data are processed through the framework is as follows (Fig. 3):

1. External spatial temporal data are located and loaded into the framework for a particular time step or at model initialization. Interchangeable datasets provide read and write access to specific spatial data storage format, such as files, geo-databases, web services, external models, or other sources of GIS data. To facilitate post-run analysis, datasets enter performed activity and decisions in the spatial operations log.

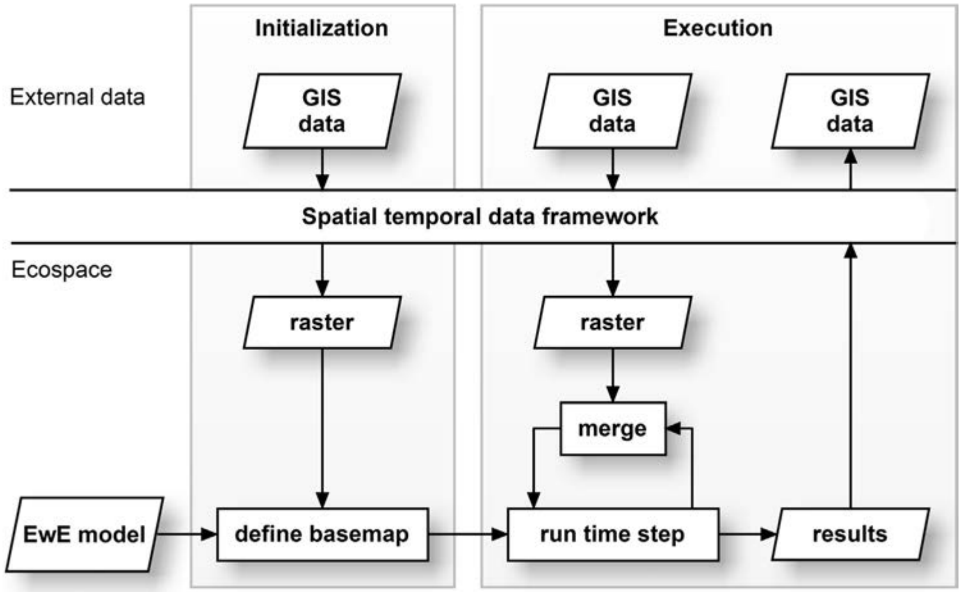

Fig. 2. Conceptual overview of the spatial–temporal data framework, which provides external GIS data to Ecospace model initialization and at runtime, and provides Ecospace results in spatial data formats when the model executes.

2. Spatial data, loaded from a data set, are passed on to the data conversion layer. Converters perform all GIS operations required to transform incoming spatial data into a raster compatible with a particular map layer in the Ecospace model. Converters are interchangeable modules capable of one type of conversion each, such as different types of raster conversions and vector to raster conversions. Additionally, raster data that are produced by converters are stored in a local file cache that serves to:
   a. preserve the outcome of conversion steps for post-run statistical analysis, and
   b. facilitate the reuse of data conversion results for next model runs which may greatly enhance the performance of the framework;

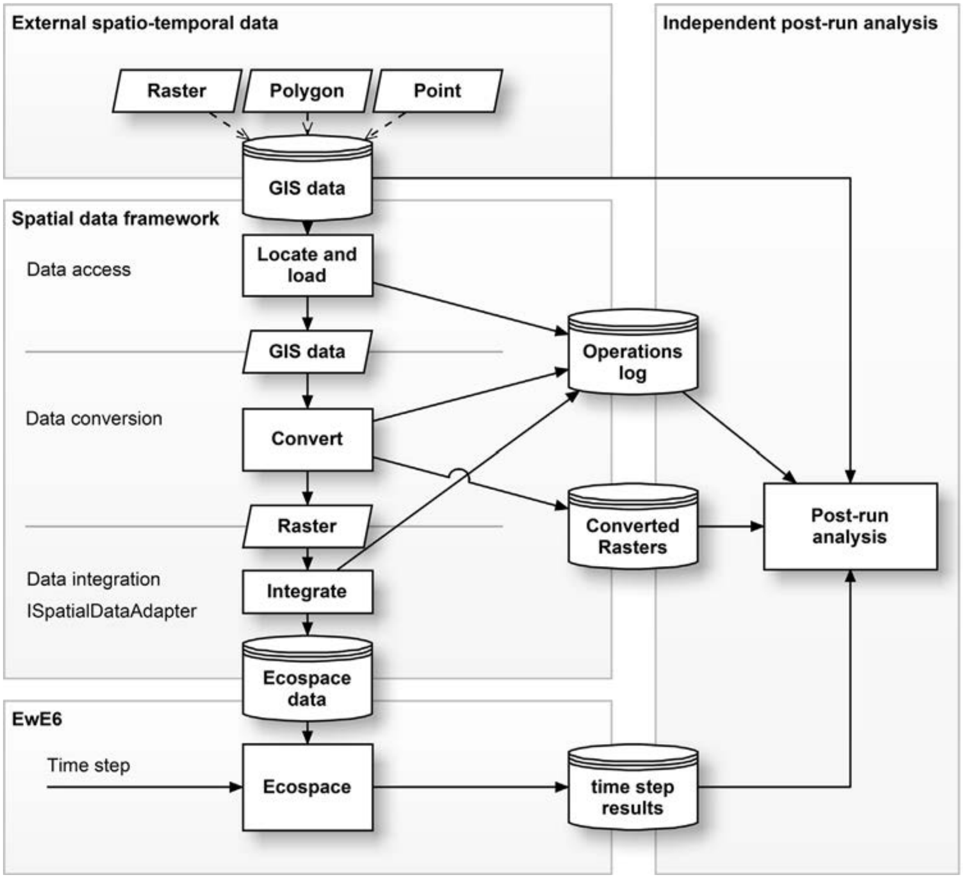

Fig. 3. A schematic functional design of the spatial–temporal data framework, displaying how external data is brought into the Ecospace model.

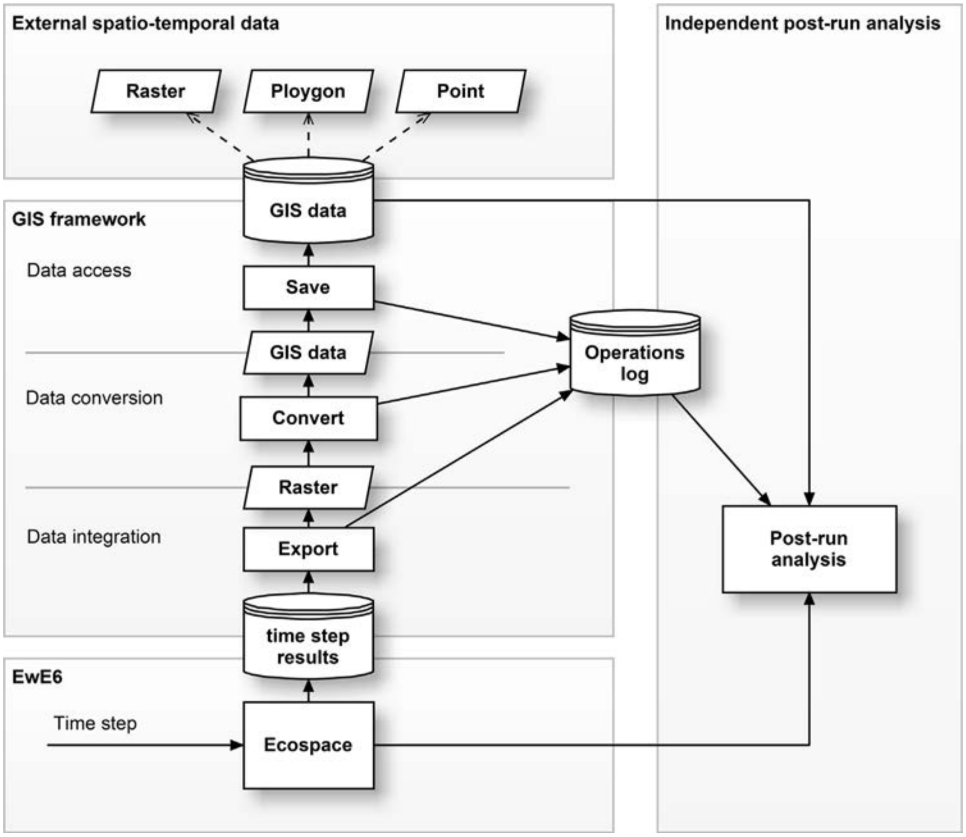

Fig. 4. A schematic functional design of the framework, displaying how external data is brought out of the Ecospace model.

3. Raster data, delivered by the converters and stored in the cache, are transferred to the data integration layer. Here, adapters place the raster data in the correct maps, and may trigger tasks to ensure that integrated data are correctly included. There is an adapter for every type of map layer that can be driven by external data. During execution, results can be exported as maps, while resulting spatial datasets can be included in any desired post-run statistical analysis.

The reverse pathway, when results are passed through the framework for delivery as GIS data, is similar (Fig. 4). Result maps are passed to an adapter for the type of result data grid for processing by the framework. The result grid is received by a converter. Any conversion that needs to be performed, such as raster-to-vector conversions, is handled here. The converted data are passed to a dataset, which then makes the data available for external use by for instance saving the data to a file, to a geodatabase, or any other destination provided by the dataset (Fig. 4).

2.2.2. Implementation and example sequence diagram

To satisfy the requirement of modular extensibility, all framework components that may require future extensions are implemented as plug-ins points (Annex A), which give the framework flexibility to incorporate new functionality modules without affecting the EwE6 source code (Fig. 5). This design provides flexibility to develop access to new data formats, media, models, using any GIS functionality, in separate plug-in modules.

2.2.3. GIS toolkit

To implement the framework, candidate GIS toolkits for collaborating with EwE were reviewed and a GIS programming toolkit was selected based on the following requirements: (i) support a range of GIS raster and vector data formats, and data connectivity methods common to the environmental sciences, (ii) provide a library of basic spatial operations for vector and raster data manipulation, (iii) permit free distribution with the open-source EwE6 software, (iv) be compatible with the Microsoft .NET environment, (v) allow open-source development to facilitate addition of new functionality at any moment, and (vi) support by an active development team and user base.

We reviewed candidate GIS programming toolkits, and found the DotSpatial toolkit (http://dotspatial.codeplex.com/) most suitable for implementing the framework. For the complete list of selection criteria and evaluated toolkits we refer to Steenbeek (Steenbeek, 2012a,b) and to Annex B.

The main purpose of this contribution is to demonstrate the feasibility of extending the Ecospace model with a framework of modular components that simplify GIS spatial–temporal data connectivity. The framework integrates with the EwE6 user interface (Annex C). Access to a wide range of GIS raster data formats was included in the framework via the DotSpatial toolkit, which provided the connectivity needed for constructing and using datasets. A suite of GIS raster operations, native to the DotSpatial toolkit, was encapsulated in the framework to convert incoming raster data to a grid compatible with an Ecospace scenario (Fig. 3).

2.3. Case study

2.3.1. Study area

The framework presented in section 2.2 was applied with external GIS data to drive the primary productivity in a food web model of the North-Central (NC) Adriatic Sea (Fig. 6), a semi-enclosed basin in the northernmost part of the central Mediterranean. The area is mostly characterized by muddy and sandy bottoms (Pinardi et al., 2006), and primary production varies from a productive shallow northern basin to an oligotrophic deeper central basin (Zavatarelli

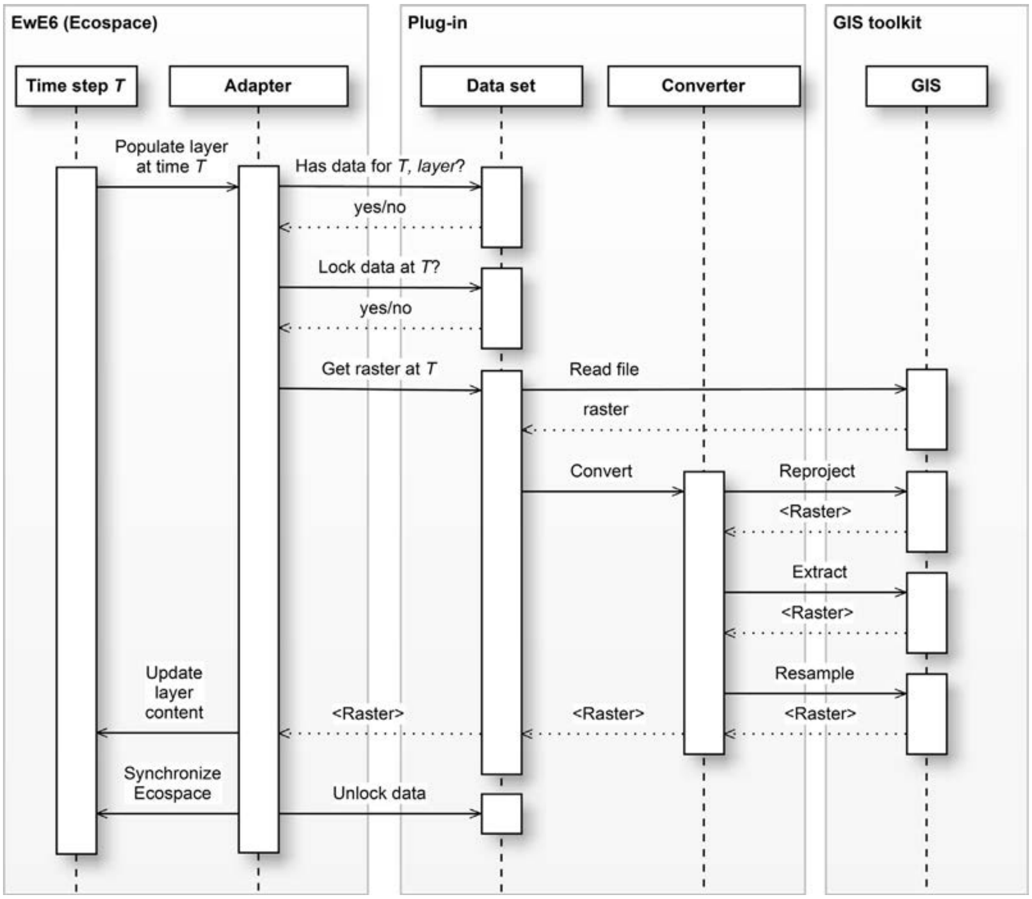

Fig. 5. Interaction diagram, showing how Ecospace, an adapter, a dataset, a converter and a GIS toolkit communicate to perform the core framework task to read external data.

et al., 2000). The production is influenced by river discharge, particularly the Po River in the northern basin (Pinardi et al., 2006).

As one of the most productive areas of the Mediterranean Sea, it is also one of the major fishing grounds in southern Europe, with a dramatic expansion of marine capture fisheries since the early 1970s (Coll et al., 2010; Fortibuoni et al., 2010; Lotze et al., 2011). This expansion has been followed by fluctuations in annual landings and a general decline of marine resources. Since the late 1980s, marine capture has progressively declined, especially for pelagic organisms such as European anchovy *Engraulis encrasicolus* and European sardine *Sardina pilchardus* stocks (Azzali et al., 2002; Santojanni et al., 2003, 2006). Several bottom-dwelling (demersal) stocks such as European hake *Merluccius merluccius* were highly exploited or overexploited already in the 1980s (Jukić-Peladić et al., 2001; Vrgoč et al., 2004), and predators have declined with time (Coll et al., 2009; Fortibuoni et al., 2010; Lotze et al., 2011).

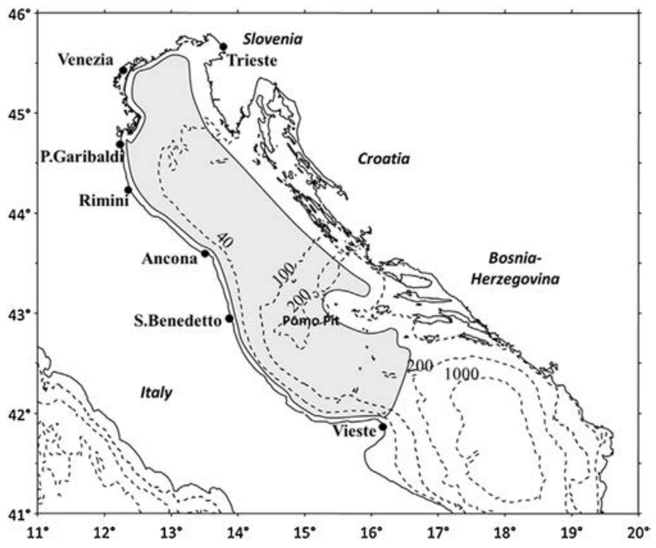

Fig. 6. The Northern-Central (NC) Adriatic Sea study area. The light-gray area represents the spatial coverage of the ecological model available.

2.3.2. *The food web model of the NC Adriatic Sea*

We use a published food web model of the NC Adriatic Sea (Coll et al., 2007). The model includes a total area of 55,500 km^2, with an average depth of 75 m, and maximum depths of 273 m (Fig. 6). The area includes Italian territorial waters and the international waters from the 12 miles off the coast of Italy to 12 miles from Croatia and Slovenia. The model describes the 1990s and includes 40 functional groups (defined as single species, trophically similar species, or just a specific life stage of an individual species), including the main trophic components of the ecosystem, from primary producers to top predators, and natural detritus and discards from fishing activities. The most common fishing activities included were bottom and beam trawls (here called bottom trawling), mid-water trawls, purse seines, and tuna fishing fleets.

The original 1990s model was fitted to historical data from 1975 to 2002 (Coll et al., 2009, 2010), and a spatial model was developed (Fouzai et al., 2012) using Ecospace to evaluate fishing management options to recover exploited marine resources.

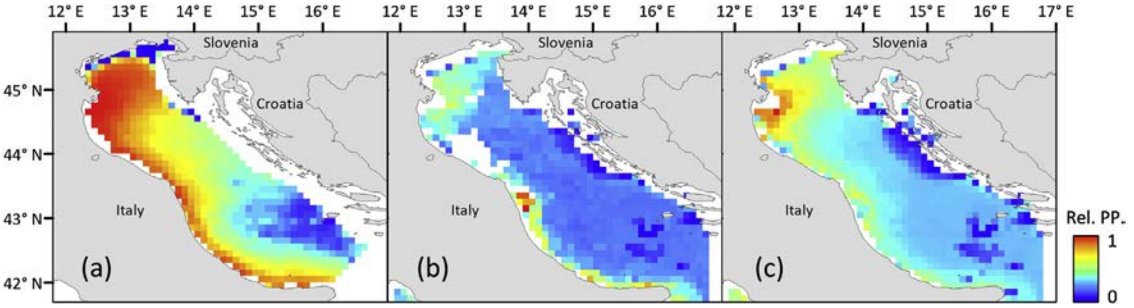

Fig. 7. (a) Original relative primary production map in the Ecospace model (Fouzai et al., 2012), and PP data distributions delivered by the framework, prior to integration in Ecospace, for (b) December 2007, and (c) annual average for 2007.

2.3.3. External primary production data

A global, monthly spatial–temporal time series of primary production data, derived from the SeaWiFS sensor with a spatial resolution of 1/12th-degree and a monthly resolution from October 1997 to December 2007 was provided by the Joint Research Centre of the European Commission (JRC) in Ispra, Italy (JRC, 2012). For each monthly global map, the data were expressed in gC/m^2/day and stored in NetCDF format after log-transformation (JRC, 2012).

The primary production calculation (Mélin and Hoepffner, 2010) is based on a depth-resolved and wavelength-resolved model following the original description of Platt and Sathyendranath (1988) and implemented at global scale by Longhurst et al. (1995). At any given location and time, the model takes into account the total irradiance available for photosynthesis between 400 and 750 nm, the phytoplankton biomass indexed by the concentration of chlorophyll-a obtained by remote sensing, as well as the physiological capacity of phytoplankton organisms to perform photosynthesis. The spatial and temporal changes in phytoplankton metabolism and its vertical distribution are considered in the model through the partition of the global ocean into biomes and provinces within each of which parameters related to photosynthesis and depth profile of chlorophyll are assigned based on field observations. In validation exercises (comparison with field measurements of primary production), the model compared favorably with respect to other models (e.g., Friedrichs et al., 2009; Saba et al., 2010, 2011). It is however acknowledged that the satellite product might be locally affected by significant uncertainties, particularly in coastal waters. In the present case study (see Section 3.1), only the spatial and temporal relative variations of the satellite primary production have an impact on the model simulations (see Section 3.1).

2.4. Zero-impact hypothesis

To ascertain that the framework was capable of correctly incorporating external data, a zero-impact analysis was developed under the following hypothesis: the original food web model should yield identical results to a food web model that is run against an external version of the PP map originally embedded in the model.

To test this hypothesis, the PP map from the NC Adriatic Sea modeling application of Fouzai et al. (2012) was exported to an ESRI-compatible ASCII raster for the model area (Fig. 7a). An external data connection to this raster file was created which was temporally aligned to the model start date. The Ecopath-to-Ecospace scaling factor for this file was calculated (Annex C), and the external data connection was linked to the Ecospace PP map layer.

This temporal, spatial and logical alignment provides the configuration needed to validate the zero-impact hypothesis.

2.5. Spatial food web scenarios

The NC Adriatic Ecospace food web model with the standard fitting to time series data and driven by fisheries data (Coll et al., 2009; Fouzai et al., 2012) was run under three scenarios: (i) without any forced primary productivity (PP) data, (ii) driven by external monthly temporal and spatial PP time series ranging from January 1998 to December 2007 (Fig. 8), and (iii) driven by external, annually averaged, temporal and spatial PP data ranging from January 1998 to December 2007 (examples of the dataset are provided in Fig. 7b and c; the time series is presented in Fig. 8).

The scenarios were run from 1975 to 2007 with monthly time steps using the Ecospace module of the EwE software. Available external data (from 1998 to 2007) were loaded and converted by the spatial–temporal data framework to the resolution and spatial extent of the Ecospace scenario, scaled to the Ecopath base value, and subsequently integrated in the Ecospace primary productivity map layer, only enhancing or lowering cell values for which external values were present. Following this data exchange Ecospace calculations resumed, applying food web dynamics and phytoplankton production to vary the biomass of phytoplankton.

After running the scenarios, results were analyzed by examining historical temporal and spatial dynamics of phytoplankton and other compartments of the food web (Fig. 9). For this, we focused on functional groups with direct or indirect relationships with phytoplankton (Coll et al., 2007, 2009): (1) phytoplankton, which serves as the nutritional basis for the food web and is directly driven by PP dynamics; (2) zooplankton, which solely consumes phytoplankton; (3) Sardine (*S. pilchardus*), with a diet that consists mostly of zooplankton, supplemented with phytoplankton; (4) anchovy (*E. encrasicolus*), with a diet that consists entirely of zooplankton; (5)

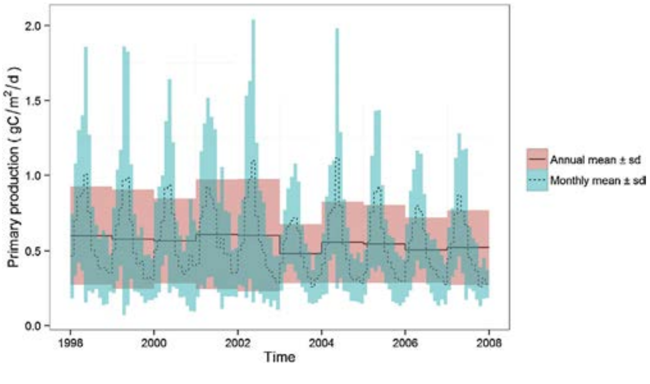

Fig. 8. Spatial mean ± standard deviation of primary productivity for the North-Central Adriatic of the monthly and annual datasets, as delivered by the spatial temporal data framework, prior to integration into Ecospace.

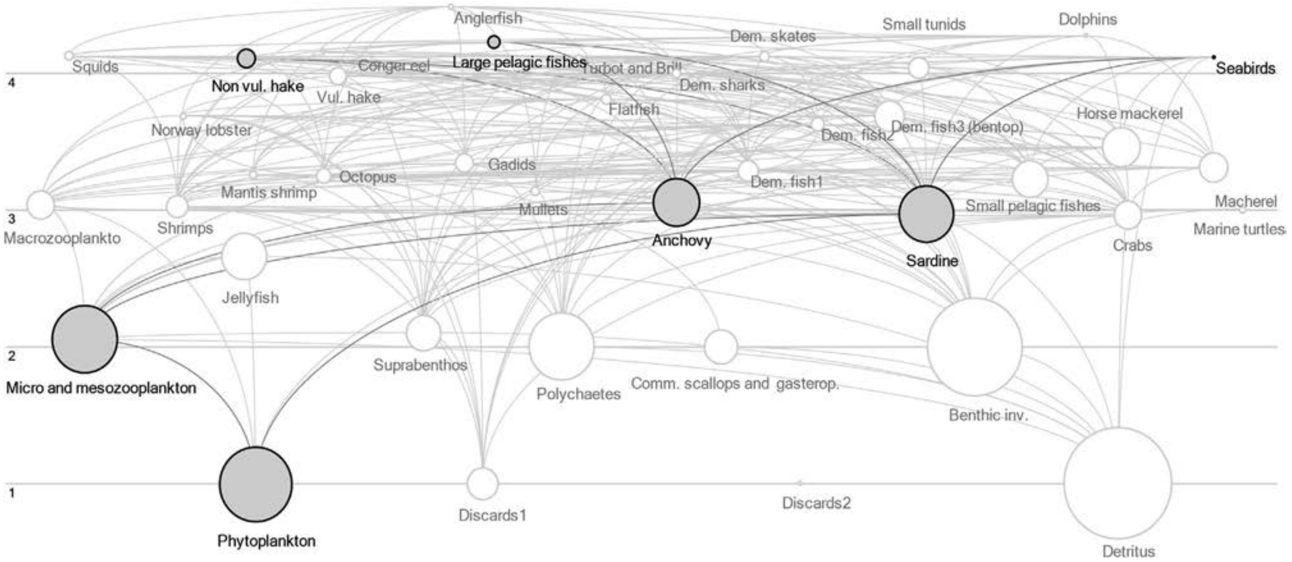

Fig. 9. Food web model of the North and Central Adriatic model, based on Coll et al. (2007, 2009). This figure highlights the groups that were used to analyze the impact of the new spatial–temporal data framework (in gray, with black outline).

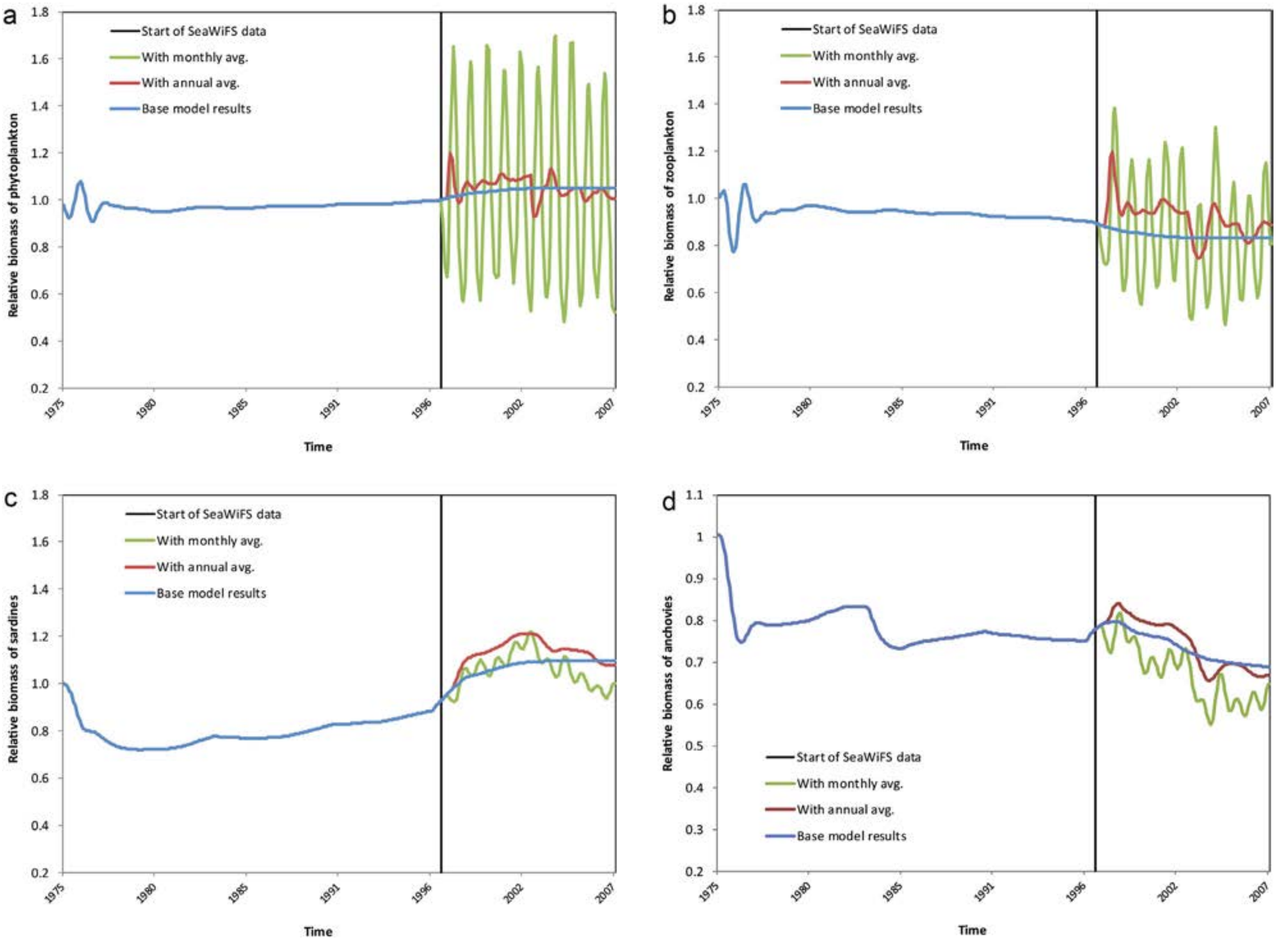

Fig. 10. (a) Predicted biomass relative (final/initial value) of phytoplankton for each of the scenario runs, and Ecospace relative dynamics of (b) zooplankton, (c) sardine and (d) anchovy biomasses, relative to the start value, for the three scenarios analyzed. The start of SeaWIFS data being read by the modeling framework is indicated by a black vertical line. (For interpretation of the references to color in the text, the reader is referred to the web version of the article.)

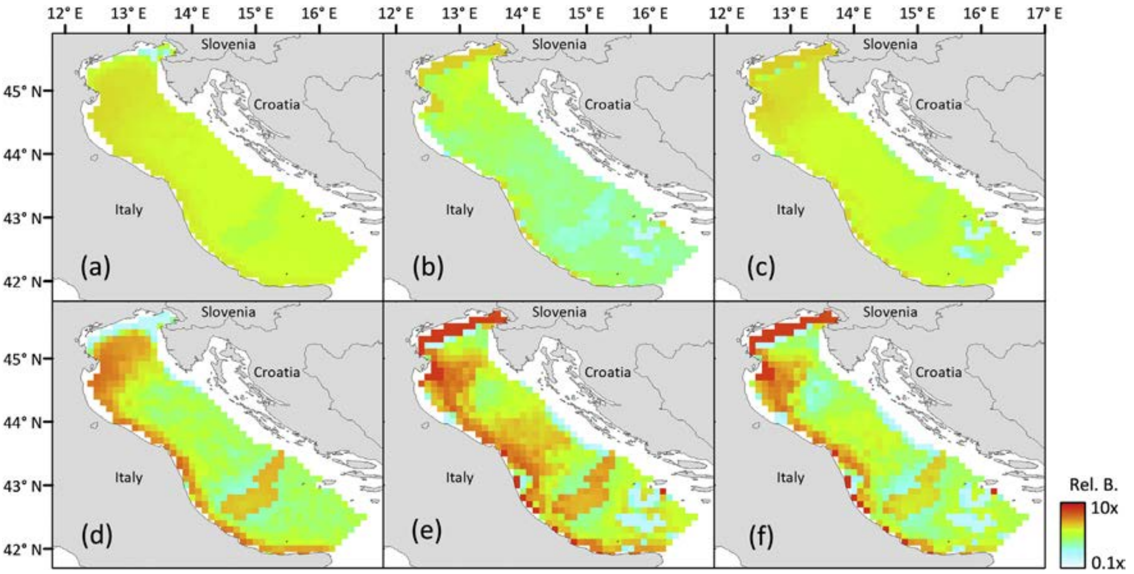

Fig. 11. Distribution of relative biomass of phytoplankton (a–c) and zooplankton (d–f) for the last year of the simulation, 2007. Results are related with the model (a and d) without external PP data, (b and e) with monthly PP data, and (c and f) with annual PP data.

seabirds, that consume mostly sardine, and some anchovy; (6) large pelagic fish (*Thunnus thynnus* and *Xiphias gladius*), with a diet that consists largely of anchovy; and (7) adult hake (*M. merluccius*), with a diet that consists of anchovy and sardine, and other demersal organisms (Fig. 9). Anchovies, sardines, large pelagic fish and adult hake are highly exploited commercial species and have been subjected to large fishing pressure from historic times (Coll et al., 2009; Lotze et al., 2011).

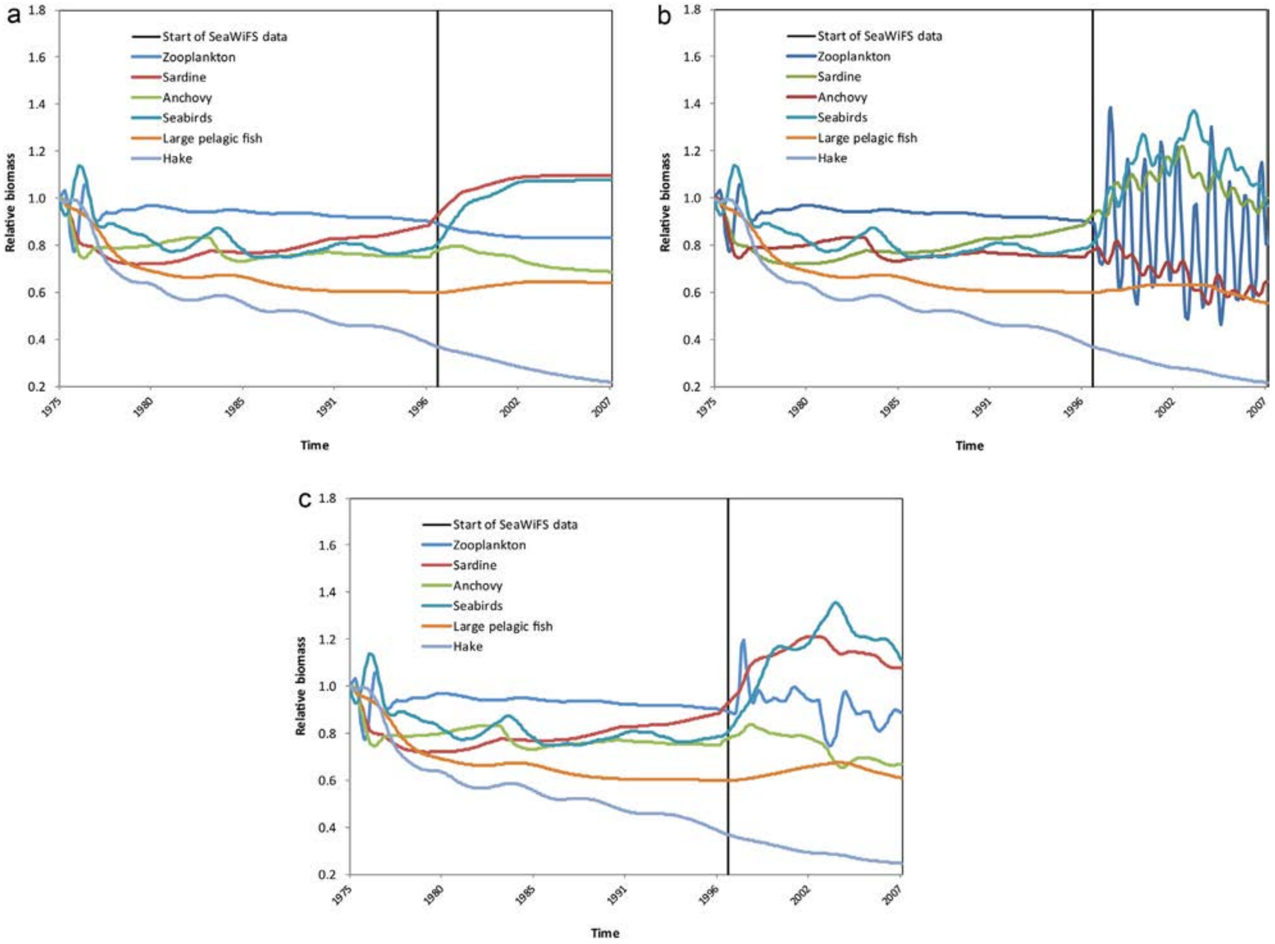

Fig. 12. Relative biomass in the NC Adriatic, as computed by Ecospace, when (a) the spatial–temporal simulation was executed without any external primary production data, (b) when forced with monthly JRC primary production data from 1997 to 2007, and (c) when forced with annual JRC primary production data from 1997 to 2007.

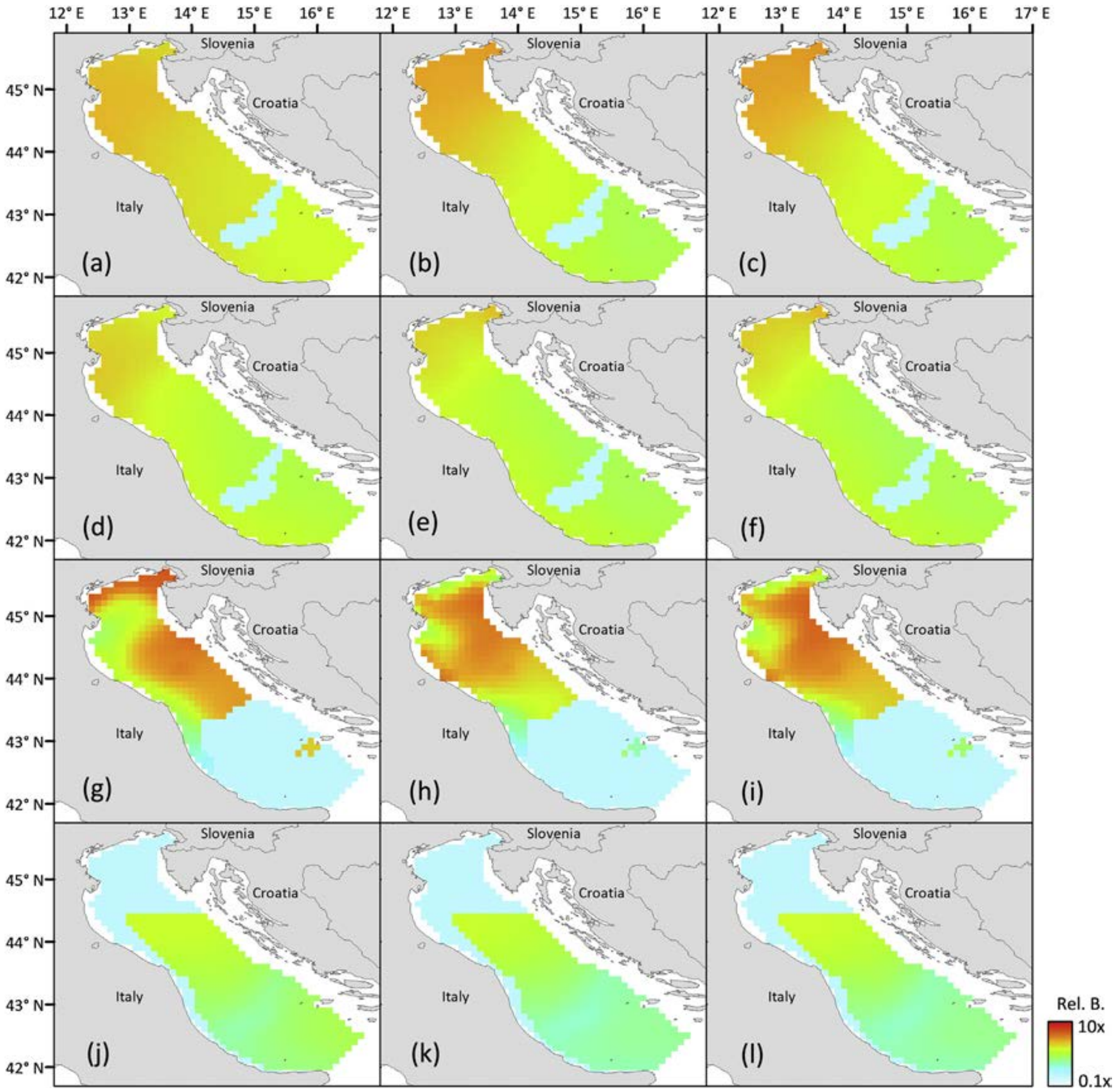

Fig. 13. Distribution of relative biomass of sardine (a–c), anchovy (d–f), seabirds (g–i) and hake (j–l) for the last year of the simulation, 2007. Results are related with the model (a, d, g and j) without external PP data, (b, e, h and k) with monthly PP data, and (c, f, I and l) with annual PP data.

3. Results

3.1. Zero-impact analysis

The zero-impact hypothesis was validated by numerically comparing the primary production maps that Ecospace produces at the end of the first time step. These maps represented the PP distribution after one month of food web effects. The classic, fitted to time series model was executed with and without the zero-impact primary production map and the resulting PP maps at the end of January 1975 were numerically identical (Annex D). This analysis confirmed that the framework was able to incorporate original driving data without producing deviating results. The framework was thus deemed suitable for incorporating external PP datasets.

3.2. Spatial–temporal simulations: phytoplankton dynamics

Results of running the NC Adriatic Sea food web model with the new spatial–temporal framework were analyzed for the three scenarios: (i) without external spatial–temporal data; (ii) with monthly spatial–temporal PP data (Fig. 8), and (iii) with annual averaged spatial–temporal PP data (Fig. 8).

Regarding the temporal pattern of phytoplankton biomass, the original run of the model, starting in 1975, hind casted a steady biomass of phytoplankton from late 1970s to late 1990s. In the last part of the time series the model showed a slight increase of phytoplankton that leveled out at the end of the time series (Fig. 10a, blue line). In contrast, results using the spatial–temporal framework with monthly PP data showed larger variations of relative biomass of phytoplankton over time starting from the beginning of the new dataset in 1997 (Fig. 10a, green line), in agreement with the monthly PP dataset (Fig. 8). Results using the annual averaged spatial–temporal PP data showed smaller fluctuations than the second scenario, a slight increase of phytoplankton biomass from late 1990s to early 2000s and then a slight decline with time (Fig. 10a, red line).

Regarding the spatial distribution of primary productivity, the satellite-derived primary production data (Fig. 7b and c) were compared with phytoplankton biomass results from the model. The spatial results of the original annual run of the model did not capture the distribution of phytoplankton biomass well enough (higher in northern and western areas and lower in southern and eastern areas) (Fig. 11a). This is due to a more homogeneous distribution of initial primary production data from the model (Fig. 7a) than the observations from the area (Fig. 7b and c). On the contrary, results of phytoplankton biomass in the second scenario with monthly spatial–temporal primary productivity data, and the third scenario with annual averaged spatial–temporal primary productivity data, better reproduced the expected spatial patterns of phytoplankton biomass that occur in the area, with less productive regions in the southern and eastern part of the maps (Fig. 11b and c).

3.3. *Temporal food web effects by functional group*

The temporal results of phytoplankton biomass changes from the original run of the model and fishing dynamics showed an increase in sardine biomass due to higher biomass of phytoplankton, their prey, and a decrease in zooplankton due to higher predation mortality by sardines (Fig. 10b and c). On the contrary, and due to high fishing pressure, anchovy firstly increased due to prey availability but then continued its historical decline (Fig. 10d). The seabirds, and to a lesser extent the large pelagic fish increased due to higher abundance of prey, mainly small pelagic fish, predominantly sardine, while hake continued to decline due to high fishing impact over time (Fig. 12a).

Under the second scenario, with monthly spatial–temporal PP data, the model showed larger variations in the biomass of zooplankton after 1997 following the variations in phytoplankton (Fig. 10b), which were translated into high variations in the biomass of sardine, anchovy and seabirds (Figs. 10c, d and 12b). Sardine and seabirds, in contrast to the first scenario and due to the pattern observed in phytoplankton biomass, showed first an increase and then a decline, which was also observed in the patterns of large pelagic fish, but with much less variability (Fig. 12b). Anchovy and hake continued to decline due to fishing impact, although anchovy showed an increase in biomass in the late 1990s, due to higher phytoplankton biomass, and overall larger variability than hake (Fig. 12b).

Under the third scenario, with annual averaged spatial–temporal PP data, the model showed lower temporal variability (as expected), but similar results to scenario 2 (Figs. 10 and 12c). Sardine increased first and then declined following phytoplankton biomass patterns, and this trend cascaded up the food web to seabirds and to a lesser extent to large pelagic fish. Zooplankton abundance/biomass decreased due to declines of the prey (phytoplankton) and higher predation mortality, and anchovy and hake continued their historical declines due to fishing impact, although again anchovy showed a slight increase in biomass late 1990s, due to higher phytoplankton biomass, and higher variability due to zooplankton dynamics.

3.4. *Spatial food web effects by functional group*

The spatial dynamics of zooplankton biomass of the original model captured some of the phytoplankton spatial dynamics (Fig. 11d), although the spatial patterns were more realistic when the external data were used under the second and third scenarios (Fig. 11e and f), showing higher zooplankton biomass in northern and western coastal areas of the study region. Differences in spatial distributions between the second and the third scenario were small, indicating that both monthly and annual average produced reasonable results at the end of the modeling runs.

The spatial dynamics of sardine biomass of the original model also captured some of the phytoplankton spatial dynamics (Fig. 13a), although the spatial patterns were clearer when the external data were used (Fig. 13b and c). Differences between the second and the third scenario were also small. The spatial dynamics of anchovy biomass of the original model and the new spatial framework showed similar patterns for anchovy distribution (Fig. 13d), although these patterns were more evident with the new spatial framework in place (Fig. 13e and f). Differences between the second and the third scenario were also small.

The spatial distribution of seabirds' biomass was similar under the three simulations (Fig. 13g–i). However, the original model hind casted less abundance of seabirds in the northern areas of the Adriatic Sea, probably due to less productivity patterns in that area. Finally, the spatial dynamics of large pelagic fish and hake biomass of the original model and the new spatial framework showed overall similar patterns (results shown for hake only, Fig. 13j–l).

4. Discussion and conclusion

This study presents the new spatial–temporal data framework developed under the Ecospace spatial and temporal modeling approach (Christensen and Walters, 2004; Walters et al., 2010). The new framework was applied to drive the dynamics of primary production of an Ecospace model representing the NC Adriatic Sea (Coll et al., 2007, 2009; Fouzai et al., 2012).

This case study is the first of its kind to drive the spatial and temporal dynamics of the Ecospace food web model with spatial–temporal time series, and it facilitates the incorporation of GIS analysis into food web models. The zero-impact analysis provided evidence that the framework is able to deliver reliable data into Ecospace. The flexible organization of the framework facilitated the execution of the Ecospace model with a minimal set of required steps while demonstrating transparent access to GIS data. Overall, results are satisfactory and by implementing the new framework biological results were consistent with historical data and improved from those of the original model (Coll et al., 2009). The distribution of phytoplankton highlighted the productive northern areas, and the influence that this production has on the western coast of the NC Adriatic Sea, while the eastern and central areas show less productivity. This is linked with the oceanography and water circulation of the area (Zavatarelli et al., 2000). The original run of the model did not hind cast correct temporal and spatial dynamics of primary production for the period with external data, from 1998 to 2007, since a slight increase in phytoplankton biomass was computed by the original model run. However, using the new spatial–temporal data framework, the dynamics of primary producers were in line with their declining trend observed in the recent past (Mozetič et al., 2010; Mélin et al., 2011; Cabrini et al., 2012). These results highlight the importance of driving the spatial Ecospace model with external observational data to improve the capability of models to better approximate observed temporal and spatial patterns of primary producers.

Changes in the temporal dynamics of phytoplankton biomasses cascaded up the food web and influenced the dynamics of zooplankton and small pelagic fish, which directly feed on phytoplankton or zooplankton (Palomera et al., 2007). The impact on the dynamics of larger predators was also noticeable, although this impact was mitigated by other factors in the food web. Seabirds and large predatory fish showed similar patterns to their prey. When the new spatial framework was in place (under the second and third scenarios), these groups showed first an increase, followed by a decrease in abundance due to dynamics of phytoplankton, then zooplankton, and following the small pelagic fish. The dynamics of adult hake were less affected by the bottom-up effects of the food web and this could be due to the lesser dependency of this species on the pelagic compartment (Coll et al., 2007), but also due to the high fishing pressure placed upon this highly exploited commercial species (Jukić-Peladić et al., 2001; Vrgoć et al., 2004).

The simulations including the external data reproduced more realistic spatial distribution of phytoplankton (Bosc et al., 2004), and thus yielded more accurate spatial distributions of zooplankton and small pelagic fish that directly feed on phytoplankton (Morello and Arneri, 2009). The differences between the three simulations regarding the spatial distribution of predators were less profound and may indicate that predator distributions are affected by other factors such as the distribution of their prey and predators, and fishing effort.

The distribution of hake hind-casted by the model was similar to that obtained from survey data (Županović and Jardas, 1986; Adriamed, 2012), suggesting that the model is providing realistic results. The distribution of seabirds computed by the original model was less realistic than results using the new spatial module given that seabird populations in the northern Adriatic Sea are known to be very abundant (Baccetti et al., 2002).

The spatial–temporal data framework provides new possibilities for climate change science, such as the integrated assessments of species distributions and food web dynamics, or driving the Ecospace food web model with the output from predictive climatological models such as used by the International Panel on Climate Change (Stock et al., 2011). The approach utilized in this framework can be also used as a foundation for simplifying and compartmentalizing complexity in order to further model interoperability and closing the gap between marine ecosystem modeling tools via geographic information systems (GIS) technology. The approach simplifies interdisciplinary model interoperability by separating its various technical and scientific challenges into a flexible and modular software system using open source GIS technology and common software development paradigms. This framework will be used in the near future for a series of ambitious model interoperability projects that will integrate the Ecospace model in GIS environments to model the global ocean through the NF-UBC Nereus Program (Christensen et al., 2012).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2013.04.027.

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ECOSYSTEMS

Representing Variable Habitat Quality in a Spatial Food Web Model

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ABSTRACT

Why are marine species where they are? The scientific community is faced with an urgent need to understand aquatic ecosystem dynamics in the context of global change. This requires development of scientific tools with the capability to predict how biodiversity, natural resources, and ecosystem services will change in response to stressors such as climate change and further expansion of fishing. Species distribution models and ecosystem models are two methodologies that are being developed to further this understanding. To date, these methodologies offer limited capabilities to work jointly to produce integrated assessments that take both food web dynamics and spatial-temporal environmental variability into account. We here present a new habitat capacity model as an implementation of the spatial-temporal model *Ecospace* of the *Ecopath with Ecosim* approach. The new model offers the ability to drive foraging capacity of species from the cumulative impacts of multiple physical, oceanographic, and environmental factors such as depth, bottom type, temperature, salinity, oxygen concentrations, and so on. We use a simulation modeling procedure to evaluate sampling characteristics of the new habitat capacity model. This development bridges the gap between envelope environmental models and classic ecosystem food web models, progressing toward the ability to predict changes in marine ecosystems under scenarios of global change and explicitly taking food web direct and indirect interactions into account.

Key words: food web model; species distribution model; ecopath; ecospace; habitat modeling; foraging capacity model; sampling; simulation model.

INTRODUCTION

Marine ecosystems are impacted by numerous anthropogenic stressors including fishing (for example, Pauly and others 2002), aquaculture (for example, Naylor and others 2000), chemical pollution (for example, Ueno and others 2004), eutrophication (for example, Vitousek and others 1997), and climate change (for example, Root and others 2003). Marine species respond differently to these stressors, and interact by complex relationships that make an assessment of human impacts a challenging endeavor (for example, Jennings and Kaiser 1998; Jackson and others 2001). Marine ecosystems are also influenced by environmental natural fluctuations and variability (Cury and others 2008; Link and others 2010). The ability to understand how human activities, environmental

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factors, and ecological components interact and influence each other, and affect ecosystem services in the future, is an issue of pressing importance (Worm and others 2006).

The scientific community is faced with an urgent need to understand ecosystem dynamics in the context of global change. This requires development of scientific tools with capability to predict how biodiversity, natural resources, and ecosystem services will change in response to stressors such as climate change and further expansion of fishing. Species distribution models and ecosystem models are two methodologies that are being developed to further this understanding.

Species distribution models use a combination of physical, environmental, ecological, and physiological data to predict where species are likely to occur (Jones and West 2005; Elith and Leathwick 2009). They aim to predict species occurrence ranges by various approaches, such as the correlation of maps with physical habitat characteristics, or by using theoretical frameworks that use the physiological responses between species distributions, or known tolerance limits to environmental predictor variables of physical, environmental, or other types. If dedicated models are used to predict future distributions of driving factors, one can then forecast possible future distributions of species under changes in predictor variables (Jones and others 2013).

Species distribution models are widely used in both terrestrial and marine ecosystems, and increasingly to predict consequences of climate change (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith and Leathwick 2009). However, most species distribution models do not take trophic interactions of predators and preys and food web dynamics into account (Micheli and others 2004; Austin 2007; Elith and Leathwick 2009), or at most consider these interactions indirectly (Albouy and others 2014). Such interactions have been shown to be key elements for understanding species and ecosystems dynamics in the ocean (Frank and others 2005; Christensen and Walters 2011). In addition, the application of species distribution models in the marine environment poses problems due to data unavailability and paucity (Kaschner and others 2006; Pearson and others 2007; Cheung and others 2009; Ready and others 2010).

Ecosystem models aim at developing a mechanistic understanding of principal species and population dynamics, which in turn can be used to predict community and ecosystem dynamics (for example, Christensen and Walters 2004; Fulton 2010). They use multiple datasets including species information (for example, abundance and distribution), population parameters (for example, growth, reproduction, feeding), community traits (for example, prey-predators information), and data from ecosystem drivers such as fishing activities and environmental dynamics. For about 30 years, ecosystem models have been used to hind cast population dynamics with considerable capability (Walters and others 2008; Christensen and Walters 2011) and are increasingly being deployed to forecast ecosystem dynamics and develop future scenarios for the ocean (Christensen 2013; Steenbeek and others 2013).

To bridge the gap between ecosystem models and species distribution models we have extended *Ecospace*, the spatial-temporal explicit module of the *Ecopath with Ecosim* (*EwE*) modeling approach, with the means to include the impacts of variable habitat quality on modeled spatial population distributions. *EwE* is the most widely applied food web model for marine ecosystems (Christensen and Walters 2004; Christensen and Walters 2011). *EwE*, which is freely available from http://www.ecopath.org, describes ecosystem food web models by means of functional groups, each representing a species, a sub-group of a species (multi-stanza groups, Walters and others 2000, 2010) or a group of species that have functional and ecological similarities. *EwE* consists of three main, linked routines that have been developed over the last three decades: *Ecopath*, *Ecosim*, and *Ecospace*. *Ecopath* is the mass-balance routine that allows building spatially and time averaged models of the trophic web (Polovina 1984; Christensen and Pauly 1992, 1993), and which serves to parameterize the dynamic modules of *EwE*; *Ecosim* is the time dynamic routine (Walters and others 1997, 2000); and *Ecospace* allows representing temporal and spatial 2D dynamics of trophic web components (Walters and others 1999, 2010).

Although no single model can capture all the relevant processes for ecological forecasting and scenarios, *EwE* can integrate a large body of information in a coherent description of aquatic food webs and places human activities in an ecosystem context that accounts for environmental changes (Christensen and Walters 2004). *EwE* models are widely used to evaluate the structure and functioning of marine ecosystems (for example, Heymans and others 2004; Coll and Libralato 2012), make ecosystem comparisons (for example, Moloney and others 2005; Coll and others 2006), derive emergent properties (for example, Pauly and Christensen 1995), assess the impacts of human activities (for example, Manickchand-Heileman and others 2004; Mackinson and others 2009) including climate change (Ainsworth and others 2011) and fishing impacts (Libralato and others 2008), analyze management options for marine resources (for example, Criales-Hernandez and others 2006; Araújo and others 2008; Walters and others 2008), and describe bioaccumulation of toxins in the food web (for example, Booth and Zeller 2005). Recently, the Institute for European Environmental Policy concluded that, among the available models of marine ecosystems, *EwE* was the most suitable for the development of scenarios for exploring future trends of marine biodiversity and changes in ecosystem services (Sukhdev 2008), and the modeling framework is indeed seeing increased use for this purpose (Wilting and others unpublished).

Ecospace, the spatially explicit model of *EwE*, has been widely applied to quantify the spatial impact of fisheries on marine species (Christensen and others 2003; in press; unpublished), to analyze impact of management scenarios such as the establishment of marine protected areas, and to assess the correlation of spatial distributions of marine species and fishing effort (Walters 2000; Martell and others 2005; Fouzai and others 2012). *Ecospace* can also be used to develop spatial optimization routines (Christensen and others 2009), to assess the impact of climate change by linking *Ecospace* with low trophic level models (Fulton 2011) or by driving *Ecospace* directly with external temporal-spatial time series (Steenbeek and others 2013).

The original *Ecospace* model has, however, been limited in the way habitat is represented as a fixed parameter in the spatial model, providing limited support to represent changes in the quality and extent of habitats. Large-scale habitat structures with associated impact on biomass distributions and trophic interactions have been represented only by a binary habitat use pattern, with each spatial cell being either entirely suitable—or entirely unsuitable—for species/functional groups. The original *Ecospace* model thus assumed homogenous conditions within each spatial cell, and local, but possibly relevant variations within cells, could not be represented. This binary formulation has been particularly troublesome for models representing ecosystems where there is strong ''sub-grid'' spatial structure of one or more key habitat types, for example, small but productive reef structures that are smaller than a single grid cell, or strong, productive, and significant coastal structures that cannot be represented as entire cells. Using smaller cells to address this limitation may adversely impact the speed of computations and the amount of memory needed at runtime, and may eventually yield unrealistic results by over-representing modeled phenomena (Fulton and Smith 2004). Further, the complex habitat gradient calculations required in the original *Ecospace* model greatly slow simulations of changing habitat usage over time, requiring re-calculation of habitat gradients whenever species habitat preference changes occur.

AIM

To date, species distribution models and ecosystem models offered limited capabilities to work jointly to produce needed integrated assessments: assessments that take both food web dynamics and spatial-temporal environmental variability into account. To overcome these problems, we have restructured the *Ecospac*e model to consider habitat quality adding a new habitat foraging capacity model. The change presented and tested here is fairly simple and mainly implies to replace a binary habitat variable with a continuous habitat suitability factor, where the area that species can feed in each cell is determined by functional responses to multiple environmental factors. This modification builds on the fact that animal populations have lower local impacts as the size of their forage area increases. The new model offers the ability to drive foraging capacity from multiple physical, oceanographic, and environmental factors such as depth, bottom type, temperature, salinity, oxygen concentrations, and so on, which have cumulative impacts on the ability of functional groups to forage. Because cell capacity is calculated for every functional group at every time step, this modification makes the model fully temporal and spatially dynamic.

In this study, we present the new habitat capacity model and we use simulation modeling to evaluate its sampling characteristics. For this, we use an artificial data set based on a spatial food web model of a marine ecosystem. We derive ''true'' distribution based on environmental preference for the functional groups in the model, and then evaluate the degree to which it is possible to recreate the ''true'' distributions from sampling. As part of this we evaluate the impact of sample size and uncertainty in key parameters. The final goal of the paper is to develop and test a continuous habitat suitability model to be used within the *Ecospace* modeling framework to address a suite of new ecological questions, such as the impact of habitat degradation due to coastal development, eutrophication, and climate change.

The Original *Ecospace* Model

The *Ecospace* model is a spatially explicit time dynamic model based on the *Ecopath* mass-balance and *Ecosim* time dynamic routines (Walters and others 1997; Christensen and Walters 2004). It applies the same set of differential equations as used in *Ecosim*, executed for each cell in a grid of cells. In *Ecosim* (Walters and others 1997; Christensen and Walters 2004), a set of differential equations is defined based on the biomass change during time for consumer functional groups, expressed as:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = g_i \sum_{j=1}^{n} Q_{ji}\big(B_j(t), B_i(t)\big) - \sum_{j=1}^{n} Q_{ij}\big(B_i(t), B_j(t)\big) + I_i - \big(M0_i(t) + F_i(t) + e_i\big)B_i(t), \qquad (1)$$

where $B_i(t)$ is the biomass of i at time t, g_i is the growth efficiency, I_i is the immigration rate; $M0_i$ is the natural mortality (mortality not due to fishing or predation from the described food web); $F_i(t)$ is the mortality rate due to harvesting (fishing mortality); e_i is the emigration rate. The term Q_{ij} represents the consumption due to predation on i by predator j and is a function of their biomasses, whereas the term Q_{ji} represent the consumption due to predation on group j by predator i. For primary producers the term $f(B_i(t))$ represents the growth term as function of the group biomass (Christensen and Walters 2004).

The consumption rates Q_{ij} are based on the foraging arena theory (see Walters and others 1997, 2000; Christensen and Walters 2004; Walters and Martell 2004; Ahrens and others 2012), where the biomass of prey i is split between a vulnerable (V_{ij}) and a non-vulnerable ($B_i - V_{ij}$) component. The transfer rate, called vulnerability (υ_{ij}) between the two fractions determines the vulnerable biomass at time interval dt:

$$\frac{\mathrm{d}V_{ij}}{\mathrm{d}t} = v_{ij}\big(B_i - V_{ij}\big) - v_{ij} \cdot V_{ij} - \frac{a_{ij}V_{ij}B_j}{1 + h_j a_{ij} V_{ij}}, \qquad (2)$$

where a_{ij} is the effective search rate for the predator (j), and h_j is handling time for the predator. The vulnerability parameter (υ_{ij}) expresses the maximum increase in predation mortality under the given predator/prey conditions. High values of υ_{ij} imply large proportions of biomass (B_i) vulnerable to predator j (V_{ij}), and thus imply $V_{ij} = B_i$, and that the predator j is far from its carrying capacity with regards to prey i.

In *Ecospace*, the spatial extent of the ecosystem is represented by a grid of cells, each of which can be defined as land or water and, and in the last case, a habitat type can be assigned to the cell. *Ecospace* represents the biomass (B) and consumption (Q) dynamics over a two-dimensional space as well as time (Walters and others 1999; Christensen and others 2008). Space, time, and state are considered discrete variables by using the Eulerian approach, which treats movements as ''flows'' of organisms among fixed spatial reference cells.

In the original *Ecospace* model, a first step of parameterizing entails the definition of a basemap based on habitat information (depth strata, bottom type, and so on) in the study area. Species preferences are then assigned to these habitat types based on the biology and ecology of the species included in each functional group of the ecosystem model, their depth distributions, their preferred sediment type, etc. In addition, the model requires (i) the dispersion rate of each functional group in ''preferred'' habitats, (ii) the relative dispersal rate in ''non-preferred'' habitats, and (iii) the relative feeding rate in non-preferred habitat by functional group.

Fishing fleets can be depicted as operating in a specific region and cells can be defined as protected areas (MPAs, for example, Walters and others 2000). Moreover, relative variations of primary productivity and fishing costs can be defined for the initial conditions of the model. For trophic interactions, fishing, and movement calculations, biomass is considered as homogeneous within each cell and movement of biomass and flows is allowed across the borders to adjacent cells. For each cell, the immigration rate I_i of equation 2 is assumed to consist of up to four emigration flows from the surrounding cells. The emigration flows ($B_{\mathrm{out},rci}$) are in turn similarly represented as instantaneous movement rates m_i times the biomass density in the cell (B_{rci}):

$$B_{\mathrm{out},rci} = \sum_{d=1}^{4} m_{i,d} \cdot B_{rci}, \qquad (3)$$

where (r,c) represents cell row and column, and d is movement direction (up, down, left, or right).

The instantaneous emigration rates m_i from a given cell in *Ecospace* are assumed to vary based on the functional group, habitat preferences, and responses of organisms to depredation risk and feeding conditions. The probability of movement of organisms toward favorable habitats is calculated by means of a ''habitat gradient function'' for each mapped habitat type and species or group i. Biomass dynamics in unsuitable cells are modified by predicting higher rates of emigration, lower feeding rates, and/or higher vulnerability to predation, a complex gradient calculation to modify dispersal rates is used to direct biomass toward suitable cells.

The Habitat Foraging Capacity Model

Using Relative Habitat Capacity to Predict Spatial Abundance

A reasonably simple and tractable way around the binary parameterization of habitat definition is to define a continuous relative habitat capacity C_{rcj} for each group j in each cell r,c, where C_{rcj} varies from 0.0 to 1.0, and is calculated for each cell as a function of a vector of habitat attributes $H_{rc} = (H_1, H_2, \ldots \mathrm{H}_v)_{rc}$ of that cell, that is, $C_{rcj} = f_j(H_{rc})$. For example H_1 might be water depth, H_2 might be proportion hard bottom, H_3 might be summer water temperature, and so on. Figure 1 provides a schematic overview of the basic calculations in the habitat capacity model.

The proportion of a cell that a species (or functional group) can use is thus a continuous value from 0 to 1, and allows inclusion of as many environmental factors as needed to define the foraging capacity of a cell for a species in an *Ecospace* model.

If the functions f_j are chosen carefully, C_{rcj} can be updated over time with relatively little computational cost, for example by loading time-varying values of H_{rc} generated by other models or remotely sensed data for physical or biophysical change, and implemented using the spatial-temporal data framework of *Ecospace* (Steenbeek and others 2013).

To use the C_{rcj} habitat assessments, the C_{rcj} values have to be linked to trophic interaction dynamics to specify how C_{rcj} impacts food consumption and predation rates. A simple and reasonable way to represent this linkage is available through the basic foraging arena equations used to predict trophic interaction (food web biomass flow) rates (equation 2). If we look at the basic way that *Ecosim* represents biomass dynamics (exclusive of spatial mixing effects), trophic interaction, and fishery effects are modeled by equations of the form:

$$\frac{\mathrm{d}B_j}{\mathrm{d}t} = \frac{g_j \cdot a_{ij} \cdot v_{ij} \cdot B_j \cdot B_i}{2 \cdot v_{ij} + a_{ij} \cdot B_j} - Z_j \cdot B_j, \tag{4}$$

where B_j is predator biomass, B_i is prey biomass, Z_j is total instantaneous mortality rate of j, g_j is growth efficiency (corresponding to the production/consumption ratio, which can vary as predators grow in size), v_{ij} is prey vulnerability exchange rate, and a_{ij} is the rate of effective search by the predator. Note that in this model, vulnerable prey density V_{ij} is represented by the foraging arena equation (equation 2), which simplified can be expressed as:

$$V_{ij} = \frac{v_{ij} \cdot B_i}{2 \cdot v_{ij} + a_{ij} \cdot B_j}, \tag{5}$$

where predation pressure in a cell depends on the foraging arena area in that cell. If we assume that variation in relative habitat capacity for the predator means variation in the foraging arena area over which a species can forage successfully, we can include variation in relative habitat capacity in the model by dividing the denominator $a_{ij} \cdot B_j$ term by relative habitat size or capacity C_{rcj}, that

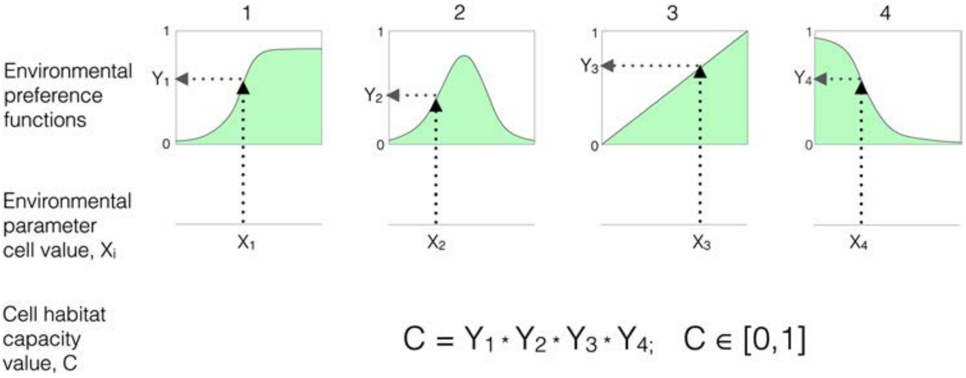

Figure 1. Schematic diagram of the habitat capacity model calculations with four (hypothetical) environmental preference functions (any number of functions is possible). During model run, cell-specific environmental parameter values can be read from data layers for each time step, and a cell-specific habitat capacity value is estimated as the product of the environmental preference values. No weighting is used, but weighting can be considered by altering the shapes of the environmental preference functions.

$$V_{ij} = \frac{v_{ij} \cdot B_i}{2 \cdot v_{ij} + a_{ij} \cdot B_j / C_{rcj}}. \qquad (6)$$

In effect, this assumption concentrates predation activity into smaller relative areas when C (foraging arena size) is small, so as to drive down vulnerable prey densities V_{ij} more rapidly as B_j increases in locales with less foraging arena area.

Importantly, including C_{rcj} as a modifier in the $a_{ij} \cdot B_j / C_{rcj}$ predation rate term results in the equilibrium predator biomass (B_j for which $\mathrm{d}B_j/\mathrm{d}t = 0$) being proportional to C_{rcj}, that is,

$$B_j = \left(g_j \cdot v_{ij} \cdot \frac{B_i}{Z_j} - 2 \cdot \frac{v_{ij}}{a_{ij}} \right) \cdot C_{rcj} \qquad (7)$$

That is, using the C_{rci} as modifiers of the foraging arena consumption rate equation results in spatial patterns of biomass of consumers being proportional to C_{rci}, other factors (prey biomasses B_i and mortality rates Z_j) being equal over space. We can of course also assume that variation in habitat capacity also affects the vulnerability exchange rates v_{ij}, search rates a_{ij}, and predation rates Z_j (and if so, add minor changes to the code to implement these assumptions), but the default assumption is that the dominant cause of ''poor'' or relatively small habitat capacity is lack of usable foraging arena area. As such, the basic change made to the rate equations is a simple division of the denominator terms for predator search term, by-arena vulnerable prey density equations, by the capacity values C_{rcj}.

The new model is made compatible with existing *Ecospace* models by providing the option to derive capacity directly from presence/absence habitats. In this case, habitat maps and habitat preferences are directly converted to a capacity map for each functional group. Cells that contain a preferred habitat will receive a full capacity of 1, other cells will receive a capacity of (almost) 0.

Setting Initial Adjusted Biomasses for *Ecospace*

In going from *Ecopath* to *Ecospace*, it is assumed that the *Ecopath* base biomasses represent the average over all modeled cells of the cell-specific biomasses. This means that *Ecospace* biomass densities can be much higher on favorable spatial cells if there are relatively few such cells. Initial biomass densities $B_{rcj}(0)$ reflecting the C_{rck} variation are assigned at the start of each *Ecospace* simulation by assuming that these biomasses are proportional to the C_{rcj}. If there are n_w water cells, such that overall biomass density for group k across the grid is given by $n_k B_i^*$ where B_j^* is the *Ecopath* base biomass for group j, the initial spatial biomass densities are assigned as,

$$B_{rcj}(0) = \left(\frac{C_{rcj}}{TC_j} \right) \cdot n_j \cdot B_j^*, \qquad (8)$$

where TC_j is a total capacity index over the grid for group j, that is,

$$TC_j = \sum_{r,c} C_{rcj} \qquad (9)$$

and the sum over r and c is over all water cells in the spatial grid. Note that $TC_j \ll n_j$ implies severe concentration of group j biomass on few cells.

Correction of Search Rate and Vulnerability Parameters for Spatial Overlap Patterns

Spatial concentration of biomass for any group implies a requirement to adjust the rates of effective search a_u and vulnerability exchange rates v_u for all foraging arenas u that are used by group j and its predators j', since without such adjustments predicted predation rates (using foraging arena equations from *Ecosim*) at the higher local densities would be artificially increased from the rates implied by *Ecopath* base consumptions. In order to make this adjustment, the rates are set so that the total consumption for each arena link is the same in *Ecospace* as in *Ecosim*, scaled up to the total number of water cells. This implies the condition

$$n_w Q_u = \frac{a_u \cdot v_u \cdot \sum_{r,c} B_{rcj} \cdot B'_{rcj}}{2 \cdot v_u + a_u \cdot B_j^*}. \qquad (10)$$

Here, Q_u is the *Ecosim* base biomass flow rate for arena link u, $B_{rcj'}$ is the initial predator abundance (biomass for non-stanza groups or sum of numbers at age times length squared for multistanza groups) for cell (r,c), and B_{ju}^* is the spatially invariant initial predator abundance obtained by noting that applying the C_{rcj} correction in equation 6 results in

$$B_j^* = \frac{n_j \cdot B_{E\cos im,j'}}{TC_j'}. \qquad (11)$$

Here $B_{Ecosim,j'}$ is the Ecosim initial predator abundance. Using the assumed relationships above between initial B_{rcj}, $B_{rcj'}$, and C_{rcj}, equation 10 can be written as:

$$Q_u = \frac{a_u \cdot v_u \cdot B_{ju}^{**} \cdot B_j^*}{2 \cdot v_u + a_u \cdot B_j^*}, \qquad (12)$$

where B^{**}_{ju} is the prey-predator "incidence weighted" mean prey biomass divided by $B_j{*}$ for link u given by

$$B^{**}_{j_u} = \frac{B^*_j \cdot \sum_{rc} C_{rcj} \cdot C'_{rcj}}{TC_j}. \tag{13}$$

Note that this reduces to just B^*_{ju} if all predator $C_{rcj'}$ are near 1.0 for the same (r,c) cells where prey C_{rcj} are near 1.0, that is, where there is strong spatial overlap of the prey and predator distributions, but can be much lower than B^*_{ju} for cases where predators occupy restricted spatial areas compared to the prey. Assuming the same vulnerability exchange rate v_u as in *Ecosim* (from total base consumption rate over all predators using arena u) where k is the user-supplied vulnerability multiplier (aka *Vulmult*), equation 12 can be solved for a_u:

$$a_u = \frac{2 \cdot v_u}{\left[B^*_{j'}\left(v_u \cdot B^{**}_{j_u}/Q_u - 1\right)\right]}. \tag{14}$$

Unfortunately, this calculation fails if $v_u B^*_{ju}/Q_u<1$, which can happen with relatively low v_u settings and weak overlap between prey and predator such that B^{**}_{ju} is much less than B_j. In that case, the assumed spatial distribution overlap pattern simply cannot support the total predation rate estimated for the link in *Ecopath and Ecosim*, and instead we simply set

$$v_u = \frac{1.001 \cdot Q_u}{B^{**}_{ju}} \tag{15}$$

before solving for a_u in equation 14 so as to provide at least some large estimate of a_u to make simulations come as close as possible to predicting the base Q_u. The rate of effective search a_u is further adjusted upward by the multiplicative factor $Qm{\cdot}Qo_{j'}/(Qm{\cdot}Qo_{j'} - 1)$ to account for handling time effects in order to create type II functional response effects by setting a low ratio of maximum (Qm) to base feeding rate (Qo).

Modification of Spatial Mixing Rates to Reflect Movement Toward Preferred Cells

For species with body sizes and mobility large enough to exhibit oriented dispersal and/or migration, it is reasonable to assume that dispersal rates between adjacent spatial cells are distorted so as to maintain abundance differences reflective of differences in habitat capacities between the cells.

Without such distortions or oriented movement, random dispersal between cells would greatly reduce abundance gradients created by the C_{rcj} capacity effects, and for species with restricted habitat use would result in too much biomass dispersing into unsuitable spatial cells so as to cause biomass to decrease substantially from *Ecopath* base biomasses, even without any changes in fishing pressure or predator abundances. For each border between cells, for example, between cell (r,c) and cell $(r,c + 1)$ to its right, *Ecospace* assumes instantaneous mixing rates $m_{1j}B_{rcj}$ to the right and $m_{2j}B_{rcj}$ to the left. Absent orientation implies $m_{1j} = m_{2j} = m_j$, where m_j is a user-supplied expected dispersal rate. To avoid smearing of the distribution, the dispersal rates are set so that

$$m_{1j}B_{rcj} = m_{2j} \cdot B_{rc+1j}. \tag{16}$$

Assuming biomasses are then to remain near or proportional to C_{rcj}, this balanced movement condition implies that the m_{1j} and m_{2j} have to be varied so as to meet the balance condition

$$\frac{m_{1j}}{m_{2j}} = \frac{C_{rc+1j}}{C_{rcj}}. \tag{17}$$

Ecospace meets this condition by setting the exit rate to m_j for whichever cell has lower capacity C_{rcj}, then adjusting the exit rate for the cell with higher C_{rcj} to m_j times the capacity ratio. Thus for example if $C_{rc+1j} > C_{rcj}$, m_{1j} to the right is set to m_j and m_{2j} to the left is set to $m_j C_{rcj}/C_{rc+1j}$ so that m_{2j} will be very small if $C_{rcj} \ll C_{rc+1j}$, that is, movement into the low capacity cell will be severely restricted.

Model Behavior and Reproducibility

Simulation Modeling Evaluation

The new habitat capacity model presented here in essence asks the question: "why are the species where they are?" and seeks to explain this based on food web characteristics, fisheries patterns, and environmental preferences, such as, for example, relationship between temperature and productivity or abundance as a function of bottom type. In applications of the model, the environmental preferences typically will be parameterized for each species (or functional group) based on a series of preference functions derived from general (literature) or specific (sampling) information, which are applied in a factorial manner.

We evaluated the performance of the habitat capacity model based on a simulation modeling where we constructed a food web model based on *EwE* (Christensen and Walters 2004), we developed a spatial version of the model with *Ecospace*, we defined environmental preference functions for a number of the groups in the model based on Table 1, and based on this we obtained (''true'') spatial distributions of the functional groups by running the food web *Ecospace* model. We then sampled spatially for abundance (with and without sampling error) and for environmental parameters for one key group, and reconstructed the environmental preference functions from this resampled data to replace those that initially were used to run *Ecospace*. We used a sampling scheme where we sampled a proportion of the spatial map (without repetition of cells) of the distributions of the functional group biomass as computed by *Ecospace* at the end of runs. For each run we varied the sampling error from 0 to 1 times the coefficient of variation for the cell abundance of the key species assuming a distribution around the mean. Using these abundance data as input in the habitat capacity model, we then ran the *Ecospace* model to obtain predicted spatial distributions for the key group, which we in turn compared to the ''true'' distribution for the group coming from the first run of *Ecospace*. Further, we evaluated how the spatial distributions for the key species are impacted by

Table 1. Functional Groups in the Food Web Model Whose Distributions are Based on Environmental Map Layers

No	Group	Environmental map layers
1	Whales	Depth, distance from coast
2	Seals	Depth, distance from coast
3	Cod	Depth, temperature, hard bottom, salinity, oxygen
4	Whiting	Depth, temperature, sand bottom, salinity, oxygen
5	Mackerel	Depth, temperature, oxygen
6	Anchovy	Depth, temperature, oxygen
7	Shrimp	Depth
8	Benthos	Depth, oxygen

For each group and layer an environmental preference function is defined and used as model input.

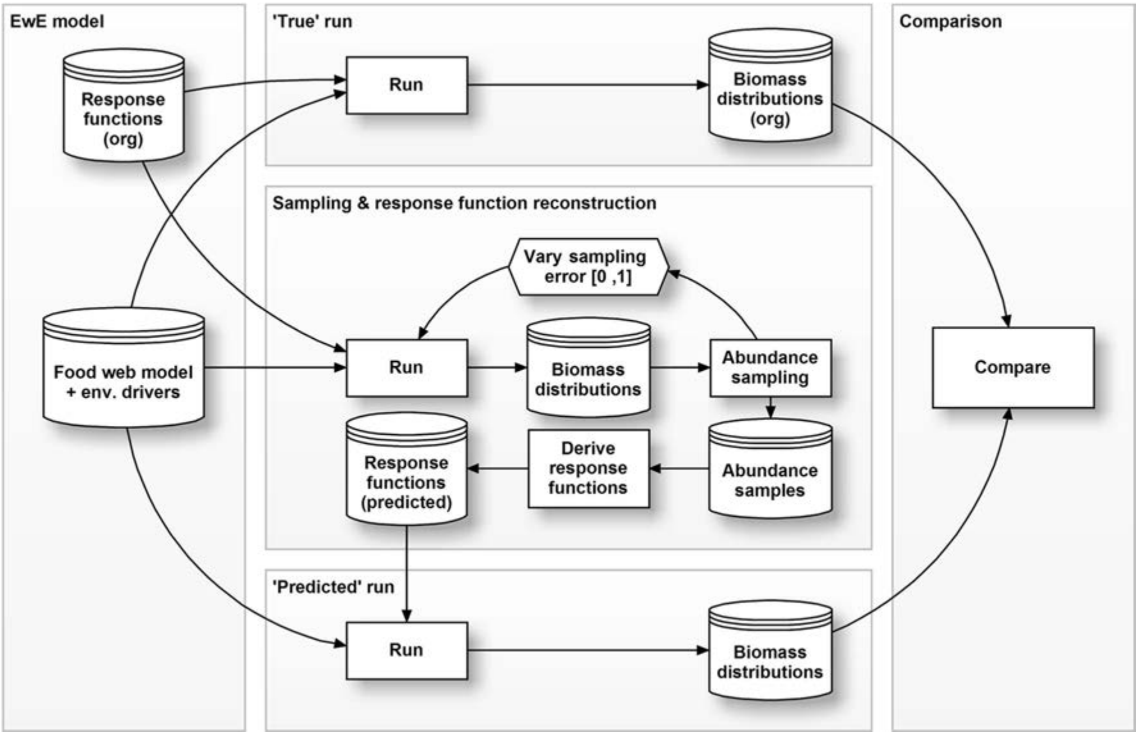

Figure 2. Simulation modeling approach for evaluating performance of the new habitat capacity model based on resampling from a simulated model data set.

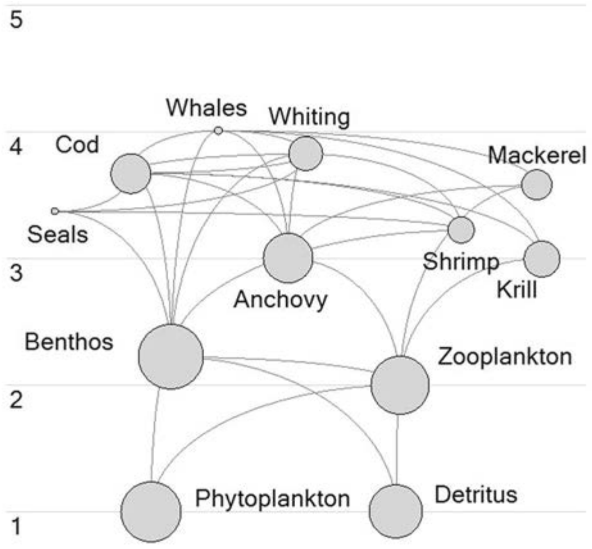

Figure 3. Food web diagram for the hypothetical food web model showing prey–predation relationships. The groups are arranged after trophic levels (TL) in the vertical plane. TLs are indicated with *numbers*.

inclusion or exclusion of environmental preference functions in the habitat capacity model. The simulation modeling procedure is described schematically in Figure 2.

For this simulation, we constructed a simple food web model with 12 functional groups, including whales, seals, whiting, cod, mackerel, anchovy, shrimp, krill, benthos, zooplankton, phytoplankton, and detritus. The model and its parameters are hypothetical, but are constructed based on experience from many other models, and are realistic as representative of a temperate ecosystems (Coll and others 2008; Heymans and others 2012; Christensen and others in press). The food web diagram for the model, showing trophic linkages between functional groups in the food web, is shown in Figure 3.

We constructed a spatial model of the food web model with 1600 spatial cells distributed over 40 rows and 40 columns. Nine of the functional groups in the food web model are distributed spatially based on environmental preference functions as indicated in Table 1. From the model groups, we chose ‘‘whiting’’ as the key group for which to evaluate how the species distribution could be replicated through sampling. Whiting was chosen because it was a high trophic level species, yet was predated upon by three other groups (Figure 3), and because it had a wide distribution with considerable variation in abundance over the map. Whiting was distributed spatially based on five environmental parameter maps (see Table 1) for which the environmental preference functions are given in Figure 4. It should be noted that the species distributions also are influenced by food web characteristics (driven by the spatial overlap of predator and prey) as well as by fisheries (for which effort is distributed spatially based on profitability, which in turn is impacted by target group abundance and the spatial cost of fishing) (Christensen and Walters 2004).

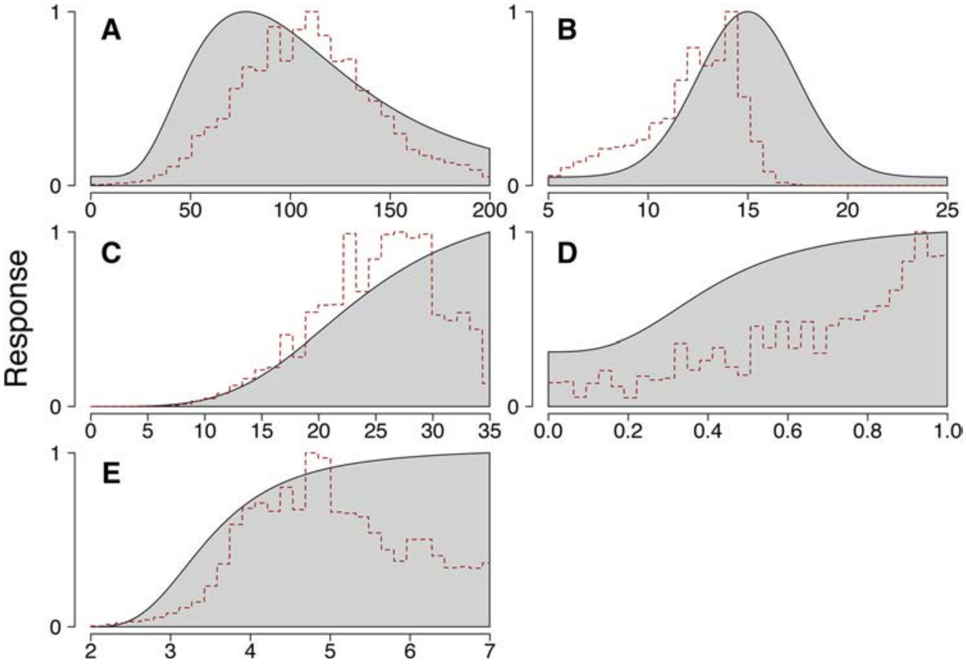

Figure 4. Environmental preference functions for ‘‘whiting’’ used to obtain the ‘‘true’’ spatial distribution for this species. **A** is used for depth (m), **B** temperature (°C), **C** salinity, **D** proportion of cell that is sand bottom, and **E** dissolved oxygen (mg O_2/ml). The *dotted lines* indicate estimated environmental functions based on sampling of all spatial cells with no sampling error.

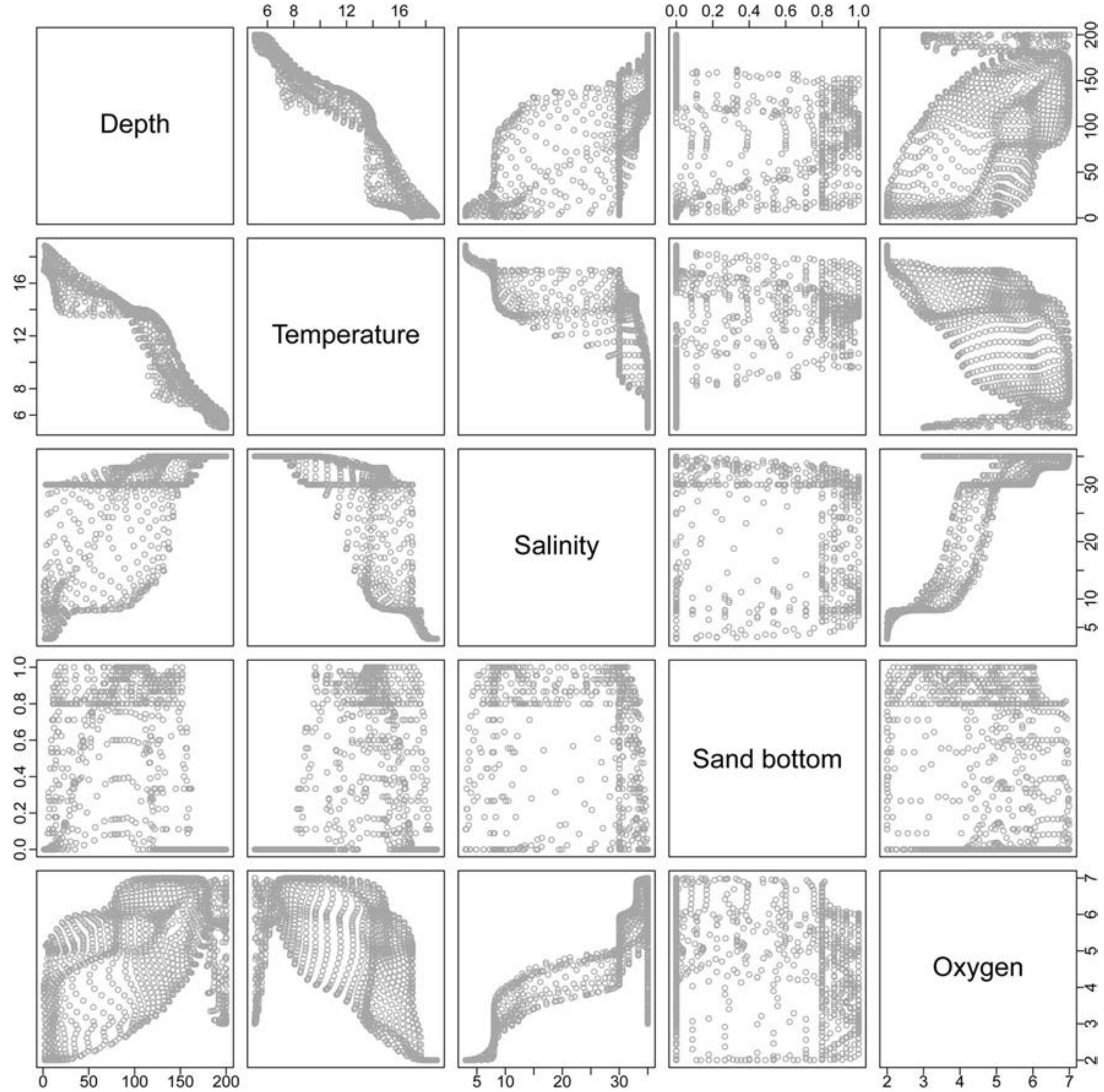

Figure 5. Pair-wise comparisons of parameters for the five environmental maps used for distributing the key group ‘‘whiting’’ spatially.

RESULTS

As a first step, we evaluated the relationships between the environmental parameters maps in the spatial model. This is shown in Figure 5, which indicates a strong negative correlation between depth and temperature ($r = -0.95$; deeper water is cold), followed by salinity with oxygen ($r = 0.77$), depth with salinity ($r = 0.74$), and temperature with salinity ($r = -0.71$), whereas at the other extreme, proportion of sand bottom and dissolved oxygen shows only very little correlation ($r = -0.30$).

We sampled the parameter space for sampling effort in steps of 200 from 200 to 1600 cells out of 1600 cells total without cell replication, and with sampling error on the biomass of the key group in steps of 0.1 from 0 to 1.0 times the coefficient of variation (CV, that is, the standard deviation / mean ratio), for a total of 48 runs. We found that as a best-case scenario, that is, based on sampling all spatial cells with no sampling error, we obtained a CV of 0.73 between the predicted and observed (or ‘‘true’’) biomasses of the key group.

This result should not be seen as surprising or disappointing; one cannot expect to replicate the environmental preference functions perfectly from sampling, as the spatial map will not cover all instances of the preference functions. Indeed, the

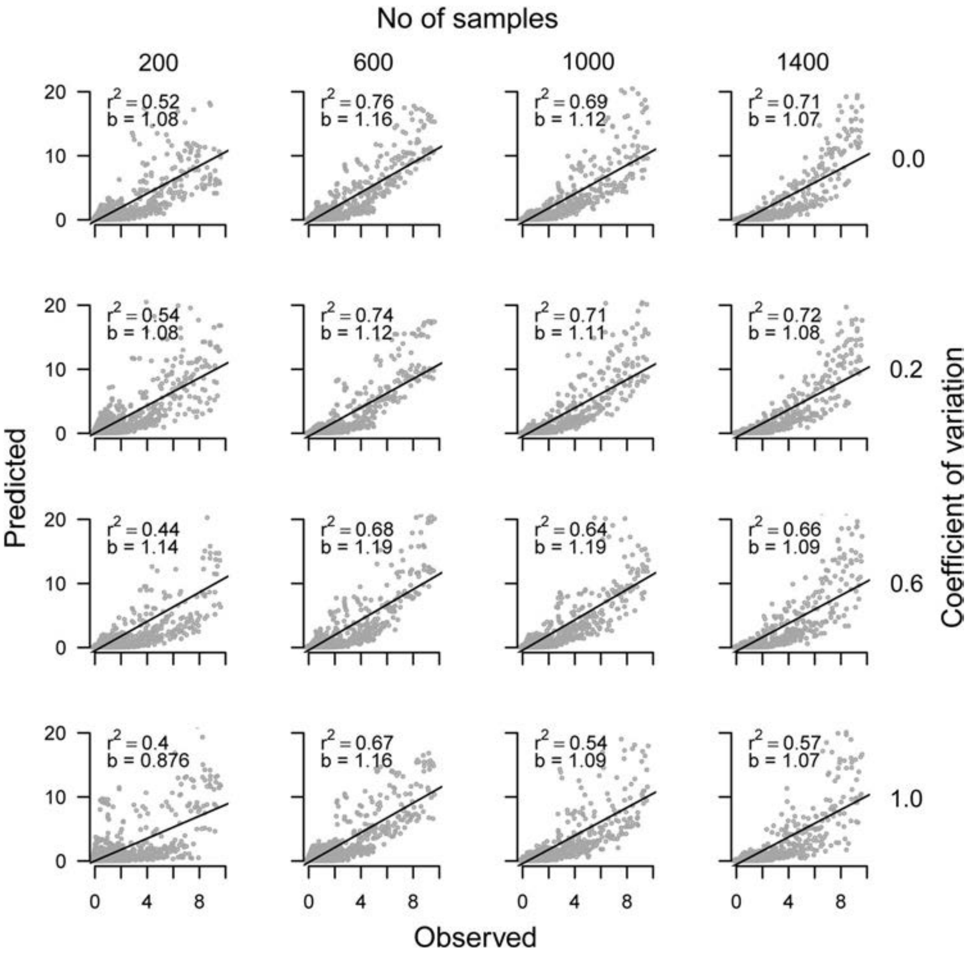

Figure 6. Predicted (*y*-axis) vs. observed (*x*-axis) biomasses of the key group in the spatial model. The number of sampled cells varies from 200 to 1400 (out of 1600) by column, and the sampling error varies with coefficient of variation from 0 to 1.0 by *rows*. The linear regressions, correlation coefficients and slopes of the regression lines are indicated on the plots.

estimated environmental preference functions based on sampling (stippled lines on Figure 4) while showing a close relationship to the ''true'' environmental preference functions (full lines on Figure 4) will differ, and therefore the predicted biomasses will differ as well.

Rather than illustrating the entire sampling state and space, we have extracted representative results as shown in Figure 6. We conclude from this (and from examining the entire space) that the parameters space with 38% or more (600+ samples) of the cells sampled and with CV of 0.2 or less does not lead to deterioration of the biomass predictions. The correlation for the 600 samples with CV of 0 indeed gave a higher correlation (r^2 = 0.76) than the full sampling scheme (r^2 = 0.73)—because of random effects in which 600 cells that were selected.

Although the observed/predicted relationship deteriorates with lower sampling effort and higher sampling error, there is still a reasonable good relationship even with low effort and high error. As an example, the case with 38% of the area sampled and a CV of 1.0 results in a correlation (r^2) of 0.67, not much below the best-case scenario.

All of the 48 runs (16 of which are shown in Figure 6) we made to evaluate impact of sample size and sampling error were biased with a trend toward overestimation of predicted biomasses at high biomasses and underestimation at low biomasses. Indicative of this is that the slopes of the linear regression lines in Figure 6 all are above 1. This is also clear from the spatial biomass maps for four representative cases as shown in Figure 7, which, however, also indicates that the habitat capacity model, while biased capture the overall trend in spatial distributions remarkably well. The species distributions based on sampling for the key group (Figure 7B–D) are very comparable to the ''true'' distribution (Figure 7A) even with low sampling effort (b, 200 cells) or high sampling error (d, CV = 1).

The ''true'' biomass distribution for the key group is derived as a function of the five environmental preference functions in combination with food web and fisheries effects. All of these factors have uncertainty and errors associated, and notably for the environmental preference functions we may never know exactly what factors cause a

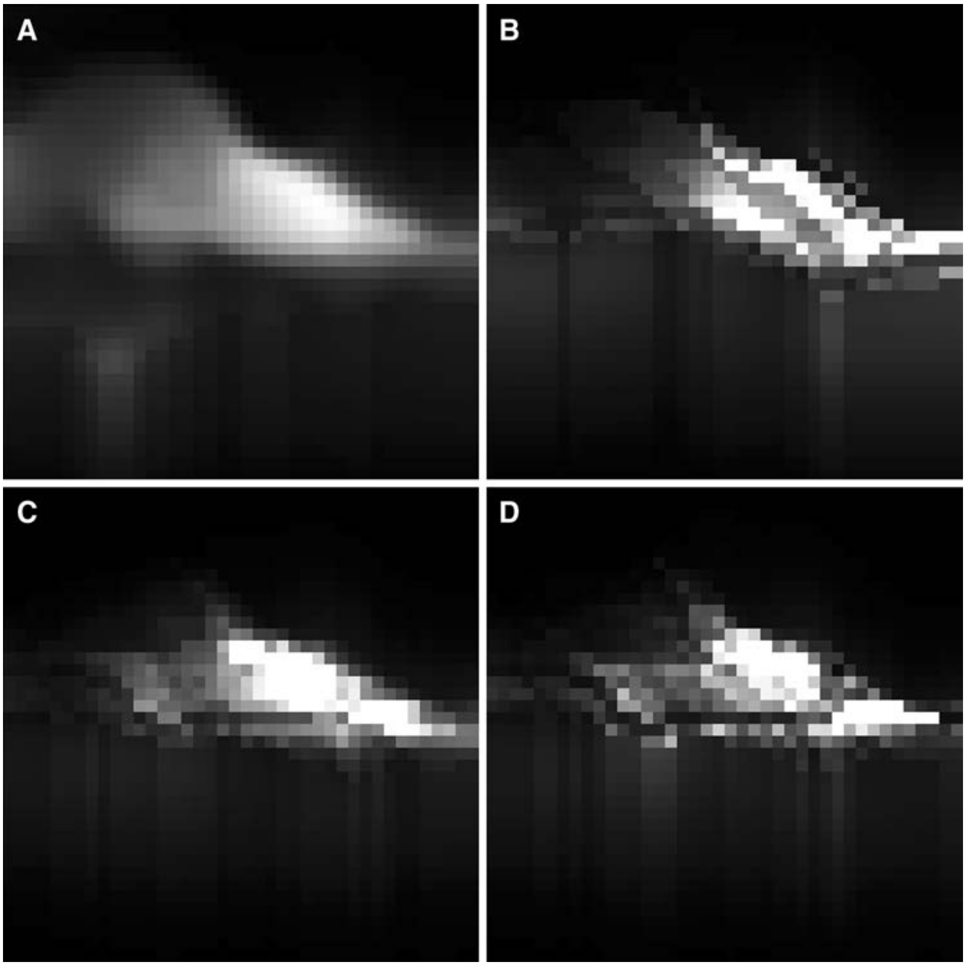

Figure 7. Biomass maps for the key group in the spatial model, white indicates higher biomass. **A** The original ''true'' biomass distribution for the key species, **B** sampling of 200 of 1600 cells with no sampling error, **C** sampling of all cells with no sampling error, and **D** sampling of all cells with sampling error equal to the coefficient of variation for the biomass.

species to occur where it does. We can often correlate the distribution with environmental factors, but these will be correlations only.

We can evaluate in the present case where we have perfect information about the ''true'' environmental preference functions and what the impact is of omitting some of these functions. As the simplest case, we did this by omitting each of the five environmental functions, one by one (Figure 8). We found the strongest effect by omitting temperature (Figure 8B), which resulted in the correlation between predicted and ''true'' biomass breaking completely down ($r^2 = 0.1$), for the other parameters the effect was much less strong (r^2 of 0.32 to 0.59). This strong impact of omitting the temperature impact is somewhat surprising given the close correlation between depth and temperature (Figure 5, $r = -0.95$). The explanation for this may be that although depth could largely substitute for temperature because of the spatial correlation, there were still parameter combinations with other factors that were not captured by depth.

It can be highlighted that the tendency toward overestimation in the predicted values is much less clear when an environmental function is omitted; we note from Figure 8 that the slope of most linear regressions is below unity.

DISCUSSION

The new habitat capacity model in *Ecospace* adds a new approach for modeling species distributions and evaluating habitat impact in the *EwE* modeling framework (Christensen and Walters 2004). There are already a number of studies in progress that use the new model and since this new capability bridges the gap between food web modeling and species distribution models, we argue that the habitat capacity model will provide a step forward for spatial food web modeling and ecological forecasting enabling the evaluation of cumulative drivers in food webs. To our knowledge, this is the first effort to bridge the gap between species distribution modeling and ecosystem food web modeling. The new approach is simple to understand,

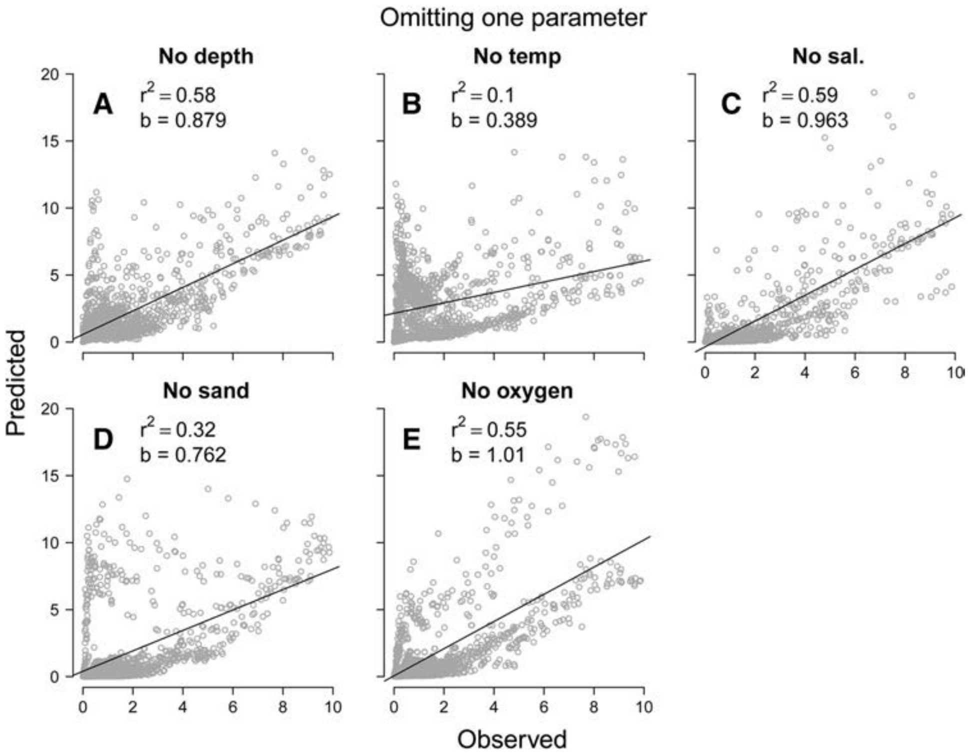

Figure 8. Effect of omitting one environmental preference function for the key group when running the spatial model. Model run are done with four out of five environmental functions with **A** depth being omitted, **B** temperature, **C** salinity, **D** proportion of cell that is sand bottom, and **E** dissolved oxygen. The linear regressions, correlation coefficients and slopes of the regression lines are indicated on the plots.

yet powerful when it comes to replicating species distributions, and it notably opens for evaluation how major habitat changes may be impacting marine resources and ecosystems. The potential uses spans wide, including evaluating impact of coastal zone development, marine protected areas, habitat impacting fishing gears, or climate change, where it, for instance, opens directly for evaluating the impact of future conditions for temperature, oxygen, and pH effects, all of which are typically simulated using biogeochemical models (Stock and others 2011).

Substantial progress has been made in the identification and quantification of multiple human threats and environmental drivers that impact marine diversity, habitats, and ecosystems (for example, Halpern and others 2008; Coll and others 2012). There is currently increasing knowledge on the identification, quantification, and distribution of these multiple stressors. However, the way these multiple stressors may interact and combine to impact productivity patterns of marine ecosystems is hardly known (Sala and others 2000). Multiple impacts may interact and their effects may accumulate, acting synergistically or antagonistically at different ecological levels, from species to community, and ecosystem levels, and may be mediated by food web effects. A comprehensive understanding of these impacts and their interactions is lacking, although it seems that synergistic effects are frequent (Folt and others 1999; Crain and others 2008; Darling and Côté 2008). Moreover, future changes of current human activities (such as climate change, or the invasion of new species), and the appearance and spread of new activities, will likely challenge our current understanding of cumulative impacts. To tackle some of these scientific challenges there is a growing need to use and develop novel methodologies of data integration, assimilation, and modeling at different scales, taking into account uncertainties in data and processes (Parravicini and others 2012). This study certainly contributes to this challenging endeavor.

There is an important caveat about using the habitat capacity model for cases with very fine spatial grids. Many organisms use one habitat type for resting or hiding, (for example, use coral reef as cover), then undertake horizontal movements into other habitats to forage, (for example, reef planktivores that move off the reef to forage). In such cases, a fine spatial grid that separates resting from foraging habitats may incorrectly represent such organisms as using only one or the other of the habitats that they depend upon. We have not yet found a good way to represent the possibility of spatially restricted utilization of adjacent habitat types by such organisms, because it is a fairly complex computational problem to allow organisms to forage in multiple spatial cells within defined distances of their ''normal'' or resting habitats.

The present study in addition to introducing and describing the new habitat capacity model also evaluated how the model can be parameterized through sampling. There is often little connection between these two entities, sampling and modeling, and the model can help bridging these two fields. From a modeling perspective, there is a clear need for understanding why species occur where they do, not just in connection with climate change studies, and we need empirical estimates for correlations with environmental parameters to bring our understanding of key ecological processes forward.

This study presents some improvements over the previous spatial-temporal model *Ecospace* (Walters and others 1999) by making it more flexible and open to external dynamic data. This new development bridges the gap between envelope environmental models and classic ecosystem food web models, progressing toward the ability to predict changes in marine ecosystems under scenarios of global change and explicitly taking food web direct and indirect interactions into account. This new capacity model is a core component of a global ocean modeling complex currently under development (Christensen and others unpublished). As a next step, we also intend to explore the functioning of the habitat capacity model when driven by spatial-temporal variations in environmental conditions as presented in Steenbeek and others (2013).

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