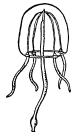


# Spatial modelling for marine resource management, with a focus on fish

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The state of the art in spatial modelling in physical and biological oceanography is reviewed in light of its relevance for marine resource management, based on discussions during a workshop in marine spatial modelling. The quality of the spatial models strongly depends on the assimilation of data. With the present level of investment in modelling and data acquisition, models can be used to obtain improved understanding of the dynamics of the ecosystems. An operational modelling approach to fisheries management will require an extensive increase in effort both with regard to data input and modelling ability. We discuss 5 different options for the use of spatial modelling in fisheries management.

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## BACKGROUND

The management of fishery resources in the North Atlantic is today based on catch statistics and data from acoustic surveys and trawl surveys. The data is typically analysed with area integrated, single species statistical calculation-tool models such as Virtual Population Analysis (VPA, Pope 1972) and prognoses are also being made with such models. These models can be used to find the historic abundance at age of a fish cohort given the observed harvest on the cohort and an assumed natural mortality rate. The current size of the cohort is then established by supplementing the VPA with landings and survey data. Multispecies VPA models that take into account predator-prey relations established through stomach sampling data have been developed (Gislason & Helgason 1985). Lately, more complex models have been attempted which allow more biological and environmental features to be implemented than in the VPA (Bogstad & al. 1997; Stefansson & Pálsson 1998; Frøysa & al. 2002). These latter types of models can include predation and migration of several target species, and represent influences from temperature on growth and maturation. Although these models aim at representing biological processes, there are no mechanistic formulations of the species interactions, and the spatial resolution is rather coarse relative to process variability.

In a report from a working group appointed by the Research Council of Norway (Anonymous 1998), the current methods for fishery resource assessment are discussed and several bottlenecks for improved stock size estimates are identified. In particular the importance of

quantifying and if possible reducing the uncertainties in the input data is emphasised. The report concludes that in a short-term perspective, the quickest improvements may come from smaller modifications and implementations of existing technology. In the longer-term perspective, it points at new technological prospects, open monitoring systems and ecosystem models for improved estimates of growth and abundance of fish stocks.

A possible way to approach fisheries assessment is through improved spatial representation of the biological processes. Hence the initiative to arrange the "Workshop on marine spatial modelling". The workshop was held in Bergen 6-8 March 2000 and gathered 59 scientists from 10 North Atlantic nations (<http://www.ifm.uib.no/msw>). Some of the presentations are printed in this issue; others are printed or will be printed elsewhere. The aim of this workshop was to discuss state of the art within marine spatial modelling and to recognise immediate and long-term research needs for utilising spatial modelling in the management of living marine resources. Based on the discussions during the workshop, we here give a short review of the state of the art in physical and biological spatial modelling, and provide recommendations for further actions for increased use of spatial models in marine resource management.

## STATE OF THE ART

### PHYSICAL MODELLING

All physical numerical ocean models try to solve one form or other of the same governing equations for oceanic motion. These equations are essentially Navier-



Stokes equations for a rotating earth and with buoyancy forces, the equation of continuity, conservation equations for salinity and temperature and an equation of state. The equations are thoroughly described in several text books in oceanography like Gill (1982) who traces the equations back to Leonhard Euler in 1755. Exact solutions of the full non-linear set of equations, initial and boundary conditions and variable topography have not been found. However, from simplified versions and for simplified conditions exact solutions have been derived, mainly during the last century, that have developed our understanding of oceanic motion considerably (Gill 1982).

To address the full set of equations, the variables are discretised on spatial grids covering the global ocean or some subset of it. Numerical ocean models estimate solutions to the physical variables at each point of such grids. The development of the first physical circulation model is often credited to Kirk Bryan at the Geophysical Fluid Dynamics Laboratory (GFDL) in the late 1960s. At the time the computers were only capable of addressing rather simple problems involving limited numbers of variables, and the number of people applying the model was also limited. Today the situation is very different. The progress in computer technology has made it feasible to address much more realistic problems. A number of numerical ocean models have been developed and there are numerous users of such models (Haidvogel & Beckmann 1999; Kantha & Clayson 2000a).

Although all these models are based on the same set of equations, and therefore might be expected to give similar results under similar conditions, the numerical results may differ widely (Lynch & Davies 1995). One reason is that the discretised forms of the governing equations may differ widely and new discretising methods continue to be developed. Another reason is limited computer power. To resolve the major length scales of the ocean, we need at least to resolve processes at the internal Rossby radius scale which is 5 to 10 km. It will require a horizontal grid size of less than 1 km to accurately describe phenomena at this scale. To cover the global ocean with such an horizontal mesh and at least 30 vertical layers is yet not feasible, and the model must therefore address smaller areas like the Skagerrak or Georges Bank. However, the quality of the interior solution will then be limited by the quality of the boundary conditions, which generally are poor. To account for sub-grid scale processes, one tries to parameterise the effects of these on the larger scales. Unfortunately there is at present no general consensus on how this should be done correctly and the model results may be very sensitive to the choice of sub-grid scale parameterisation (Kantha & Clayson 2000b).

Despite the above shortcomings, today's physical ocean models have proven to be useful tools in under-

standing oceanic processes. The creation of such models has also opened tremendous possibilities for interdisciplinary studies. They may be used to investigate pathways of tracers, chemicals, algae, or fish egg and larvae. They are at present coupled to a variety of biological models. The number of combinations of models and the number of possible applications are both virtually unlimited. Thus the prediction is that the use of physical ocean models will grow strongly in the years to come. Progress in computer technology, improvements in discretisation techniques and sub-grid scale parameterisations will be important to support the growing number of applications and to improve the quality of the model outputs.

#### BIOLOGICAL MODELS

Spatial modelling of the lower levels of the marine food chain goes back to Fleming (1939), Sverdrup & al. (1942) and Riley (1946). In recent years, numerical model systems that include physical variables, nutrients, phytoplankton and zooplankton have been developed for several marine ecosystems (Hofmann & Ambler 1988; Fasham & al. 1990; Baretta & al. 1995; Skogen & al. 1995; Skogen 1999; Broström & Drange 2000), and the state of the art is documented in a series of reviews and text books (Steele 1974; Kremer & Nixon 1978; Evans & Fasham 1993; Anderson & al. 1993; Hofmann & Lascara 1998; Carlotti & al. 2000). Generally, the success of these models is highest at the lower levels of the food chain, where physical forces dominate abundance and spatial distribution. With short generation times, population sizes of microbial organisms will be adjusted towards the ever fluctuating carrying capacities over short time scales. And with low individual locomotory ability, local population densities may be understood from local conditions and physical transportation. Therefore, element-based biogeochemical models have had high success at these trophic levels. However, already for long-lived zooplankton, this modelling approach has had poorer predictive ability (Salvanes 2001, this issue). As diel and seasonal migration, energy allocation, and life cycle of mesozooplankton are evolved by natural selection, fitness-based behavioural models have been used in spatial models in recent years (Aksnes & Giske 1990; Eiane & al. 1998; Fiksen & Carlotti 1998; Steele & Henderson 1998).

In the pelagic water column there may be hundreds of species of phytoplankton, and a similar number of zooplankton taxa. It is not possible to represent all these units in a model. Most models study only one species, and ecosystem models commonly group ecologically similar species into functional categories as diatoms and flagellates, or mesozooplankton and macrozooplankton (Carlotti & al. 2000). The stability and dynamics of ma-



rine pelagic food webs is generally poorly understood (Steele 1974; Ulanowicz & Platt 1985), and it may be hard to predict whether an extra nutrient supply is likely to produce food for a fish larva or a jellyfish.

Spatial modelling of fish has a more recent history, especially models with individually varying fish behaviour. Models of dispersing fish larvae, where migration is driven by physical processes (Bartsch & al. 1989; Hinckley & al. 1996), have been present long before models of migration of adult and juvenile fish (Dagorn & al. 1995, 1997; Fiksen & al. 1995; Huse & Giske 1998; Kirby & al. 2000). While fish larvae spatial modelling has been developed as an extension of physical modelling (Werner & al. 1997) and individual-based modelling (Heath & Gallego 1997), spatial modelling of adults have also been relying on evolutionary models of animal behaviour (Tyler & Rose 1994; Giske & al. 1998). Still, model ability of representing drift of eggs and larvae depends largely on improved physical representations, while developments in habitat selection models of animals with high locomotory ability depend on improved representation of sensing and preferences (Giske & al. 1998).

#### INPUT DATA AND DATA ASSIMILATION

As discussed for physical modelling, the availability and quality of marine spatial data is severely restricting the quality of the marine spatial modelling. This applies to biological data even more than to physical. However, our ability to collect data has increased tremendously with remote sensing and buoys. GIS-databases (Isaak & Hubert 1997; Kracker 1999) allow easily retrieval of spatially structured data in dynamic models and statistical analyses (this issue: Harbitz & Lindstrøm 2001; Meester & al. 2001; Souissi & al. 2001; Wieland & Rivoirard 2001). Vessels, remote sensing (Petit 1991; Cracknell 1999; Kracker 1999), buoys (Ji & Leetmaa 1997; Johnsen & Sakshaug 2000) and other technological developments may now provide real time input data to the modelling systems (Josse & al. 1998, 1999; Dagorn & al. 2000), and there has been major progress in data assimilation in large, spatially distributed systems (Wunsch 1996). In this issue, Grønnevik & Evensen (2001) discuss data assimilation in fisheries assessment. Still, data availability restricts hindcast studies, and nowcast modelling is presently possible only for specifically designed situations. Even the meteorological nowcast and forecast modelling of waves and tides use statistical data for the marine environment and real-time assimilated data for the atmosphere (Daley 1991). To obtain ability to model biological marine spatial processes in nowcast or forecast, an observing system in space and time is required. As for physical modelling, the needed resolution of the monitoring of the phenomena

depends on the spatial and temporal scales of the variation. Fish stocks vary slowly with time, compared to physical factors. But the spatial resolution needed is generally much smaller than for physical factors, implying a far denser observing system for biological variables. Still, the system depends on the goal: to monitor the slow decline in abundance of 4 year old herring, vessel surveys a few times each year is probably sufficient, while to monitor the survival of herring larvae will require daily observations on a fine spatial grid. Further, any rich trophodynamics model will quickly go astray without data correction. However, the data requirement for theoretical modelling is far lower, although the reliability of the output also here depends on the data set available.

#### TOWARDS COUPLED PHYSICAL-BIOLOGICAL MODEL SYSTEMS

Coupling of models is not always straightforward. The main reason nutrient-phytoplankton-zooplankton models and models of drifting fish larvae were developed at such an early stage, is that they are readily coupled to physical models (this issue: Werner & al. 2001). The earliest transportation models of eggs and larvae (Bartsch & al. 1989) considered them as physical particles whose motion was fully determined by physical forces. Likewise, biogeochemical models assume that the biological components can be described by 1 or 2 limiting elements, e.g. nitrogen or carbon, and that the biological dynamics depend on the concentration of these elements (this issue: Allen & al. 2001). This approach works well at lower trophic levels, and for organisms where physical forces determine their spatial position. In dynamic models of populations of mobile organisms, the intention of the organism must also be considered. Therefore, models of zooplankton and fish behaviour and life cycle often will be solved as an optimization. In Stochastic Dynamic Programming (SDP, Mangel & Clark 1988; Clark & Mangel 2000), the behavioural trait that maximises evolutionary fitness in the given environment will be found. However, this method requires that the environment is specified before the optimal policy can be found. Such models, although often ideal for studying marine populations, are unsuited for coupling with physical models in nowcasting or forecasting. They have, however, been used to re-analyse previous events (e.g. Fiksen & al. 1995; Kirby & al. 2000). Recently, new methods of adaptive behaviour, based on artificial life methods, have been developed (Dagorn & al. 1995, 1997; Huse & Giske 1998; Huse & al. 1999), and two contributions are found in this issue (Eiane & Parisi 2001; Huse 2001). These methods allow coupling with physical models for nowcasting and forecasting while still maintaining adaptive behaviour in the modelled fish or zooplankton populations. Examples of model integration approaches are given by Meester & al. (2001) in this issue.



A possible 4-D (space and time) monitoring system will also require powerful computers. Over the last 20 years the peak performance of computers has on average improved with a factor of 10 in 3 years. Computers are now approaching a power that could make it feasible to set up a 4-D ecosystem model with focus on fish, that resolves the major time and length scales.

#### RECOMMENDATIONS

Marine spatial modelling can be of use to management in two different ways: 1) for analysis of previous events and system dynamics, and 2) for simulation of the present and the future. As a method of analysis, spatial modelling can be a tool for understanding dynamics and interactions in the ecosystem. This is the traditional use of marine spatial modelling, and can be used to evaluate effects of management options. The new availability of data from buoys, satellites, and vessels allows for much more precise and extensive analyses (e.g. Turk & al. 2001), and the new methods for individual-based adaptive modelling allow inclusion of fish and zooplankton in nowcasting (Bowen & al. 1995) and perhaps also in forecasting. However, there is not a simple route towards a management of marine living resources based on spatial models and data assimilation, and we will therefore point at some options:

1. *Action: Maintain today's level of effort.* At today's level of investment in modelling and data acquisition, marine spatial modelling can be used to obtain an improved understanding of physical and biological processes, and of interactions and dynamics in the ecosystem. Such modelling is of benefit to resource management by clarifying consequences of decisions, and of simulating natural variability. The current developments in state of the art in physical and biological modelling will continue to yield improved spatial models. However, it is uncertain whether results from such modelling may become of immediate use for short-term management decisions.
2. *Action: Develop institutionalised GIS databases.* GIS databases are still under-utilised as a meeting point between model results and field studies. Both modellers and field scientists can benefit from a much more systematic storage and access to spatial data. These databases should be run by institutions close to the management decisions, but universities should also be strongly encouraged to deliver data. Funding agencies should see to it that publicly funded data are made publicly available.

3. *Action: Extend operational physical oceanography.* Operational oceanography, in the sense of active assimilation of field observation in nowcast and forecast modelling, as now used in e.g. marine weather forecasts and harmful algal blooms, can be strongly improved by further development of models and observing systems. However, to expand operational oceanography into fish and zooplankton, will require both new modelling paradigms and new types of observation platforms.
4. *Action: Develop 4-D operational ecosystem models.* A spatial modelling concept for management of fisheries resources without extensive data input is not realistic. A 4-D monitoring system for simulation of the present and the future fish stock sizes is necessary, and will require an observing system that resolves the major space and time scales for the fish stocks. Statistical properties of the basic input data must be known. To achieve this, substantial investments in new observing technology like buoys and satellites will be necessary. Fundamental improvements in the modelling methodology will also be needed, particularly of trophic interactions and animal behaviour. Before the development of 4-D monitoring systems for estimation of fish stock sizes, one should perform cost-benefit-analyses for different levels of precision in estimates.
5. *Action: Develop a coarse resolution observation grid.* An observing system with a coarse resolution will have great scientific value for theoretical modelling, and will allow modelling of problems and situations that without such data only can be sketched. With a gradual refinement of the grid, the number of management situations for which operational oceanography can be used, will increase.

Actions 2, 3, and 5 will require a gradual increase of today's effort. This higher effort will give improved understanding, which obviously will be valuable for long-term management strategy decisions. Several examples are found in this issue (Meester & al. 2001; Souissi & al. 2001). However, is it not given that gradual increases along the lines of these actions ever will improve short-term management decisions. Action 4 will require a substantial increase in effort. If the major space and time scales are resolved, then action 4 will lead to spatial models of immediate value for management.

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## REFERENCES

- Aksnes DL, Giske J. 1990. Habitat profitability in pelagic environments. *Marine Ecology Progress Series* 64:209-215.
- Allen JJ, Blackford J, Holt J, Proctor R, Ashworth M, Siddorn J. 2001. A highly spatially resolved ecosystem model for the North West European Continental Shelf. *Sarsia* 86:423-440.
- Anderson TR, Andersen V, Fransz HG, Frost BW, Klepper O, Rassoulzadegan F, Wulff F. 1993. Modelling zooplankton. In: Evans GT, Fasham JR, editors. *Towards a model of ocean biogeochemical processes*. p 177-192. NATO ASI Series, Vol. 10. 350 p.
- Anonymous 1998. Methods for fishery resources assessment – status and potentials of marine resource and environment monitoring. <http://nrcwg.imr.no>
- Baretta JW, Ebenhov W, Ruardij P. 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. *Netherlands Journal of Sea Research* 33:233-246.
- Bartsch J, Brander K, Heath M, Munk P, Richardson K, Svendsen E. 1989. Modelling the advection of herring larvae in the North Sea. *Nature* 340:632-636.
- Bogstad B, Hauge KH, Ulltang Ø. 1997. A multispecies model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fisheries Science* 22:317-342.
- Bowen AJ, Griffin DA, Hazen DG, Matheson SA, Thompson KR. 1995. Shipboard nowcasting of shelf circulation. *Continental Shelf Research* 15:115-128.
- Broström G, Drange H. 2000. On the mathematical formulation and parameter estimation of the Norwegian Sea plankton system. *Sarsia* 85:211-225.
- Carlotti F, Giske J, Werner F. 2000. Modeling zooplankton dynamics. In: Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M, editors. *ICES zooplankton methodology manual*. p 571-667. Academic Press.
- Clark CW, Mangel M. 2000. *Dynamic state variable models in ecology: methods and applications*. New York: Oxford University Press.
- Cracknell AP. 1999. Remote sensing techniques in estuaries and coastal zones – an update. *International Journal of Remote Sensing* 20:485-496.
- Dagorn L, Bach P, Josse E. 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* 136:361-371.
- Dagorn L, Petit M, Stretta JM, Bernardet X, Ramos AG. 1995. Towards a synthetic ecoethology of tropical tunas. *Scientia Marina* 59:335-346.
- Dagorn L, Petit M, Stretta JM. 1997. Simulation of large-scale tropical tuna movements in relation with daily remote sensing data: the artificial life approach. *Biosystems* 44:167-180.
- Daley R. 1991. *Atmospheric data analysis*. Cambridge: Cambridge University Press.
- Eiane K, Aksnes DL, Ohman MD. 1998. Advection and zooplankton fitness. *Sarsia* 83:87-93.
- Eiane K, Parisi D. 2001. Towards a robust concept for modelling zooplankton migration. *Sarsia* 86:465-475.
- Evans GT, Fasham MJR. 1993. *Towards a model of ocean biogeochemical processes*. Springer Verlag. 350 p.
- Fasham M, Ducklow H, McKelvie S. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *Journal of Marine Research* 48:591-639.
- Fiksen Ø, Carlotti F. 1998. A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia* 83:129-147.
- Fiksen Ø, Giske J, Slagstad D. 1995. A spatially explicit fitness-based model of capelin migrations in the Barents Sea. *Fisheries Oceanography* 4:193-208.
- Fleming RH. 1939. The control of diatom populations by grazing. *J. Cons. perm. explor. Mer.* 14:210-227.
- Frøysa KG, Bogstad B, Skagen DW. 2002. Fleksibest - an age-length structured fish stock assessment model. *Fisheries Research* 55:87-101.
- Gill AE. 1982. *Atmosphere-Ocean Dynamics*. Academic Press. International Geophysics Series, Vol. 30, 662 p.
- Giske J, Huse G, Fiksen Ø. 1998. Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries* 8:51-91.
- Gislason H, Helgason T. 1985. Species interaction in assessment of fish stocks with special application in the North Sea. *Dana* 51:1-44.
- Grønnevik R, Evensen G. 2001. Application of ensemble-based techniques in fish stock assessment. *Sarsia* 86:517-526.
- Haidvogel DB, Beckmann A. 1999. *Numerical ocean circulation modeling*. Imperial College Press. Series on environmental science and management, Vol. 2. 318 p.
- Harbitz A, Lindstrøm U. 2001. Stochastic spatial analysis of marine resources with application to minke whales (*Balaenoptera acutorosatrata*) foraging: A synoptic case study from the southern Barents Sea. *Sarsia* 86:485-501.
- Heath M, Gallego A. 1997. From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. *Journal of Fish Biology* 51A:1-29.
- Hinckley S, Herman AJ, Megrey BA. 1996. Development of a spatially explicit, individual-based model of marine fish early life history. *Marine Ecology Progress Series* 136:47-68.
- Hofmann EE, Ambler JW. 1988. Plankton dynamics on the outer southeastern U.S. continental shelf. Part II: A time-dependent biological model. *Journal of Marine Research* 46:883-917.
- Hofmann EE, Lascara C. 1998. Overview of interdisciplinary modeling for marine ecosystems. In: Brink KH, Robinson AR, editors. *The Sea*, Volume 10, Chapter 19. p 507-540. John Wiley and Sons. 604 p.
- Huse G, Giske J. 1998. Ecology in the sea of Pentium: An individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research* 37:163-178.
- Huse G, Strand E, Giske J. 1999. Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evolutionary Ecology* 13:469-483.
- Huse G. 2001. Modelling habitat choice in fish using adapted random walk. *Sarsia* 86:477-483.



- Isaak DJ, Hubert WA. 1997. Integrating new technologies into fisheries science: The application of geographic information systems. *Fisheries* 22:6-10.
- Ji M, Leetmaa A. 1997. Impact of data assimilation on ocean initialization and El Nino prediction. *Monthly Weather Review* 125:742-753.
- Johnsen G, Sakshaug E. 2000. Monitoring of harmful algal blooms along the Norwegian coast using bio-optical methods. *South African Journal of marine Science* 22:309-321.
- Josse E, Bach P, Dagorn L. 1998. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia* 372:61-69
- Josse E, Dagorn L, Bertrand A. 2000. Typology and behaviour of tuna aggregations around fish aggregating devices from acoustic surveys in French Polynesia. *Aquatic Living Resources* 13:183-192
- Kantha LH, Clayson CA. 2000a. *Numerical models of oceans and oceanic processes*. Academic Press. International Geophysics Series, Vol. 66. 940 p.
- Kantha LH, Clayson CA. 2000b. *Small scale processes in geophysical fluid flow*. Academic Press. International Geophysics Series, Vol. 67. 888 p.
- Kirby DS, Fiksen Ø, Hart PJB. 2000. A dynamic optimisation model for the behaviour of tunas at ocean fronts. *Fisheries Oceanography* 9:328-342.
- Kracker LM. 1999. The geography of fish: The use of remote sensing and spatial analysis tools in fisheries research. *Professional Geographer* 51:440-450.
- Kremer JN, Nixon SW. 1978. *A coastal marine ecosystem. Simulations and analysis*. Ecological studies 24. Berlin: Springer-Verlag.
- Lynch DR, Davies AM, editors. 1995. *Quantitative skill assessment for coastal ocean models*. Washington DC: American Geophysical Union. 510 p.
- Mangel M, Clark CW. 1988. *Dynamic modeling in behavioral ecology*. Princeton University Press. 308 p.
- Meester GA, Ault JS, Smith SG, Mehrotra A. 2001. An integrated simulation modeling and operations research approach to spatial management decision making. *Sarsia* 86:543-558.
- Petit M. 1991. Aerospatial remote sensing as catalyst of an operational marine fishery (halieutic) science. *International Journal of Remote Sensing* 12:713-724.
- Pope JG. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *Research Bulletin of the International Commission for North West Atlantic Fisheries* 9:65-74
- Riley GA. 1946. Factors controlling phytoplankton populations on George's Bank. *Journal of marine Research* 6:54-73.
- Salvanes AGV. 2001. Review of ecosystem models of fjords; new insights of relevance to fisheries management. *Sarsia* 86:441-463.
- Skogen MD, Svendsen E, Berntsen J, Aksnes D, Ulvestad KB. 1995. Modelling the primary production in the North Sea using a coupled 3-dimensional physical-chemical-biological ocean model. *Estuarine Coastal and Shelf Science* 41:545-565.
- Skogen MD. 1999. A biophysical model applied to the Benguela upwelling system. *South African Journal of marine Science* 21:235-249.
- Souissi S, Ibanez F, Ben Hamadou R, Boucher J, Cathelineau AC, Blanchard F, Poulard JC. 2001. A new multivariate mapping method for studying species assemblages and their habitats: example using bottom trawl surveys in the Bay of Biscay (France). *Sarsia* 86:527-542.
- Steele J. 1974. *The structure of marine ecosystem*. Cambridge, MA: Harvard University Press. 128 p.
- Steele JH, Henderson EW. 1998. Vertical migration of copepods. *Journal of Plankton Research* 20:787-799.
- Stefansson G, Palsson OK. 1998. A framework for modelling of Arcto-boreal systems. *Reviews in Fish Biology and Fisheries* 8:101-104.
- Sverdrup HU, Johnson MW, Fleming RH. 1942. *The oceans*. New York: Prentice-Hall. 1087 p.
- Turk D, McPhaden MJ, Busalacchi AJ, Lewis MR. 2001. Remotely sensed biological production in the equatorial Pacific. *Science* 293:471-474.
- Tyler JA, Rose KA. 1994. Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries* 4:91-123.
- Ulanowicz RE, Platt T. 1985. Ecosystem theory for biological oceanography. *Canadian Bulletin of Fisheries and Aquatic Sciences* 213. 260 p.
- Werner FE, Quinlan JA, Blanton BO, Luettich RA Jr. 1997. The role of hydrodynamics in explaining variability in fish populations. *Journal of Sea Research* 37:195-212.
- Werner FE, Quinlan JA, Lough RG, Lynch DR. 2001. Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. *Sarsia* 86:411-421.
- Wieland K, Rivoirard J. 2001. A geostatistical analysis of IBTS data for age 2 North Sea haddock (*Melanogrammus aeglefinus*) considering daylight effects. *Sarsia* 86:503-516.
- Wunsch, C. 1996. *The ocean circulation inverse problem*. Cambridge University Press, Cambridge.

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