

# Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modelling approach

Ute Daewel, Myron A. Peck, and Corinna Schrum

**Abstract:** We employed a suite of coupled models to estimate the influence of environmental variability in the North Sea on early life stages of sprat (*Sprattus sprattus*), a small pelagic clupeid, and Atlantic cod (*Gadus morhua*), a demersal gadoid. Environmentally driven changes in bottom-up processes were projected to impact the survival and growth of eggs and larvae of these marine fish species in markedly different ways. We utilized a spatially explicit, individual-based model (IBM) to estimate larval fish survival and a 3D ecosystem model (ECOSMO) to provide variable prey fields. The model was applied to each of 3 years (1990, 1992, 1996) specifically characterized by interannual differences in water temperature in late winter and spring. Our results indicated that an important mechanism connecting environmental factors to larval fish survival was the match–mismatch dynamics of first-feeding larvae and their prey, which was species-specific because of (i) differences in the timing and locations of spawning, (ii) the duration of endogenously feeding life stages, and (iii) prey thresholds required for larval survival. Differences in transport processes also played an important role for the potential survival of larvae of both species.

**Résumé :** Nous employons une série de modèles couplés pour estimer l'influence de la variabilité environnementale dans la mer du Nord sur les premiers stades de vie du sprat (*Sprattus sprattus*), un petit clupéidé pélagique, et de la morue franche (*Gadus morhua*), un gadoïde démersal. Nous avons prédit que les changements causés par l'environnement dans les processus ascendants devraient affecter la survie et la croissance des œufs et des larves de ces espèces marines de poissons de manière nettement différente. Nous utilisons un modèle basé sur l'individu (IBM) et spatialement explicite pour estimer la survie des larves de poissons et un modèle 3D de l'écosystème (ECOSMO) pour fournir des champs variables de proies. Nous avons utilisé cette modélisation avec les données de chacune de 3 années (1990, 1992, 1996) qui sont spécifiquement caractérisées par des différences interannuelles de température de l'eau à la fin de l'hiver et au printemps. Nos résultats indiquent qu'un important mécanisme qui relie les facteurs du milieu à la survie des larves de poissons est la dynamique d'appariement–mésappariement entre les larves lors de leur première alimentation et leurs proies; cette dynamique est spécifique à chaque espèce à cause (i) des différences dans le calendrier et la localisation de la fraie, (ii) de la durée des stades du cycle à alimentation endogène et (iii) des seuils de proies requis pour la survie des larves. Des différences dans les processus de transport jouent aussi un rôle important dans la survie potentielle des larves des deux espèces.

[Traduit par la Rédaction]

## Introduction

The North Sea (Fig. 1) is a highly dynamic shelf sea system in terms of both physical and biological processes. The main cyclonic circulation pattern that comprises transport processes at the open boundaries as well as residual currents (e.g., wind, tides, and baroclinic currents) is superimposed by smaller scale dynamics with high frequencies that are

ecologically highly relevant. For example, strong tides and river runoff interact with bottom topography to produce a complex hydrographical situation including frontal zones separating well-mixed, shallow, near-coastal regions from deeper, seasonally stratified areas in the southern North Sea (e.g., Otto et al. 1990; Schrum 1997). These frontal zones can be extremely productive areas supporting a high biodiversity of marine fauna, including relatively dense aggrega-

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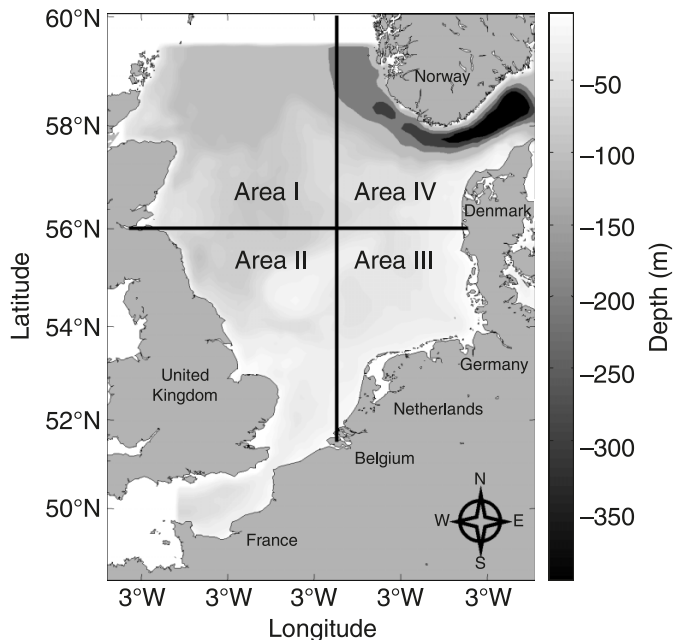
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**Fig. 1.** North Sea model domain and topography and the locations of the four North Sea subareas (partitioned at 4°E and 56°N) employed in the analyses of 3D model results.



tions of larval fish, their prey, and their predators (e.g., Kjørboe et al. 1988; Munk et al. 1999). Both physical and biological features of the North Sea (and other shelf seas) are directly impacted by changes in atmospheric forcing (e.g., air temperature, wind velocity), and the link between environmental variability and productivity in North Sea fish fauna has been discussed for the last century (Hjort 1914). Given the pronounced seasonality in physical and biological factors, species that spawn at different times of the year in the North Sea have likely adopted different life history strategies that may make them either more or less vulnerable to environmental changes. The fact that some fishes exist at their latitudinal extreme in the North Sea is a second feature that makes the composition of the fish assemblage dynamic with respect to environmental changes (Beare et al. 2004; Alheit et al. 2005).

Sprat (*Sprattus sprattus*) and Atlantic cod (*Gadus morhua*) are two important members of the North Sea fish community that have different life history strategies and different trophodynamic roles. Sprat is a small, pelagic “wasp-waist” species (e.g., Cury et al. 2000), important to both “top-down” and “bottom-up” processes (e.g., Köster and Möllmann 2000), whereas Atlantic cod is a demersal gadoid that has traditionally been one of the most abundant predatory fish in the North Sea. The North Sea forms the southern limit of the distribution of Atlantic cod (Planque and Frédou 1999) and the northern limit of the distribution of sprat, and this is reflected in the difference in life cycle scheduling observed for these species. North Sea cod spawns in winter and spring (January–May, peak February and March; Rogers et al. 2001), while the warmer-water sprat spawns in the spring and summer (April–August, peak in May and June; Munk 1993). Both of these species produce pelagic eggs that hatch into pelagic larvae and, owing to the different spawning times, early life stages of these species experience

markedly different North Sea environments (e.g., temperatures, prey fields).

During the last 30 years, spawning stock biomass of sprat has been stable or increasing while that for Atlantic cod has markedly declined in the North Sea (Heath 2005; International Council for the Exploration of the Sea 2005). Unfortunately, explaining these patterns is difficult, since both species are commercially exploited and disentangling the influence of multiple drivers (such as climate and fishing pressure) remains problematic. In North Sea cod, a clear relationship between cold mean water temperatures and high levels of cod recruitment has been reported by several investigators (e.g., Planque and Frédou 1999; Brander and Mohn 2004), but the impact of water temperature appears strongest at low levels of cod spawning stock biomass (O’Brien et al. 2000). Causal mechanisms (e.g., predator–prey match–mismatch dynamics) behind these temporal trends have been inferred from correlations between climate-driven changes in both the size and species composition of calanoid copepods in the North Sea and changes in cod recruitment strength (Beaugrand et al. 2003). Clearly, one can assume that changes in both water temperature and prey availability can impact the recruitment of North Sea cod (and other marine fish species in other regions), and these statistical (correlative) studies are an extremely important first step towards understanding which physical and biological processes may be important regulators of marine fish recruitment.

Many recruitment hypotheses suggest that rates of survival and growth are linked during the early life of marine fish (Houde 2002) and that small changes in these rates can cause large differences in recruitment (e.g., Houde 1989; Campana 1996) because of the interaction between body size and the risk of mortality in marine food webs (Shin and Cury 2004; Pope et al. 2006). A number of biophysical individual-based models (IBMs) have been employed to examine how different environmental factors influence growth and survival of early life stages of a variety of species, including Atlantic cod (Fiksen and MacKenzie 2002; Lough et al. 2005) and sprat (Kühn et al. 2008; Peck and Daewel 2007). These mechanistic IBMs include species-specific physiological attributes and can provide estimates of environmental requirements (e.g., temperature–prey combinations) for larval survival. A recent advancement has been to couple a three-dimensional (3D) biophysical IBM to a 3D NPZD (nutrient, phytoplankton, zooplankton, detritus) ecosystem model (Daewel et al. 2008a, 2008b) to include spatially explicit changes in key abiotic (hydrographic environment) and biotic (prey fields) factors. Daewel et al. (2008a) utilized this coupled modelling approach to investigate the spatial variability in survival, growth, and aggregation of sprat larvae on a seasonal time scale in the North Sea. They identified spatial and temporal differences in growth rates (driven by differences in temperature and prey fields) and suggested that these differences were the likely mechanism responsible for the accumulation of larval fish at frontal areas in the southern North Sea (Daewel et al. 2008a).

The objective of the current modelling study was to illustrate how interannual, atmospherically driven bottom-up changes in key abiotic and biotic factors could influence the

survival of early life stages of two species having somewhat different life history strategies (e.g., spawning season, larval energetics). We employed the coupled model system in each of 3 years (1990, 1992, and 1996) that differed with respect to North Sea winter–spring water temperature to investigate spatial–temporal differences in rates of survival and growth in early life stages of both Atlantic cod and sprat. Our modelling study was designed to identify causal factors and key processes that help explain recent trends in North Sea populations of cod and sprat. On a more generic level, we wanted to explore how interspecific differences in life history might mediate the effects of environmentally driven changes in bottom-up factors on growth and survival of marine fish early life stages.

## Materials and methods

### Model description

A coupled model system (hydrodynamic model, NPZD model, fish early life stage IBM) previously described by Daewel et al. (2008a) was utilized to assess the impact of both abiotic and biotic factors on the transport, growth, and survival of eggs and larvae of sprat and cod. An IBM was used to depict the development, growth, and potential survival of fish early life stages (eggs and larvae) as well as advective and diffusive transport (Lagrangian approach). The IBM was coupled online to a hydrodynamic model (Schrum and Backhaus 1999). Finally, prey fields required for simulating the foraging, growth, and survival of larval fish were derived from the 3D output of a biophysical ecosystem model “ECOSMO” (Schrum et al. 2006a). The IBM was coupled to the 3D hydrodynamic model using a 20 min time step, which allowed the impacts of tidal dynamics as well as the diurnal changes in short-wave radiation to be resolved, an important prerequisite for adequately depicting the transport and foraging by larval fish.

### Coupled hydrodynamic–NPZD model ECOSMO

Detailed descriptions were previously published regarding the 3D hydrodynamic core (that provided temperature, turbulence, and transport) by Schrum and Backhaus (1999) and the NPZD module (from which prey fields were obtained) by Schrum et al. (2006a). The model equations were solved on a staggered Arakawa-C-grid for the North Sea and Baltic Sea with a horizontal resolution of 6 nm (1 nm = 1852 m). To resolve stratification, a 5 m vertical grid was used in the upper 40 m. Besides atmospheric boundary conditions at the surface (provided by NOAA National Centers for Environmental Prediction (NCEP)–National Center for Atmospheric Research (NCAR) reanalysis data; Kalnay et al. 1996), monthly means of land-based freshwater runoff and nutrient loads were required to run the model, and details on data sources were given by Schrum and Backhaus (1999). At the open boundaries to the North Atlantic and the English Channel, changes in sea surface elevation were prescribed to introduce tidal dynamics via the dominant, partial  $M_2$ ,  $S_2$ , and  $O_1$  components. The model provides realistic estimates of the hydrodynamics of the North Sea and Baltic Sea and its spatial and temporal variability on time scales of days to years as was shown by Janssen (2002).

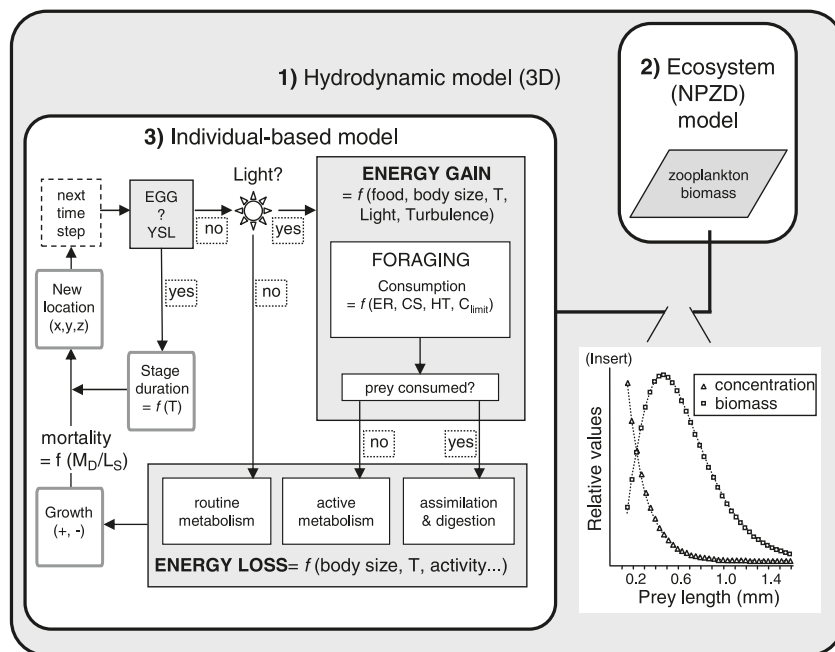
The ecosystem (NPZD) model was developed, tested, and validated by Schrum et al. (2006a, 2006b). This model has 12 state variables and was developed to simulate different macronutrient limitation processes that are particularly important to lower trophic level dynamics in the North Sea (Schrum et al. 2006a). For this purpose, it included three nutrient cycles (nitrogen, phosphorus, and silicon), two phytoplankton functional groups (diatoms and flagellates), and two zooplankton groups (herbivores and omnivores). Climatic boundary and initial conditions for the NPZD model were prescribed for nutrients, temperature, and salinity. Details about data sources are provided by Schrum et al. (2006a). Schrum et al. (2006a) published results from 1-year model integrations for few selected years, with initial condition of winter plankton concentrations obtained from World Ocean Atlas 2001 (WOA2001, Conkright et al. 2002). Neither the WOA2001 nor any other sources provide coherent and adequate estimates for climatic zooplankton biomass data for the North Sea. In our climatic simulations, we therefore related the initial zooplankton carbon biomass to the climatic winter phytoplankton concentration, with the zooplankton biomass chosen to be 20% of the climatic winter phytoplankton biomass. As shown in the model validation performed by Schrum et al. (2006a), our initial condition underestimated the observed zooplankton winter biomass. Moreover it does not allow for good representation of interannual variability in winter zooplankton estimates, since the 1-year runs always started from the same climatic conditions. For the study presented here, therefore, we used the zooplankton data from a 24-year (1980–2004) continuous model integration (S. Svendsen, University of Bergen, Geophysical Institute, N-5007 Bergen, Norway, unpublished data), starting from the initial conditions as described in Schrum et al. (2006a). This simulation improved the modelled levels of winter (February to mid-March) zooplankton ( $\sim 3 \text{ mg C} \cdot \text{m}^{-3}$ ) compared with the climatic 1-year simulation ( $\sim 0.1 \text{ mg C} \cdot \text{m}^{-3}$ ). Similarly to Schrum et al. (2006a), we assessed the zooplankton biomass against winter average values from in situ experiments. For example, the SAHFOS continuous plankton recorder (CPR) scaled biomass estimates were  $1.0\text{--}4.0 \text{ mg C} \cdot \text{m}^{-3}$  and  $\ll 1.0 \text{ mg C} \cdot \text{m}^{-3}$  for carnivorous and omnivorous zooplankton, respectively, in the majority of the North Sea (Broekhuizen et al. 1995). Furthermore, measurements performed between February and March 1987 during the “ZISCH” project (German Federal Ministry of Education and Research, BMBF) reported a North Sea-wide mean zooplankton biomass of  $7.0 \text{ mg C} \cdot \text{m}^{-3}$  for the respective time period (Krause and Knickmeyer 1992; Krause et al. 1995).

The NPZD model was coupled offline to the spatially explicit IBM using methods described by Daewel et al. (2008b), which converted estimates of bulk zooplankton biomass ( $\text{mg C} \cdot \text{m}^{-3}$ ) into a prey size spectrum (using specific size bins) required for foraging by larval fish. The conversion is based on the assumption that the size spectrum of zooplankton in the North Sea follows an exponential decrease in abundance with increasing zooplankton size (Fig. 2, insert).

### Individual-based model

The IBM was structured as an *i*-state configuration model,

**Fig. 2.** Conceptual diagram of the coupled model structure. The IBM is implemented in the hydrodynamic core. The IBM consists of the egg, yolk-sac larval, and feeding larval stages (EGG, egg stage; YSL, yolk sac larvae;  $L_S$ , larval length;  $M_D$ , larval dry mass;  $T$ , temperature; ER, encounter rate; CS, capture success; HT, handling time) and a Lagrangian transport module. The ecosystem model “ECOSMO” (Schrum et al. 2006a) provides zooplankton biomass that is converted into a size-specific prey field (Insert) and utilized in the IBM foraging subroutine according to Daewel et al. (2008b).



treating individuals as explicit entities (Caswell and John 1992). The development of endogenously feeding life stages (eggs and yolk-sac larvae) was parameterized based on empirical (laboratory-derived) relationships. The formulation for exogenous feeding larvae was more complex and based on a balanced bioenergetics approach that accounted for energy gain (ingestion: represented by food consumption  $C$  and assimilation efficiency  $\beta$ ) and energy loss due to metabolism ( $R$ ) and specific dynamic action (SDA) (Fig. 2):

$$(1) \quad G = C\beta(1 - \text{SDA}) - R$$

The IBM parameterizations were species-specific and based on previously published models for both sprat (Daewel et al. 2008a) and Atlantic cod (Lough et al. 2005), while the latter needed to be slightly modified for use in our coupled model system. In the following section, we provide a general description of the IBM and the major differences between the formulations for Atlantic cod and sprat, while details about the model parameterization and its implementation for both species are given in Appendix A.

#### IBM: nonfeeding stages

The development of eggs and yolk-sac larvae was based upon previously published functions estimating the time to hatch for eggs and the time required for 95% yolk absorption in yolk-sac larvae at different temperatures. These functions were available for Atlantic cod (Jordaan and Kling 2003; Geffen et al. 2006) and sprat (Thompson et al. 1981; Alshuth 1988). Based upon these functions, the duration of the endogenous feeding period was longer in sprat compared with cod at the same (constant) temperature. However, eggs

and yolk-sac larvae of cod can survive and develop at colder water temperatures than those of sprat (see Fig. 3a).

#### IBM: food consumption

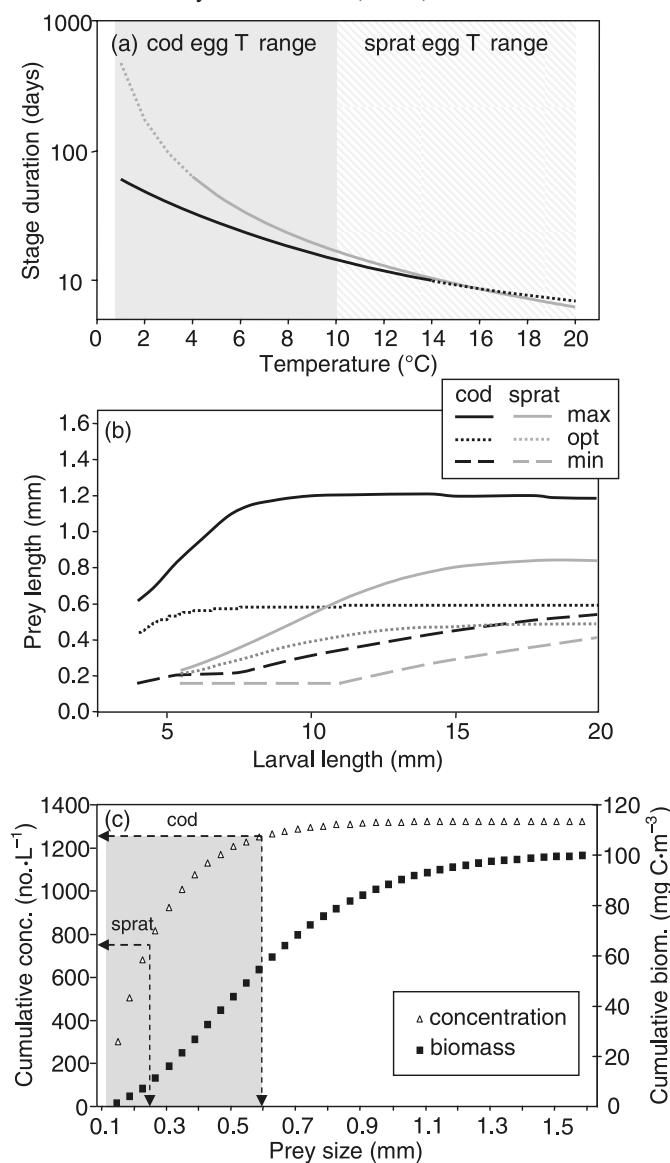
In exogenously feeding larvae, foraging and growth were depicted using subroutines that had the same structure for both cod and sprat but with species-specific parameter estimates. The mass of total prey consumed was calculated according to Letcher et al. (1996) as a function of encounter rate ( $N_{L_S,i}$ ), capture success ( $CS_{L_S,i}$ ), and handling time ( $HT_{L_S,i}$ )

$$(2) \quad C = \frac{\sum_i m_i \times N_{L_S,i} \times CS_{L_S,i}}{1 + \sum_i N_{L_S,i} \times HT_{L_S,i}} \times \Delta t$$

where  $i$  represents the index of a certain prey type with a specific prey length ( $pl_i$ ) and prey mass ( $m_i$ ). Larval sprat and cod were not expected to feed on all prey sizes available, but select from encountered prey using an optimal foraging approach (Letcher et al. 1996). Specifically, the different prey types were ranked according to three factors ( $m_i$ ,  $CS_{L_S,i}$ ,  $HT_{L_S,i}$ ) and sequentially included in the diet on the basis of rank until the profitability decreased. The maximum prey size that a larva with a certain length is able to ingest is determined by its mouth gape opening, which is markedly different in early life stages of cod and sprat. Formulations of the maximum prey size versus larval size were based upon measurements made of the prey in gut contents of sprat (Voss et al. 2003; Dickmann et al. 2007) and Atlantic cod (G. Lough, Northeast Fisheries Science Center, Na-



**Fig. 3.** IBM estimates based upon simple, species-specific parameterizations, including (a) cumulative duration of the egg and yolk-sac stages: the dashed line denotes ranges in temperatures ( $T$ ) causing increased egg mortality based upon published laboratory data; the shaded area in the background indicates the potential range of temperatures likely experienced by eggs and yolk-sac larvae in the North Sea. (b) Prey size (length, mm) consumed by Atlantic cod and sprat versus larval fish standard length (mm). All prey sizes between minimum (dashed line) and maximum (solid line) were included in the modelled larval diet. Dotted lines indicate optimal prey sizes calculated by the model. (c) Cumulative prey abundance (open triangles) and biomass (solid squares) versus prey size class and the prey size classes utilized by first-feeding cod and sprat larvae (grey shaded areas). Cumulative prey size and biomass distributions were based upon a total zooplankton biomass of  $100 \text{ mg C} \cdot \text{m}^{-3}$  that was separated into  $40 \text{ } \mu\text{m}$  size classes using methods outlined by Daewel et al. (2008b).



tional Marine Fisheries Service, Woods Hole, MA 02543, USA, unpublished data). A comparison between the species indicated that cod was able to profitably feed on larger prey

items and on a larger prey size spectrum compared with similar-sized sprat larvae (Fig. 3b). Young (first-feeding) larval sprat are able to ingest relatively small prey items (prey size  $< 250 \text{ } \mu\text{m}$ ) compared with first-feeding cod (prey size  $< 600 \text{ } \mu\text{m}$ ). The fraction of the total prey biomass (range in prey lengths between 150 and 1600  $\mu\text{m}$ ) available to first-feeding sprat was predicted to be quite small (10%) compared with that available to cod (50%) (Fig. 3c).

One difference between the model formulations for cod and sprat was the parameterization for  $N_{L,i}$  that depends on the reactive distance ( $\text{RD}_i$ ) and the velocity component of encounter rates ( $V$ ). Here, sprat was considered to be a cruise predator (see Daewel et al. 2008a for details), while cod larvae were considered pause-travel predators, searching for prey during pauses between swimming events (Lough et al. 2005).

The daily food consumption ( $C_{\text{day}}$ ) was restricted to an upper limit ( $C_{\text{day}} = \min(\sum_{\text{day}} C, C_{\text{max}})$ ), representing a satiation effect incorporated into the model to prevent overfeeding (e.g., Letcher et al. 1996). Maximum consumption ( $C_{\text{max}}$ ) in sprat was based on an empirically derived formulation (for details see Daewel et al. 2008a), while a mechanistic approach was taken to prevent overfeeding by cod. Here, the maximum gut content ( $\text{GC}_{\text{max}}$ ) and gut evacuation rate (GER) determined the space available in the gut and hence the amount of prey that could be ingested by a larva during any model time step.

#### IBM: metabolic losses

Consumed prey mass was reduced by an assimilation efficiency ( $\beta$ ), specific dynamic action ( $\text{SDA}_{\text{mi}}$ ), and other metabolic losses. The latter included components accounting for standard ( $R_S$ ) and active ( $R_A$ ) rates of energy loss. Metabolic losses due to activity occurred during the day and were approximated by increasing standard metabolism by a factor ( $k$ ) to account for activity.

#### IBM: length growth and mortality

For exogenously feeding sprat and cod larvae and postlarvae (7.0–40.0 mm  $L_S$ ), allometric relationships between dry mass and standard length were available (Peck et al. 2005). Potential larval survival (PLS) was included in both the cod and sprat IBMs. In cod, PLS was equal to the percentage of larvae remaining above a critical minimum mass ( $M_{\text{min}}$ ) at age ( $t$ ). Larvae that lost mass and were  $< M_{\text{min}}$  were considered to have died from starvation and were removed from the simulation. For sprat, partitioning between growth in mass and length depended upon larval condition factor ( $\phi$ ) (mass-at-length). If growth in dry mass was positive and  $\phi \geq 1$ , the larva increased its standard length. If growth in dry mass was continually negative and  $\phi$  was  $< 0.4$ , the larva died. Mortality due to predation was not included in this study.

#### 0D model runs: experimental setup

To compare the performance of the IBM for exogenously feeding larvae of Atlantic cod and sprat, 0D model runs were performed. Here the IBM was not coupled to the hydrodynamic or ecosystem models, but environmental conditions (e.g., temperature, prey biomass, light, turbulence level) were predefined and kept constant during each simu-

lation. Two numerical experiments were conducted to assess the impacts of temperature and prey availability on simulated growth and survival. In experiment 1, larval growth rate in length ( $\text{mm}\cdot\text{day}^{-1}$ ) was calculated under ad libitum feeding conditions ( $150 \text{ mg C}\cdot\text{m}^{-3}$ ) at two different temperatures. The second 0D experiment examined the inter-relationship between temperature and prey requirements by performing simulations at five different constant temperatures (4, 8, 12, 16, 20 °C) and at different levels of prey biomass ranging from 10 to  $250 \text{ mg C}\cdot\text{m}^{-3}$  for sprat and from 5 to  $100 \text{ mg C}\cdot\text{m}^{-3}$  for cod. At each temperature, the prey biomass level at zero growth rate was iteratively determined. The simulations were stopped when the larvae reached a length of 10 mm, and the mean growth rate in length for the whole simulation period was calculated. In both 0D experiments, light intensity was set to be sufficient for feeding, and photoperiod was maintained at 14 h.

Note that these 0D simulations were conducted under relatively low levels of turbulence ( $10^{-8} \text{ W}\cdot\text{kg}^{-1}$ ). The maximum turbulent dissipation rates encountered by larvae in the North Sea can be  $>10^{-6} \text{ W}\cdot\text{kg}^{-1}$  (e.g., Simpson et al. 1996), constituting environmental conditions where larval survival would only be possible at higher levels of prey biomass. A sensitivity study previously conducted on the sprat IBM indicated a dome-shaped relationship between growth and turbulence and that larvae feeding was poor at high turbulent dissipation rates (Daewel et al. 2008a). However, the analysis also indicated that larvae did not die of starvation at high turbulence levels if prey biomass levels were high.

### 3D model runs: experimental setup

In 3D-coupled model simulations, particles representing cohorts of eggs that could develop into larvae were released each day during the North Sea spawning period for cod (1 January to 30 April) and sprat (1 April to 31 July). A total of 72 506 cohorts was released each day in a homogeneous distribution (horizontal  $6 \text{ nm} \times 6 \text{ nm}$  grid, vertical every 5 m) across the entire North Sea (see Daewel et al. 2008a, their figure 1b). Although sprat and cod do not spawn throughout the entire North Sea, utilizing a homogeneous distribution of release areas provided spatial estimates of habitats that supported potential larval survival (PLS) independent of previously observed (realized) spawning grounds. An estimate of PLS was obtained for each horizontal grid point from the average percentage of surviving cohorts that were released at all depths on each day within that grid box throughout the entire spawning season of cod (January–April) and sprat (April–July). We then could compare the spatial estimates of PLS to the locations of known spawning grounds to help verify the model approach. We also calculated the duration of endogenously feeding stages and the position of each cohort prior to first feeding with respect to spawning time and location to identify the role of transport patterns in terms of predator (larvae) – prey (zooplankton) overlap. An estimate of the potential magnitude of match–mismatch was obtained by comparing the seasonal variability of mean zooplankton biomass in each subarea to depth-averaged larval concentrations (the sum of all larvae from first-feeding to 20 mm  $L_S$  within each horizontal grid box divided by the total depth (m) at the horizontal position) for each day of a simulation.

We chose to compare 3D simulation results of PLS, transport, and match–mismatch among 3 years (1990, 1992, and 1996) that display different mean (North Sea-wide) winter water temperatures. The years 1990, 1992, and 1996 represented a relatively warm winter, an average winter ( $\Delta T_{1992-1990} \sim -0.6 \text{ °C}$ ), and an extremely cold winter ( $\Delta T_{1996-1990} \sim -1.7 \text{ °C}$ ), respectively. As a justification for basing our choice on winter temperatures, the largest inter-annual variability in simulated water temperatures (Fig. 4) exists in the North Sea during the coldest period of the year (February and March) (Janssen 2002), which coincides with the main spawning period for Atlantic cod in this region. An empirical orthogonal function (EOF) analysis conducted on spatiotemporal variability in water temperature (Janssen 2002) and modelled zooplankton biomass (Schrum et al. 2006b, their figure 8) indicated that the prevailing patterns were strongly correlated with the North Sea hydrography. For example, the largest seasonal temperature differences and variability in zooplankton biomass were estimated for shallow, tidally well-mixed areas along the coast, particularly in the southern North Sea, while the central and northern portions of the North Sea exhibited less temperature variability, are seasonally stratified, and are less productive. To simplify the interpretation of our 3D model results (as well as provide spatially explicit analyses of the results), we separated the North Sea into four different areas (see Fig. 1) based upon regional differences in prey and temperature predicted by the coupled hydrodynamic and NPZD models.

## Results

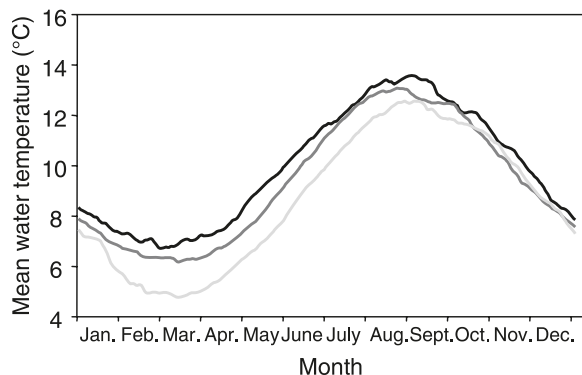
### 0D model simulations

Despite differences in the formulations and parameterizations of the cod and sprat foraging and growth IBM subroutines, the results of 0D model simulations indicated that temperature-specific growth rates of cod and sprat larvae  $<20 \text{ mm } L_S$  were quite similar when larvae were not food-limited (Fig. 5a). However, more prey was required for maximum growth at any temperature in sprat ( $\sim 30\text{--}200 \text{ mg C}\cdot\text{m}^{-3}$ ) compared with cod ( $\sim 7\text{--}50 \text{ mg C}\cdot\text{m}^{-3}$ ), and model growth rates of cod and sprat were markedly different when food was limiting (Fig. 5b). Although the zooplankton biomass (concentration) required for survival increased with increasing temperature in both species (owing to temperature-dependent metabolic costs), interspecific requirements were markedly different. The results indicated that the critical amount of prey required to support the survival of first-feeding larval sprat was about fivefold higher than that for larval cod (Fig. 5b).

### 3D results: potential larval survival

When sprat and cod eggs were released homogeneously in the North Sea, not all areas supported PLS. Based upon spawning location and spatial variability in mean PLS, suitable spawning grounds for both sprat and cod were restricted to the southern North Sea (Fig. 6). The highest mean PLS resulted from spawning in nearshore areas of the Dutch and German coasts and in the vicinity of Dogger Bank. Although the location of suitable spawning grounds estimated for sprat (Figs. 6d–6f) appeared to be similar in each of the 3 years, this was not the case for Atlantic cod

**Fig. 4.** North Sea mean water temperature in 1990 (black line), 1992 (dark grey line), and 1996 (light grey line) as estimated by the hydrodynamic model employed in this study.



(Figs. 6a–6c), where the spatial extent and magnitude of areas supporting PLS varied among the years.

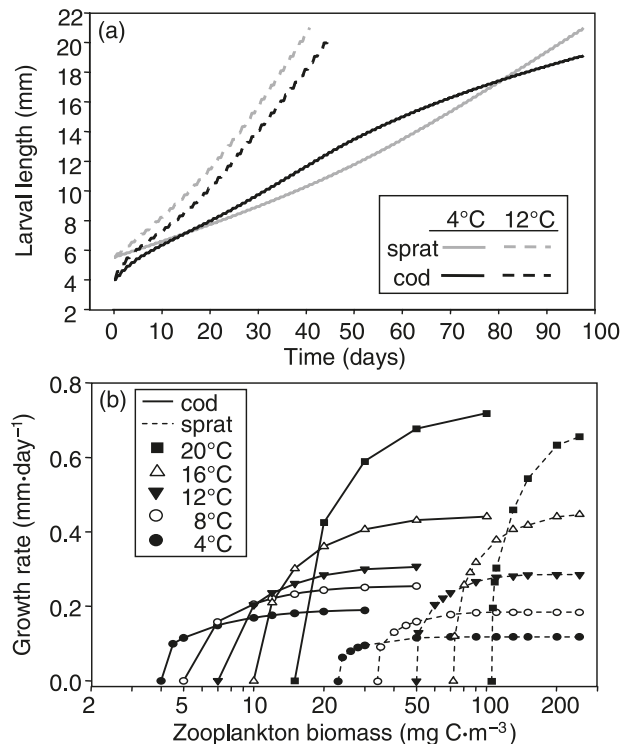
Our results also predicted an interannual trend as well as differences among the four North Sea regions in PLS. Among the years, cod PLS decreased with increasing average winter water temperature (January–April) (Fig. 7a), a trend that was consistent within each of the four subareas. However, at the same average winter water temperature, PLS was always two to four times higher for spawning (particle releases) in the southern areas (Areas II and III) compared with northern areas (Areas I and IV) of the North Sea. For sprat, PLS was also greatest in southern areas but was unrelated to interannual changes in the average water temperature (April–July) (Fig. 7b). Intraannual differences in monthly mean PLS were also evident, with largest differences for cod during the earliest spawning months (January–February: relative low PLS) compared with later spawning months (March–April: relative high PLS) (Fig. 7, Insert 1). Specifically, cod PLS during the coldest year (1996) was higher compared with the warmer years. In contrast, interannual differences in sprat PLS were much smaller when compared with cod. Furthermore, PLS in sprat was generally higher in earlier spawning months (April–May) compared with later spawning months (June–July) (Fig. 7, Insert 2).

### 3D results: transport

Despite the difference in spawning time, the general transport pattern for cod and sprat cohorts prior to first feeding was similar in each of the four potential spawning regions (Areas I–IV; Fig. 8). Generally, stronger transport was projected for cod cohorts compared with sprat in all areas except within Area I, where larvae were strongly transported into the northern and central North Sea (Fig. 8a). From the German Bight (Area III, Fig. 8c), there was a strong northward transport of early life stages of both species and a low percentage of westward transport into the Southern Bight (Area II). Similar percentages of cohort released in the Southern Bight drifted into Areas I and III (Fig. 8b). Some larval cohorts were lost from the model domain. For example, up to 5% of larval sprat or cod cohorts were transported northward out of Area IV (Fig. 8d) before they started exogenously feeding. This transport is caused by the Norwegian coastal current and appears to be more important for the spring- and summer-spawned sprat individu-

**Fig. 5.** IBM, 0D simulation results for sprat and Atlantic cod.

(a) Larval standard length ( $L_S$ ) vs. time at 4 and 12 °C under ad libitum feeding conditions (prey biomass = 150 mg C·m<sup>-3</sup>). (b) Growth rates for <10 mm  $L_S$  sprat and Atlantic cod larvae versus total zooplankton (prey) biomass at each of five different temperatures. Note that the prey spectrum that first-feeding larvae are able to utilize is not the same for sprat and Atlantic cod.



als. On the other hand, a greater part of cod cohorts were exposed to a westward transport pattern.

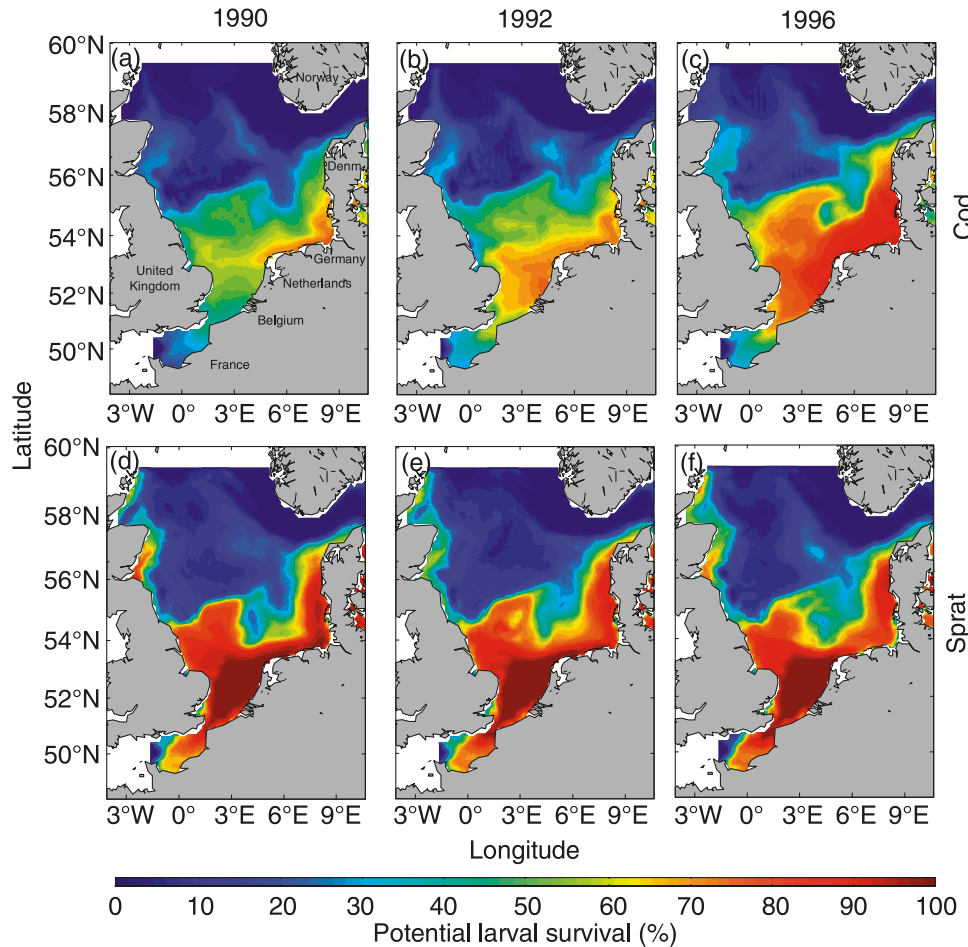
The results indicated stronger transport of eggs and yolk-sac larvae for cod spawned in 1990 and 1992 compared with sprat (Figs. 8a–8d). Moreover, the transport of cod exhibits a more pronounced interannual variability than that of sprat (Figs. 8a–8d). This was particularly evident in 1996, an exceptionally cold year that exhibited a markedly different transport pattern compared with either 1990 or 1992. Despite the very cold temperatures (and hence slow rates of development and longer durations of endogenous feeding periods for cod compared with sprat), transport out of the southern areas (Areas II and III) was lower for cod compared with sprat in that year. Moreover, the number of individuals leaving Areas II and III in a northward direction was much lower in 1996 (~4.4 times greater in 1990), and the dominant direction of transport of individuals spawned in the German Bight (Area III) was in a westward direction, following a weak anticyclonic circulation pattern.

### 3D results: match–mismatch dynamics

A comparison of monthly mean values of larval cod and sprat concentration and zooplankton biomass in each sub-area revealed the potential for larvae to match with favourable feeding conditions (Fig. 9). In general, the modelled seasonal zooplankton dynamics indicated a slightly later onset of the zooplankton production in the western parts of the



**Fig. 6.** Model estimates of spawning grounds supporting potential survival of larval Atlantic cod (*a–c*) and larval sprat (*d–f*) for 1990, 1992, and 1996. Estimated potential survival was the mean value calculated for the whole spawning period (Atlantic cod: January–April; sprat: April–July) at each spawning location.



North Sea in Area I (Fig. 9c) and Area II (Fig. 9f) compared with the eastern regions in Areas III and IV (Figs. 9i and 9l). Furthermore, the spring peak in biomass (February–March) was accompanied by higher maximum values in the east, with highest zooplankton biomass obtained in 1990 and 1992 compared with 1996.

The seasonality in the concentration of feeding larvae was markedly different in Atlantic cod and sprat, particularly in relation to temporal changes in zooplankton biomass. While the occurrence of larval sprat (Figs. 9b, 9e, 9h, 9k) overlapped (matched) the timing of maximum prey biomass, the maximum occurrence of cod larvae (Figs. 9a, 9d, 9g, 9j) appeared earlier in the season and suggested mismatch situations with prey early in the year (January–March). Specifically during the warmer years (1992, 1993), our results suggest lower larval concentrations in months with relatively high prey biomass (March–July) compared with the colder year 1996 (Figs. 9a, 9d, 9g, 9j). In contrast, sprat larvae experienced favourable feeding situations (a match with zooplankton biomass) in all 3 years. However, simulations also predicted marked interannual variability in the seasonality of sprat larval concentration. The first increase in sprat larval concentration occurred in May, where higher concentrations were predicted during the warmest year (1992) in each area (Figs. 9b, 9e, 9h, 9k). In contrast, the concentra-

tion of sprat larvae was higher somewhat later in the year during 1996.

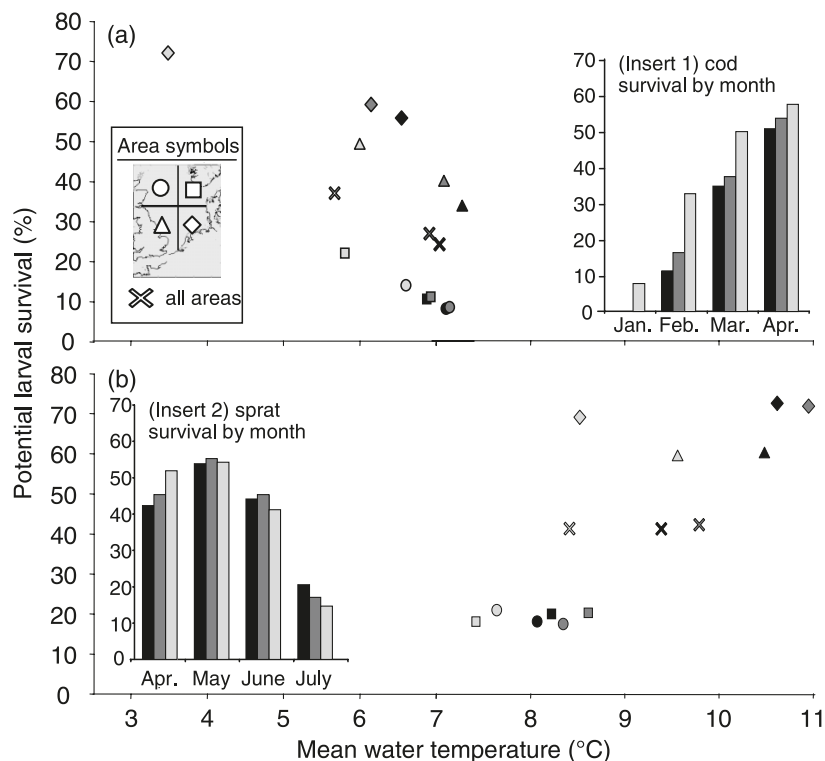
## Discussion

### Observed vs. predicted spawning sites

The model simulations for Atlantic cod and sprat identified potential spawning grounds (PSG, based upon larval survival) mainly in the southern part of the North Sea that coincided with areas observed (e.g., Pitois and Fox 2006) and predicted by our NPZD model to have maximum amounts of secondary production and zooplankton biomass. For both sprat and Atlantic cod, coarse maps of spawning activity were published by Rogers et al. (2001, their figures 3.2.2.1 and 3.2.13.1, respectively), and more detailed maps of North Sea cod spawning activity were published by Fox et al. (2008). Spawning by sprat takes place over broad areas of the southern North Sea and along the English coast (Rogers et al. 2001), a spatial pattern that agrees well with our model-based estimates of sprat PSG. For Atlantic cod, the spatial extent of peak spawning activity also agreed with our PSG. However, over a broad area, spawning appears to be restricted to a number of smaller “pockets”, including areas associated with Dogger Bank, the Elbe estuary, and the central German Bight, where highest con-



**Fig. 7.** Potential larval survival (PLS) versus average water temperature experienced during the spawning season (upper panel: Atlantic cod; lower panel: sprat). The symbols indicate the respective spawning area (Areas I–IV, see Fig. 1), and lines having different shades of grey denote each of the simulated years (black: 1990; dark grey: 1992; light grey: 1996). (Insert 1 and 2) North Sea-wide mean PLS in each spawning month for the 3 years.



centrations of cod eggs were normally found within frontal zones (Munk et al. 2009). Interestingly, most cod spawning areas determined from that (2004) survey agreed well with historical records of active spawning grounds (Fox et al. 2008) and include areas where genetic differences between spawning populations have been identified (Hutchinson et al. 2001). Besides their genetic dissimilarity, other studies have reported differences in spawning characteristics of cod at different North Sea spawning sites that could potentially influence PLS (e.g., International Council for the Exploration of the Sea 2005; Harrald et al. 2010). For example, cod in the German Bight have a later spawning period (February–May) than cod in the Southern Bight (January–April) (International Council for the Exploration of the Sea 2005), which, according to our results, would increase the annual PLS of cod progeny in the former area.

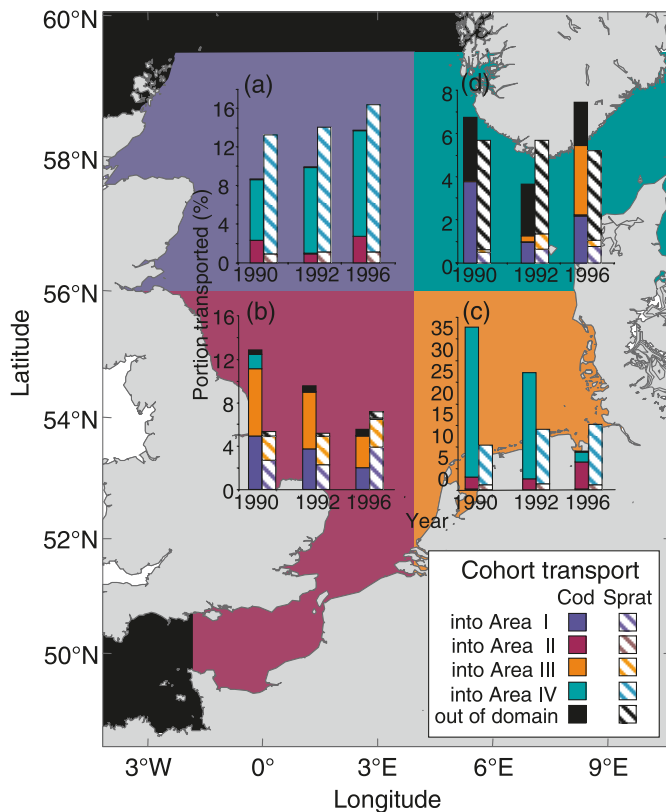
Although the spatial extent of cod spawning also agreed well with our model-based estimates of PSG (e.g., little spawning activity in the central and northwestern part of the North Sea; Fox et al. 2008), the spatial complexity of observed spawning pockets was not captured by our model system. It appears as though “realised” spawning areas by cod do not reflect all of the areas where spawning could potentially result in high levels of early life stage survival and that additional factors contribute to the choice of spawning areas by this demersal species. For example, cod are known to avoid spawning in turbid waters and have an affinity towards spawning in areas with specific topographic characteristics (Brander 1994; Begg and Marteinsdottir 2002; Rindorf and Lewy 2006). Our model did not include these

habitat features. Regardless, the general agreement between observed spawning grounds and modelled PSGs in both sprat and cod help validate our model approach, since spawning grounds utilized by these species in the North Sea were those projected in our model system to promote increased survival of early life stages (exogenously feeding larvae).

#### Larval survival: detecting relevant processes

The influence of differences in life history strategy and early life stage physiology on the relative impacts of environmental factors was evident from a comparison of the results of our simulations for North Sea cod and sprat. A critical factor influencing survival was the match or mismatch of first-feeding larval fish with their prey (Cushing 1990). A priori to understanding match–mismatch dynamics occurring in the field, a thorough examination of the interrelationships between physical environmental factors and the onset of zooplankton production is required. Unlike temperate lakes where phenological changes in primary and secondary production are often tightly coupled to changes in water temperature via changes in winter ice cover (Weyhenmeyer et al. 1999; Weyhenmeyer 2001), long-term observations in the North Sea at Helgoland Roads (located in our Area III) indicated that even in the coldest years (e.g., 1996), sea ice cover was absent and the dynamics (phenology and biomass) of the spring phytoplankton bloom were comparable to those observed after warmer winters (Wiltshire and Manly 2004). Those findings agree well with our NPZD model estimates, indicating no phenological

**Fig. 8.** Transport processes impacting nonfeeding developmental stages in Atlantic cod and sprat in the North Sea. The bars indicate the percentage of individuals that left each spawning area (a–d) (Areas I–IV, see Fig. 1) prior to exogenous feeding. The colours represent the area within which the larvae started to feed (colour code is given by the background colour of each of the four areas). Black indicates the percentage of larvae that were transported out of the model domain.



shifts in the timing of zooplankton production in the German Bight despite relatively large differences in mean winter water temperatures among the 3 years examined here.

In the North Sea, cod spawn during the winter and early spring (January–April) prior to the spring zooplankton bloom, and therefore their progeny (eggs and larvae) can be exposed to both cold water temperatures and also unfavourable feeding conditions. At typical North Sea winter water temperatures ( $<8^{\circ}\text{C}$ ), our IBM estimated that at least  $5\text{ mg C}\cdot\text{m}^{-3}$  would be required for the survival of cod larvae. Although the comparison of modelled and observed values indicated that the model underestimated zooplankton biomass in those winter months, observed (in situ) zooplankton estimates also suggest that cod larvae may routinely encounter prey fields during the winter that are close to (or fall below) our physiological-based estimate of the threshold needed for survival (CPR:  $\sim 1.0\text{--}4.0\text{ mg C}\cdot\text{m}^{-3}$ ; ZISCH:  $7.0\text{ mg C}\cdot\text{m}^{-3}$ ).

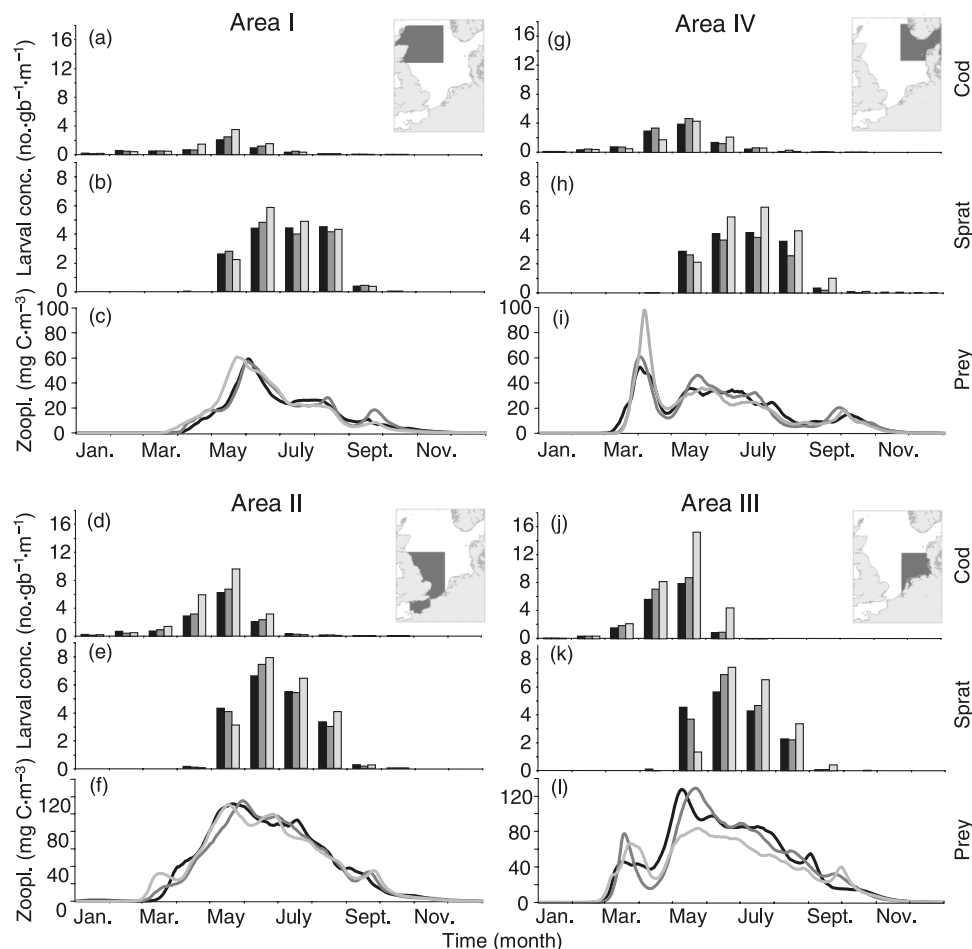
Because of longer duration of the time lag between spawning and zooplankton production in cod compared with sprat, match–mismatch dynamics are expected to play a much larger role in controlling larval survival of the former compared with the latter species. This is particularly the case since cod has a somewhat faster rate of development

through nonfeeding stages compared with sprat at the same water temperature. On the other hand, first-feeding larval cod have a larger potential prey size spectrum (up to  $600\text{ }\mu\text{m}$ ) compared with sprat (up to  $200\text{ }\mu\text{m}$ ) and thus have the ability to survive at lower levels of zooplankton biomass compared with sprat larvae. Since developmental rates and feeding requirements of fish larvae are both strongly temperature-dependent, whereas the timing of secondary production in the North Sea is not, potential survival of larval cod is expected to decline with increasing water temperature. In relatively warm years (e.g., 1990, 1992), development of cod will be relatively rapid, leading to an earlier transition to exogenous (first-) feeding for larvae with relatively higher metabolic requirements, all of which will exacerbate any potential mismatch situation. These mechanisms explain why a negative correlation between potential larval survival and average winter water temperature was observed in the results of our simulations for cod but not for sprat.

Although water temperatures and prey fields interact to place clear, physiological constraints on the survival of marine fish early life stages, our results stress that the ultimate success of larval cohorts in the North Sea will also depend upon changes in transport processes. During the years with strong westerly winds (e.g., 1990 and 1992, the two warmer years simulated in the present study), pelagic eggs and larvae of both cod and sprat were transported away from the spawning area following the general circulation pattern described by Otto et al. (1990). However, a different transport pattern was observed in the drift trajectories of cod eggs and larvae during the exceptionally cold year (1996). In that year, a higher proportion of larvae was retained within favourable feeding areas. Based on positive correlations between the North Atlantic Oscillation (NAO) and water temperature (Becker and Pauly 1996) and wind stress (Siegmund and Schrum 2001), colder years are expected to have lower dispersal and a higher retention of larvae within spawning areas. Moreover, these colder years also delay the timing of first feeding by cod, thus acting to increase the temporal match of larvae with suitable prey. In this manner, temperature, prey, and transport mechanisms interact to influence spatiotemporal patterns in PLS in North Sea cod.

For sprat, our model system projected no interannual differences in PLS or correlation between PLS and temperature. However, our results suggested that first-feeding sprat larvae require relatively high levels of zooplankton biomass for survival compared with cod. This physiological characteristic likely restricts the spatiotemporal occurrence of successful larval sprat cohorts (and thus the spawning of adults) to places and times coinciding with high zooplankton biomass. The highest levels of zooplankton biomass correspond to well-mixed and transitional (frontal) zones between well-mixed and seasonally stratified waters in the southern North Sea (e.g., LeFèvre 1987). Our model suggests that interannual differences in PLS in sprat are most likely related to the position and strength of tidal-mixing fronts (e.g., Munk 1993; Daewel et al. 2008a). Frontal residence might increase prey concentrations experienced by sprat, but it would also increase the potential for mortality via predators targeting accumulations of larvae and their zooplankton prey (Floeter 2005). Although predation was not included in our model simulations, we suggest that variability in predation pressure

**Fig. 9.** Simulated larval concentration vs. time (month) for Atlantic cod and sprat as well as the seasonal dynamics of mean (ECOSMO simulated) zooplankton biomass versus time (days) for Areas I–IV (see insert maps). Years are indicated by different shading of bars and lines (black: 1990; dark gray: 1992; light gray: 1996).



(mortality) may explain a larger portion of the interannual variability in landings and recruitment reported for sprat (e.g., Heath 2005; International Council for the Exploration of the Sea 2007) and other small pelagic species that spawn in the late spring and summer such as newly (re-) established populations of European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the North Sea compared with bottom-up controls such as mismatch events.

### Coupled modelling and marine fish early life stages

One of the assumptions used to set up the model experiments in this study was that cod and sprat larvae were exposed to the general circulation pattern as passive drifters. In the earliest life stages (eggs and yolk sac larvae), this appears to be a reasonable assumption because of limited swimming ability. However, for older larvae, the consideration of vertical (and (or) horizontal) migratory behaviour might be necessary. Although we could not find any evidence in the literature for vertical migration of cod and sprat larvae in the North Sea, evidence exists that the larvae of both species can perform vertical migration in other areas. For example, working in the Baltic Sea, Voss et al. (2007) reported the presence of diel vertical migration behaviour in sprat larvae >10 mm SL in the early 1990s and the absence

of this behaviour in the same area in the early 2000s. The two periods were characterized by large changes in key prey species (calanoid copepods in the *Acartia*, *Temora* and *Pseudocalanus* genera) and changes in water temperature. Although it is difficult to know whether those results apply to the North Sea system, those Baltic observations suggest a potential for diel vertical migration in older sprat larvae. Similarly, in cod larvae >9 mm SL, Lough and Potter (1993) reported that individuals were evenly distributed throughout the water column under well-mixed conditions but were concentrated at the thermocline and performed diel vertical migration in stratified conditions on Georges Bank (Northwest Atlantic). Both studies support our assumption that larvae <10 mm SL can be considered passive particles and, since large parts of the North Sea are well mixed throughout the year (particularly the highly productive southern areas), our assumption also appears valid for larger larvae. However, extending the model into the post-larval and juvenile stages will require additional components depicting active movements such as migratory behaviour.

When searching for critical life stages in marine fish larvae, the relationship among ontogenetic changes in foraging ability versus the available prey fields as well as starvation resistance versus growth potential need to be considered. In



sprat larvae, the first-feeding period was considered “critical” because of low feeding success, but suboptimal prey fields of larger larvae (10–15 mm SL) can also hamper growth performance and survival (Voss et al. 2003). In cod larvae, Jordaan and Brown (2003) identified clear trade-offs among body size, growth performance, and starvation resistance. In that laboratory study, ~12 mm SL cod larvae had the highest potential for growth as well as starvation-induced mortality, while, in contrast, first-feeding larvae had a higher potential to withstand periods of prey deprivation (within limits imposed by the timing of complete yolk absorption and the point of no return (Overton et al. 2010). These and studies conducted on other marine fishes (e.g., Bochdansky et al. 2008) reveal that larvae may need to pass through multiple “critical periods” and that relationship between prey field characteristics and vital rates (growth and survival) can often remain dynamic through the early larval and into the late larval and early juvenile periods (Baumann et al. 2007). Thus, extending our coupled (IBM–NPZD) model approach to later life stages is warranted.

The present study provided an example of how a coupled model systems can provide important tools to move beyond mere statistical analyses (correlations) between climate variability (e.g., changes in the NAO index) and changes in the productivity of fishes in the North Sea and elsewhere. Gaining process understanding of historical changes in fish stocks is particularly difficult in the North Sea, a region where large differences exist among species in terms of their life history strategies (Houde 1989), physiological tolerances (Pörtner et al. 2001; Pörtner and Farrell 2008), and (or) key trophodynamic relationships (Rijnsdorp et al. 2009). Our North Sea simulations for cod and sprat included environmental changes in key physical and biological factors as well as species-specific differences in life history (reproductive) strategies and growth physiology of early life stages. Although longer-term (decadal) simulations will ultimately be required to link the mechanisms identified here (match-mismatch and transport dynamics) to variability in climate and recruitment, our results suggest that the likelihood of mismatch events between first-feeding cod larvae and their prey in the North Sea is clearly correlated to changes in climatic conditions. It is important to note that our model system was designed to explicitly test for climate impacts on bottom-up processes. Thus, one cannot conclude that top-down processes (and the effects of climate on those processes) are not also relevant causal factors affecting the vital rates of marine fish early life stages within our model domain (the North Sea).

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## Appendix A

Appendix A continues on following pages.



IBM parameterization

All model parameters and the associated units are listed in Table A1.

Table A1. List of parameters and units used in the individual-based model.

Variable	Parameter	Units
$H_{ep}$	Development rates of eggs	%·day <sup>-1</sup>
$H_{ys}$	Development rates of yolk-sac larvae	%·day <sup>-1</sup>
$\beta$	Assimilation efficiency	—
$R_A$	Active metabolism	µg DM·h <sup>-1</sup>
$k$	Activity multiplier	—
$\alpha$	Angle of visual acuity	°
$CS_{L_S,i}$	Capture success	—
$C_{day}$	Daily food consumption	µg·day <sup>-1</sup>
$N_{L_S,i}$	Encounter rate	no·s <sup>-1</sup>
$C$	Food consumption	µg·Δt <sup>-1</sup>
$HT_{L_S,i}$	Handling time	s
$M_D$	Larval dry mass	µg
$G$	Larval growth	mm·Δt <sup>-1</sup>
$GC_{max}$	Gut content	µg
$GER$	Gut evacuation rate	%·h <sup>-1</sup>
$L_S$	Larval length	mm
$SS_{L_S}$	Larval swimming speed	mm·s <sup>-1</sup>
$pl_{i\ max}$	Maximum prey size	mm
$pl_i$	Prey length	mm
$m_i$	Prey mass	µg
$PS$	Prey swimming speed	mm·s <sup>-1</sup>
$RD_i$	Reactive distance	mm
$SDA_{m_i}$	Specific dynamic action	—
$R_S$	Standard metabolism	µg DM·h <sup>-1</sup>
$T$	Temperature	°C
$\Delta t$	Time interval	s
$w$	Turbulence-generated velocity difference	mm·s <sup>-1</sup>
$C_{MAX}$	Upper limit to food consumption	µg
$V$	Velocity component of contact rates	mm·s <sup>-1</sup>
$\gamma$	Oxycaloric equivalent	cal µL·O <sub>2</sub> <sup>-1</sup>
$\chi$	Calorie to microgram mass conversion factor	µg DM·cal <sup>-1</sup>

Note: 1 calorie = 4.185 J.

IBM: nonfeeding stages

The duration of the nonfeeding life period is temperature-dependent and was calculated using empirically derived functions (Table A2).

Table A2. Equations for developmental rates during nonfeeding life stages (eggs, yolk-sac larvae).

				Citation	
Eq.	Variable	Sprat	Atlantic cod	Sprat	Atlantic cod
A.1	$H_{ep}$	$1.30 T^{1.26}$	$\frac{1}{10^{[1.871 - 0.79 \log_{10}(T+2)]}}$	Thompson et al. 1981	Geffen et al. 2006
A.2	$H_{ys}$	$0.27 T^{1.495}$	$e^{(-3.6 + 0.22T)}$	Alshuth 1988	Jordaan and Kling 2003

**IBM: food consumption**

The equations required to simulate larval food consumption are given in Table A3. The encounter rate of larvae with their prey (eq. A.3) depends not only on larval reactive distance (eq. A.3.1) and prey density, but also on larval swimming behavior and turbulence. A cruise predator formulation was used for sprat (see Daewel et al. 2008b for details), while cod larvae were considered pause-travel predators, searching for prey during pauses between swimming events. Hence, in the case of cod, prey encounter rates were determined by pause frequency ( $P_f$ ) and pause duration ( $P_d$ ) (MacKenzie and Kiørboe 1995). According to Lough et al. (2005),  $P_d = 1.7$  s for small cod ( $<5.5 L_S$ ) and 1.4 s for larger cod and  $P_f = 30/60$  pauses·s<sup>-1</sup> and 32/60 pauses·s<sup>-1</sup>, respectively. Turbulence was included into the expression of encounter rate as described by Evans (1989). The velocity component of contact rates (eq. A.3.3) was composed of the predator swimming speed (eq. A.3.4), the prey speed (eq. A.3.5), and the turbulence-generated velocity difference, which was calculated according to Rothschild and Osborn (1988). Additionally, the encounter rate was multiplied with a turbulence-dependent ingestion probability calculated according to MacKenzie et al. (1994). Feeding was also sensitive to the prevailing light intensity, where the threshold was set to 0.1 lx ( $\sim 0.017 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) as observed for feeding by herring larvae (Blaxter 1986).

**Table A3.** IBM equations relevant for larval food consumption of Atlantic cod and sprat and the respective references.

Eq.	Variable			Citation	
		Sprat	Atlantic cod	Sprat	Atlantic cod
A.3	$N_{L_S,i}$	$\frac{1}{2} \pi R D^2 p_i V$	$(\frac{2}{3} \pi R D^3 p_i P_f) + (\pi R D^2 p_i P_f P_d V)$	Letcher et al. 1996	MacKenzie and Kiørboe 1995
A.3.1	$R D_i$	$\frac{p_i}{2 \tan(\frac{\pi}{6})}$	$\frac{p_i}{2 \tan(\frac{\pi}{6})}$	Breck and Gitter 1983	Breck and Gitter 1983
A.3.2	$\alpha$	$0.0167 e^{9.14 - 2.4 \ln(L_S) + 0.229 [\ln(L_S)]^2}$	$0.0167 e^{9.14 - 2.4 \ln(L_S) + 0.229 [\ln(L_S)]^2}$	Breck and Gitter 1983	Breck and Gitter 1983
A.3.3	$V$	$\sqrt{P S^2 \times S S_{L_S}^2 \times 2 w^2}$	$\sqrt{P S^2 \times S S_{L_S}^2 \times 2 w^2}$	Evans 1989	Evans 1989
A.3.4	$S S_{L_S}$	$\frac{181.15}{1 + e^{\left[\frac{-(L_S - 29.52)}{5.57}\right]}}$	$0.261 L_S^{(1.552 L_S^{0.92})} - \frac{5.289}{L_S}$	Munk 1992	Peck et al. 2006
A.3.5	$P S$	$3 p_i$	$3 p_i$	See Daewel et al. 2008a	See Daewel et al. 2008a
A.4	$C S_{L_S,i}$	$1.1 - \left(a \times \frac{p_i}{L_S}\right)$	$1.1 - \left(a \times \frac{p_i}{L_S}\right)$	Munk 1992	Munk 1992
A.4.1	$a$	$\frac{1.1 L_S}{p_{i \max}}$	$\frac{1.1 L_S}{p_{i \max}}$	Daewel et al. 2008a	Daewel et al. 2008a
A.4.2	$p_{i \max}$	$\frac{1524.9}{1 + \left(\frac{L_S}{14.0}\right)^{-1.63}}$	$\frac{1.2936}{1 + e^{-(L_S - 2.8579)/1.2758}}$	Daewel et al. 2008a	Unpublished data (see text)
A.5	$H T_{L_S,i}$	$e^{0.264 \times 10^{7.0151} \left(\frac{p_i}{L_S}\right)}$	$e^{0.264 \times 10^{7.0151} \left(\frac{p_i}{L_S}\right)}$	Walton et al. 1992	Walton et al. 1992
A.6.1	$C_{\max}$	$1.315 M_D^{0.83} \times 2.872 \left[\frac{(T-15)}{10}\right]$	—	Daewel et al. 2008a	—
A.6.2	$G C_{\max}$	—	$3.24 + 0.064 M_D$	—	Lough et al. 2005
A.6.3	$G E R$	—	$1.792 L_S^{-0.828} \times Q_{10}^{\left(\frac{T-12}{10}\right)}$	—	Peck and Daewel 2007

Capture success (eq. A.4) has been parameterized as a function of prey length and larval length (Munk 1992) and differs for Atlantic cod and sprat in the formulation of the maximum prey size versus larval size (eq. A.4.2). This formulation was based upon measurements made of the prey in gut contents of sprat (Voss et al. 2003; Dickmann et al. 2007) and Atlantic cod (G. Lough, Northeast Fisheries Science Center, NMFS, NOAA, Woods Hole, MA 02543, USA, unpublished data).

In the cod IBM, the majority of the parameter estimates was the same as utilized by Lough et al. (2005), including parameterizations needed for the foraging and growth submodule. One parameter that prevented overfeeding (gut evacuation rate, GER) needed to be modified so that modelled growth matched observations of larval cod growth over a broad range of temperatures (Otterlei et al. 1999). GER was adapted from a generalized formulation published by Peck and Daewel (2007) (eq. A.6.3) and included a  $Q_{10}$  of 3 and a threefold increase in GER during feeding, adjustments well within the range of values observed for the larvae of a number of different species (see Peck and Daewel 2007). In the sprat IBM, a maximum consumption parameter ( $C_{\max}$ ) (eq. A.6.1) was utilized (instead of GER) to prevent overfeeding and unrealistically high growth rates (see Daewel et al. 2008b).

IBM: metabolic losses and length growth

Equation for larval mass–length relationships (eq. A.11) and metabolic losses including assimilation efficiency (eq. A.7), specific dynamic action (eq. A.8), and standard and active metabolic rates (eqs. A.9 and A.10) are given in Table A4.

Table A4. Model equations for metabolic losses and the mass–length relationship for Atlantic cod and sprat.

	Variable	Sprat	Atlantic cod	Citation	
				Sprat	Atlantic cod
A.7	$\beta$	$0.7\left[1-0.3\mathrm{e}^{-0.003(M_D-M_{D\text{MIN}})}\right]$	$0.7\left[1-0.4\mathrm{e}^{-0.003(M_D-50)}\right]$	Buckley and Dillmann 1982	Lough et al. 2005
A.8	$SDA_{m_i}$	$0.11+4.91\times10^{-7}\times m_i$	0.35	See Daewel et al. 2008a	Lough et al. 2005
A.9	$R_s$	$b\times0.00272\times M_D^{0.80}\times2.57^{\left[\frac{(T-8)}{10}\right]}$	$b\times0.00114\times M_D^{(1.02900-0.00774\times\ln M_D)}\times\mathrm{e}^{[(0.10720-0.00320\times\ln M_D)\times T]}$	Kjørboe et al. 1987	Lough et al. 2005
A.9.1	$b$	$\gamma\times\chi$	$\gamma\times\chi$	Hinckley et al. 1996	Hinckley et al. 1996
	$\gamma$	0.00463	0.00463	Brett and Groves 1979	Brett and Groves 1979
	$\chi$	227.0	227.0	Theilacker and Kimball 1984	Theilacker and Kimball 1984
A.10	$R_A$	$k\times R_s$	$k\times R_s$	—	—
A.10.1	$k$	$k=\begin{cases}1.9+0.0076m_i & \forall m_i\leq 800\text{ g}\\2.5 & \forall m_i> 800\text{ g}\end{cases}$	$k=\begin{cases}1.4 & \forall L_S< 5.5\text{ mm}\\2.5 & \forall L_S\geq 5.5\text{ mm}\end{cases}$	Beyer and Laurence 1980	Lough et al. 2005
A.11	$L_s$	$3.928M_D^{0.199}$	$1.935M_D^{0.247}$	Peck et al. 2005	Lough et al. 2005

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