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

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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 Ecopath 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.

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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,
maritime 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). Geographical 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) modeling receives significant scientific interest in peer-reviewed literature (e.g., Travers et al., 2007; Libralato and Soliddoro, 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; Fouza 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).
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.
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. 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.

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

### 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 km², 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.

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**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.

**Fig. 6.** The Northern-Central (NC) Adriatic Sea study area. The light-gray area represents the spatial coverage of the ecological model available.
2.3.3. 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/m²/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 Ecopath 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. 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.)
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. 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.

**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.
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 (Zavattarelli 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; Mlinč 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-Peledić et al., 2001; Vrgoč 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-cast by the model was similar to that obtained from survey data (Zupanović 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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