



THEME SECTION

# Advances in modelling physical–biological interactions in fish early life history

*Idea and coordination:* Alejandro Gallego\*, Elizabeth W. North, Pierre Petitgas, Howard I. Browman

CONTENTS

**Gallego A, North EW, Petitgas P**

Introduction: status and future of modelling physical–biological interactions during the early life of fishes ..... 121–126

**Miller TJ**

Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations ..... 127–138

**Osborn T**

Applicability of turbulence measurement technology to small-scale plankton studies ..... 139–143

**Thygesen UH, Ådlandsvik B**

Simulating vertical turbulent dispersal with finite volumes and binned random walks ..... 145–153

**Mariani P, MacKenzie BR, Visser AW, Botte V**

Individual-based simulations of larval fish feeding in turbulent environments ..... 155–169

**Peck MA, Daewel U**

Physiologically based limits to food consumption, and individual-based modeling of foraging and growth of larval fishes ..... 171–183

**Leis JM**

Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography ..... 185–193

**Fiksen Ø, Jørgensen C, Kristiansen T, Vikebø F, Huse G**

Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal ..... 195–205

**Vikebø F, Jørgensen C, Kristiansen T, Fiksen Ø**

Drift, growth and survival of larval Northeast Atlantic cod with simple rules of behaviour ..... 207–219

**Christensen A, Daewel U, Jensen H, Mosegaard H, St. John M, Schrum C**

Hydrodynamic backtracking of fish larvae by individual-based modelling ..... 221–232

**Sentchev A, Korotenko K**

Modelling distribution of flounder larvae in the eastern English Channel: sensitivity to physical forcing and biological behaviour ..... 233–245

**Lett C, Veitch J, van der Lingen CD, Hutchings L**

Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems ..... 247–259

**Huret M, Runge JA, Chen C, Cowles G, Xu Q, Pringle JM**

Dispersal modeling of fish early life stages: sensitivity with application to Atlantic cod in the western Gulf of Maine ..... 261–274

**Brickman D, Marteinsdottir G, Taylor L**

Formulation and application of an efficient optimized biophysical model ..... 275–284

**Paris CB, Chérubin LM, Cowen RK**

Surfing, spinning, or diving from reef to reef: effects on population connectivity ..... 285–300

**Hannah CG**

Future directions in modeling physical–biological interactions ..... 301–306

Resale or republication not permitted without written consent of the publisher

\*Email: a.gallego@marlab.ac.uk

# Introduction: status and future of modelling physical–biological interactions during the early life of fishes

Alejandro Gallego<sup>1,\*</sup>, Elizabeth W. North<sup>2</sup>, Pierre Petitgas<sup>3</sup>

<sup>1</sup>FRS Marine Laboratory, PO Box 101, Victoria Road, Aberdeen AB11 9DB, UK

<sup>2</sup>University of Maryland, Center for Environmental Science, Horn Point Laboratory, Cambridge, Maryland 21613, USA

<sup>3</sup>IFREMER, Centre de Nantes, rue de l'Île d'Yeu, BP 21105, 44311 Nantes Cedex 03, France

**ABSTRACT:** Modelling physical–biological interactions in the early life of fish is becoming an integral part of theoretical and applied marine ecology. A workshop on 'Advancements in modelling physical–biological interactions in fish early-life history' (WKAMF) was held in April 2006 to review recent developments and identify future research directions. Here we provide an overview of the information presented at WKAMF (some of which is published in this Theme Section), discussions that took place at the workshop, and the authors' perspectives as workshop co-Chairs. The major themes identified at the workshop were the need for enhanced model validation and sensitivity methods and improved understanding of physical and biological processes. Using the appropriate level of model complexity required for each model application is important; developing quantitative consistency of model results with good quality observational data is critical. In addition, improving our prediction of physical processes, such as circulation patterns and turbulence, will advance our knowledge of fish early life, as will a better understanding of biological processes like mortality, behaviour, and energetics. The latter stage-dependent, often species-specific, processes pose particular challenges, although technical advances in field and laboratory observations are likely to result in considerable progress in the near future. Finally, there is a clear requirement for interdisciplinary collaboration between modellers, field scientists and laboratory scientists. Studies receiving input from a wide range of disciplines will increase our understanding of fish early-life ecology and prediction of recruitment to fish populations.

**KEY WORDS:** Biophysical modelling · Fish · Eggs · Larvae · Individual-based methods · Workshop

*Resale or republication not permitted without written consent of the publisher*

Modelling physical–biological interactions in the early life history of fish has expanded considerably in the last decade (Miller 2007, this Theme Section [TS]). It is increasingly becoming an integral tool for understanding the processes that affect interannual variability in fish recruitment (Werner et al. 1997) and the degree of connectivity between fish sub-populations (Cowen et al. 2006). These themes are crucially important in the global context of anthropogenic and climatic pressure on marine ecosystems in general and on fished species in particular.

The International Council for the Exploration of the Sea (ICES) Working Group on Modelling Physical–Biological Interactions (WGPBI) called for a review of recent developments in the field of modelling fish early life history, in order to evaluate the current state-of-the-art, compile a manual of 'best practices' and identify future research directions. In response, the workshop on 'Advancements in modelling physical–biological inter-

actions in fish early-life history' (WKAMF), was held in Nantes, France, in April 2006 under the auspices of WGPBI and the ICES Working Group on Recruitment Processes (WGRP). Papers in this TS are based on research presented at WKAMF. This introduction to the TS provides an overview of work presented at WKAMF, a synthesis of open discussions that took place at the workshop, and the authors' perspectives as workshop co-Chairs. Products of the workshop can be found at <http://northweb.hpl.umces.edu/wkamf/home.htm>.

The WKAMF workshop was focused on the main aspects of biophysical models of fish early life history, and addressed numerical techniques, validation issues, and case studies. It was organized around 7 core information sessions, from eggs to juveniles and from smaller to larger scales, with discussion and consensus-building sessions. This introduction follows the thematic structure of the workshop core information sessions.

\*Email: a.gallego@marlab.ac.uk

**Initial conditions: egg production, spawning location/time.** The level of detail required for initial conditions depends upon the objectives of the model. Models are often used in a heuristic way, i.e. to increase our understanding of complex processes, or in a predictive role. Even beyond this general classification, specific objectives (e.g. predicting recruitment vs. identifying population connectivity) will have a major influence on the required level of complexity in initial conditions. For example, particles can be distributed uniformly over wide spatial and temporal scales to investigate whether hydrographic conditions prevent transport between ecosystems (e.g. Lett et al. 2007, this TS). Alternatively, a model that predicts spatial and temporal patterns in the recruitment process (i.e. how the recruits are distributed in time and space) requires input in the form of spatially and temporally resolved egg production (e.g. Heath & Gallego 1998).

Numerical techniques are available that can help fill in gaps in understanding of spatial and temporal patterns in spawning. Sensitivity analyses can be used to estimate which characteristics of spawning (e.g. patchy vs. uniform, higher/lower frequency, spawning location/time, depth) are important for the model application. Pattern-oriented modelling is a useful strategy for identifying the patterns in observational data that can be used to determine model complexity and optimize model structure (Mullon et al. 2002, Grimm & Railsback 2005, Grimm et al. 2005). A promising technique to derive initial conditions is backtracking by individual-based modelling (Batchelder 2006, Christensen et al. 2007, this TS) which, by moving particles 'backwards' through a flowfield, can be applied to estimate the original distribution of fish eggs or early larvae from observations of the distribution of later stages. Although these techniques are useful, they supplement, not supplant, basic biological information on spawning processes that are required to predict recruitment. For many fish species, information is lacking on the factors that control the spatial and temporal patterns in spawning, including the potentially important effects of adult characteristics (e.g. maternal effects; Marteinsdottir & Steinarsson 1998).

**Small-scale processes (turbulence, feeding success).** The effect of turbulence on larval fish feeding and growth has been the object of considerable modelling and experimental effort since the pioneering work of Rothschild & Osborn (1988). However, *in situ* measurements of kinetic energy do not seem to fit turbulence theory in coastal environments (Osborn 2007, this TS), where many larval fish live. On the shelf, dissipation appears to be anisotropic, resulting in higher measured dissipation than predicted by isotropic theory. A better understanding of basic turbulent processes is required, as are measurements of turbulence relevant

to larval fish at the scales of predator-prey interactions (i.e. from 1 mm to 1 m) instead of averaging turbulent dissipation over depths  $\geq 1$  m.

Observational data needed to parameterize predator escape and prey encounter, capture, and feeding processes at scales relevant to larval fish are scarce (e.g. Browman 1996, Skajaa et al. 2004, Skajaa & Browman *in press*). The influence of turbulence on feeding success is sensitive to the size and shape of the predator's perceptual field for prey (Galbraith et al. 2004, Mariani et al. 2007, this TS). Therefore, detailed species-specific observations (in the laboratory or *in situ*) of the feeding process are critical for improving and validating this component of biophysical models of larval fish. New observational techniques (e.g. Osborn 2007) show considerable promise in the laboratory and in the field; these are labour-intensive and rely on new technologies that are often expensive, but the information gained may be quite useful depending on the objectives of the model.

**Mesoscale transport processes: physics and behaviour.** Three-dimensional hydrodynamic models are increasingly being used as the basis for modelling fish early life history and, consequently, a well-validated hydrodynamic model is a fundamental requirement. The horizontal resolution of hydrodynamic models can influence predicted fish egg and larval trajectories. As a rule of thumb, the model grid size should be fine enough to capture the appropriate horizontal mixing processes (e.g. smaller than the internal Rossby radius; Hinrichsen et al. 2002).

Development of particle-tracking techniques and parameter optimization frameworks is improving the efficiency of individual based models (IBMs) and their integration into life cycle models. For example, although the majority of biophysical models are Lagrangian IBMs (Miller 2007), a computationally efficient compromise between Eulerian and Lagrangian models can be achieved by using a 'biased binned random walk', which does not track the exact vertical position of the particles but instead the layer in which they reside (Thygesen & Ådlandsvik 2007, this TS). In addition, a probability density function (PDF) can be used to condense the results of tens of thousands of particle trajectories and integrate tFhem into an optimization framework that estimates biological parameters, including larval mortality and growth (Brickman et al. 2007, this TS). Finally, the interaction between environmental variability and population change over decades can be simulated with Lagrangian trajectories coupled to evolutionary algorithms that include adaptive behaviour and fitness characteristics that can be passed on to subsequent generations (Huse 2005).

The need for parameterization of sub-grid scale mixing processes in particle tracking models (i.e. pro-

cesses that occur on scales smaller than the grid size of the hydrodynamic model) is now increasingly recognized (Hunter et al. 1993, Visser 1997, North et al. 2006, Christensen et al. 2007); however, important differences in parameterization remain, depending on the characteristics of different physical models and individual applications. Some models are implemented with only vertical sub-grid scale processes (e.g. Huret et al. 2007, this TS), some with only horizontal processes (e.g. Brickman et al. 2007), and others include both vertical and horizontal parameterizations (e.g. Paris et al. 2007, Sentchev & Korotenko 2007; both in this TS). A systematic assessment of the influence of these processes on model predictions, and guidelines for their appropriate use, is needed.

Larval vertical swimming behaviour can critically influence transport (e.g. Fiksen et al. 2007, Vikebø et al. 2007; both in this TS). Therefore, biophysical models should incorporate at least vertical movements instead of assuming that simulated larvae are passive (inanimate) particles. Horizontal orientation, and directed horizontal swimming, are greater unknowns as most models assume passive drift in the horizontal plane. Although *in situ* observations of tropical coral reef fish larvae demonstrate that they can be strong, directed (i.e. non-random) swimmers (Leis 2007, this TS), considerable differences in swimming ability exist between these and temperate fish larvae. Moreover, horizontal orientation of temperate fish larvae has not been sufficiently studied.

It is important to identify the internal (e.g. physiological) and external (environmental) drivers that control the behaviour of the early life stages of fish. Perspectives derived from behavioural ecology can enhance our understanding of fish early life and help identify processes that emerge from the interplay of physiological mechanisms and fitness. For example, realistic patterns can emerge from models that incorporate tradeoffs between growth and survival (Fiksen et al. 2007). Larval behaviour could influence growth as well as mortality by, for instance, influencing vertical position, which in turn affects light-dependent feeding success and predation risk (Fiksen et al. 2007, Vikebø et al. 2007). Given the potential for transport patterns to vary with depth when the flow is not vertically homogeneous, behaviour can also link the biological processes of growth and mortality to physical transport processes.

**Biological processes: growth and mortality.** Survival of fish throughout the early life stages is the outcome of a trade-off between growth and mortality. Some modelling studies have focused on growth processes, applying a simple size-dependent mortality function. Others have concentrated on mortality, especially that resulting from predation.

Knowledge of a hierarchy of factors is required to parameterize the growth and development of fish early-life stages. Although temperature and body size are often identified as primary factors (e.g. Heath & Gallego 1997, 1998), some models incorporate prey concentration (Bartsch & Coombs 2004) and increasingly complex mechanistic sub-models of feeding processes and bioenergetics (e.g. Werner et al. 1996, Hinckley et al. 2001). Many of these models are parameter-rich and/or empirically derived from specific environmental conditions, and there is often considerable uncertainty about the universal applicability of functional forms and specific parameter values. Care should be taken in understanding the model assumptions and the consequences of model formulation (e.g. Peck & Daewel 2007, this TS).

Our understanding of larval mortality in the field is incomplete and is challenged by the need to detect often subtle (Houde 1989) or sporadic variations in mortality rates over time. Predictions of predator feeding rates (and consequently mortality on young fish) from laboratory, field and simple models can differ by an order of magnitude (Paradis et al. 1996, Pepin 2004, 2006). Consequently, modelling predator feeding requires better observations and greater effort to validate model formulations (especially functional responses). Adequate knowledge of the degree of spatio-temporal overlap between (vertebrate and invertebrate) predators and larval fish prey is a critical pre-requisite for understanding predation mortality, which appears to follow a random encounter pattern on the local scale (Poisson distributed; Pepin 2004).

**Biological processes: juvenile recruitment and settlement.** Explicit modelling of post-larval stages through to recruitment is rare (Hinckley et al. 1996) and sometimes adding complexity (e.g. a simple settlement process) does not enhance the model fit to the observations (Brickman et al. 2007). The role of settlement and density dependence in nature needs to be further investigated and incorporated into models, where appropriate (e.g. see Gallego & Heath 2003). The study of older stages can also provide some insight into earlier life history, e.g. by backtracking (Christensen et al. 2007). Biophysical models can be used to generate indices (e.g. a coefficient of overlap between modelled larval and idealized prey distributions [Hinrichsen et al. 2005]) that can be correlated to juvenile recruitment and may complement traditional methods for recruitment prediction.

**Future directions: integration with observing systems, operational models, monitoring programs, and management recommendations.** Spatially-explicit coupled models have been useful for studying the transport of planktonic stages of marine fish. Further uses of these models to investigate more complex

mechanisms (see Miller 2007) such as recruitment, growth, predation, stock structure, effects of climate change, as well as optimal survey/marine protected area design, are becoming more commonplace in the scientific literature. These models have the potential to improve our predictions of population variability and ecosystem dynamics, and will advance our knowledge of important biophysical processes when used for hypothesis testing (Miller 2007).

The way forward entails overcoming many technical issues, including assessment of (1) model resolution in space (grid size and bathymetry) and time (time step), (2) particle tracking algorithms and interpolation schemes, (3) implementation of biological models within hydrodynamic models (on-line) or separate from them (off-line), (4) temporal resolution of physical forcing (e.g. hourly vs. daily wind data) and hydrodynamic model output (e.g. tidally explicit vs. averaged output), (5) sensitivity analysis, visualization and validation methods, (6) benchmark test cases for particle tracking models, and (7) data assimilation techniques. An important challenge is to integrate bio-physical models with monitoring programs to enhance model validation. We need to incorporate the data generated by monitoring programmes and even influence their design so that they generate the measurements that are useful to parameterize and validate biophysical models.

**Consensus discussion.** Workshop participants identified several major themes that would result in advances in the field of biophysical modelling of the early life stages of fish. The need for, and utility of, validation and sensitivity methods was addressed in every theme session and figured prominently in group discussions. Consistency between model predictions and observational data is crucial; quality of data is paramount. Methods of model-data comparison need to be applied and developed and the validity of quantitative metrics should be addressed. In addition, models should be as simple as possible but as complex as necessary. There are no fixed rules to determine the appropriate complexity of a model, although some useful tools (e.g. sensitivity analysis, pattern-oriented modelling) can provide guidance. The level of model complexity should also be adjusted to the model objectives and the observed biological patterns that it aims to reproduce.

Biophysical model results are critically influenced by hydrodynamic model predictions. Therefore, basic improvements in understanding of turbulence and in predicting mixing and circulation patterns will advance the field of larval fish modelling. Additionally, ensemble methods (combining a suite of simulations that have slightly different starting conditions or model assumptions [Gneiting & Raftery 2005]) and probabilistic approaches (e.g. Brickman et al. 2007) have been proposed as useful tools for integrating complex 3-

dimensional predictions, environmental variability and uncertainty into biological life cycle models.

Fundamental information is needed on the biological processes of mortality, behaviour, and energetics to advance models of fish early life. These stage-dependent, and often species-specific, processes pose challenges for investigation; however, recent advances in field and laboratory techniques will likely revolutionize the field of larval fish modelling.

Finally, general recommendations were made at the WKAMF workshop: (1) models and model results should be made accessible to managers and other users, but mainly in close collaboration with scientists to ensure that model results are interpreted and applied appropriately; and (2) laboratory, field and modelling scientists must work together to advance the field. The groups that come to grips with both the rhomboidal approach to model complexity (with greatest complexity at the level of the target organism and decreasing towards higher and lower trophic levels; deYoung et al. 2004) and the laboratory/model/observation triad (Hannah 2007, this TS) will lead the advances in the field of fish early life ecology.

*Acknowledgements.* We thank WKAMF workshop participants and sponsors. WKAMF was hosted by the French Research Institute for Exploitation of the Sea (IFREMER) Centre de Nantes with support from IFREMER (France), the US National Science Foundation (OISE-0527221), Fisheries Research Services (Scotland, UK), the University of Maryland Center for Environmental Science (USA), and the US National Marine Fisheries Service. It was endorsed by GLOBEC and Eur-Oceans. Support for this publication was provided for E.W.N. by NSF (OCE-0424932, OCE-0453905). Partial support for P.P. was provided by Eur-Oceans (EC FP6 Network of Excellence). We also thank Howard Browman for his constructive comments on this manuscript.

#### LITERATURE CITED

- Bartsch J, Coombs SH (2004) An individual-based model of the early life history of mackerel (*Scomber scombrus*) in the eastern North Atlantic, simulating transport, growth and mortality. *Fish Oceanogr* 13(6):365–379
- Batchelder HP (2006) Forward-in-time-/backward-in-time-trajectory (FITT/BITT) modeling of particles and organisms in the coastal ocean. *J Atmos Ocean Technol* 23(5): 727–741
- Brickman D, Marteinsdottir G, Taylor L (2007) Formulation and application of an efficient optimized biophysical model. *Mar Ecol Prog Ser* 347:275–284
- Browman HI (ed) (1996) Predator–prey interactions in the sea: commentaries on the role of turbulence. *Mar Ecol Prog Ser* 139:301–312
- Christensen A, Daewel U, Jensen H, Mosegaard H, St. John M, Schrum C (2007) Hydrodynamic backtracking of fish larvae by individual-based modelling. *Mar Ecol Prog Ser* 347:221–232
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311(5760):522–527



- deYoung B, Heath M, Werner F, Chai F, Megrey B, Monfray P (2004) Challenges of modelling decadal variability in ocean basin ecosystems. *Science* 304:1463–1466
- Fiksen Ø, Jørgensen C, Kristiansen T, Vikebø F, Huse G (2007) Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Mar Ecol Prog Ser* 347:195–205
- Galbraith PS, Browman HI, Racca RG, Skiftesvik AB, Saint-Pierre JF (2004) Effect of turbulence on the energetics of foraging in Atlantic cod *Gadus morhua* larvae. *Mar Ecol Prog Ser* 281:241–257
- Gallego A, Heath MR (2003) The potential role of settlement on the stock-recruitment relationship: numerical experiments using biophysical modelling simulations. *ICES CM/P:11*
- Gneiting T, Raftery AE (2005) Weather forecasting with ensemble methods. *Science* 310:248–249
- Grimm V, Railsback SF (2005) Individual-based modelling and ecology. Princeton University Press, Princeton, NJ
- Grimm V, Revilla E, Berger U, Jeltsch F and 6 others (2005) Pattern-oriented modelling of agent-based complex systems: lessons from ecology. *Science* 310:987–991
- Hannah CG (2007) Future directions in modeling physical-biological interactions. *Mar Ecol Prog Ser* 347:301–306
- Heath MR, Gallego A (1997) From the biology of the individual to the dynamics of the population: bridging the gap in fish early life studies. *J Fish Biol* 51(suppl A):1–29
- Heath MR, Gallego A (1998) Bio-physical modelling of the early life stages of cod and haddock in the North Sea. *Fish Oceanogr* 7(2):110–215
- Hinckley S, Hermann AJ, Megrey BA (1996) Development of a spatially explicit, individual-based model of marine fish early life history. *Mar Ecol Prog Ser* 139:47–68
- Hinckley S, Hermann AJ, Mier KL, Megrey BA (2001) Importance of spawning location and timing to successful transport to nursery areas: a simulation study of Gulf of Alaska walleye Pollock. *ICES J Mar Sci* 58(5):1042–1052
- Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can J Fish Aquat Sci* 59: 1858–1873
- Hinrichsen HH, Schmidt JO, Petereit C, Möllmann C (2005) Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies. *ICES J Mar Sci* 62:878–885
- Houde ED (1989) Subtleties and episodes in the early life of fishes. *J Fish Biol* 35:29–38
- Hunter J, Craig P, Phillips H (1993) On the use of random-walk models with spatially-variable diffusivity. *J Comp Physiol* 106:366–376
- Huret M, Runge JA, Chen C, Cowles G, Xu O, Pringle JM (2007) Dispersal modeling of fish early life stages: sensitivity with application to Atlantic cod in the western Gulf of Maine. *Mar Ecol Prog Ser* 347:261–274
- Huse G (2005) Artificial evolution of *Calanus* life history strategies under different predation levels. *GLOBEC Int Newsletter* 11(1):19
- Leis JM (2007) Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Mar Ecol Prog Ser* 347:185–193
- Lett C, Veitch J, van der Lingen CD, Hutchings L (2007) Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems. *Mar Ecol Prog Ser* 347:247–259
- Mariani P, MacKenzie BR, Visser AW, Botte V (2007) Individual-based simulations of larval fish feeding in turbulent environments. *Mar Ecol Prog Ser* 347:155–169
- Marteinsdottir G, Steinarsson A (1998) Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *J Fish Biol* 52(6):1241–1258
- Miller TJ (2007) Contribution of individual-based coupled physical-biological models to understanding recruitment in marine fish populations. *Mar Ecol Prog Ser* 347:127–138
- Mullon C, Cury P, Penven P (2002) Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela. *Can J Fish Aquat Sci* 59:910–922
- North EW, Hood RR, Chao SY, Sanford LP (2006) Using a random displacement model to simulate turbulent particle motion in a baroclinic frontal zone: a new implementation scheme and model performance tests. *J Mar Syst* 60: 365–380
- Osborn T (2007) Applicability of turbulence measurement technology to small-scale plankton studies. *Mar Ecol Prog Ser* 347:139–143
- Paradis AR, Pepin P, Brown JA (1996) Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. *Can J Fish Aquat Sci* 53: 1226–1235
- Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar Ecol Prog Ser* 347:285–300
- Peck MA, Daewel U (2007) Physiologically-based limits to food consumption, and individual based modeling of foraging and growth of larval fishes. *Mar Ecol Prog Ser* 347:171–183
- Pepin P (2004) Early life history studies of prey-predator interactions: quantifying the stochastic individual responses to environmental variability. *Can J Fish Aquat Sci* 61:659–671
- Pepin P (2006) Estimating the encounter rate of Atlantic capelin (*Mallotus villosus*) with fish eggs, based on stomach content analysis. *Fish Bull* 104:204–214
- Rothchild BJ, Osborn TR (1988) Small-scale turbulence and plankton contact rates. *J Plankton Res* 10:465–474
- Sentchev A, Korotenko K (2007) Modelling distribution of flounder larvae in the eastern English Channel: sensitivity to physical forcing and biological behaviour. *Mar Ecol Prog Ser* 347:233–245
- Skajaa K, Browman HI (in press) The escape response of food-deprived cod larvae (*Gadus morhua* L.). *J Exp Mar Biol Ecol*
- Skajaa K, Fernf A, Folkvord A (2004) Ontogenetic- and condition-related effects of starvation on responsiveness in herring larvae (*Clupea harengus* L.) during repeated attacks by a model predator. *J Exp Mar Biol Ecol* 312:253–269
- Thygesen UH, Ådlandsvik B (2007) Simulating vertical turbulent dispersal with finite volumes and binned random walks. *Mar Ecol Prog Ser* 347:145–153
- Vikebø F, Jørgensen C, Kristiansen T, Fiksen Ø (2007) Drift, growth and survival of larval Northeast Atlantic cod with simple rules of behaviour. *Mar Ecol Prog Ser* 347:207–219
- Visser AW (1997) Using random walk models to simulate the vertical distribution of particles in a turbulent water column. *Mar Ecol Prog Ser* 158:275–281
- Werner FE, Perry RI, Lough RG, Naimies CE (1996) Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep-Sea Res II* 43:1793–1822
- Werner FE, Quinlan JA, Blanton BO, Luettich RA Jr (1997) The role of hydrodynamics in explaining variability in fish populations. *J Sea Res* 37:195–212