THE INFLUENCE OF BIOPHYSICAL FACTORS ON THE CONNECTIVITY OF HOLOPLANKTONIC COPEPODS

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Abstract

Although there are few obvious physical dispersal barriers in the ocean, holoplanktonic copepods exhibit species-specific distribution patterns and significant genetic structure within ocean basins and gyres. To explain these patterns, a flexible biophysical model to examine connectivity of various species of holoplanktonic copepods across the Atlantic Ocean basin was developed and implemented. These tools include an individual-based model (IBM) forced by a physical model to examine the effects of interactions among biological traits and the physical environment on connectivity. This model allows for the characterization of meaningful variability in biological responses to the environment both among individuals and across species. First, distribution and connectivity patterns for a generic model species are explained by linking influential life history traits, including ontogenetic vertical migration, diel vertical migration, reproduction, development, and mortality, to environmental factors such as food concentration, temperature, and ocean currents. Results are discussed with respect to distributions of various life history traits, and resulting community dynamics across the ocean basin, including how these might vary with environmental changes in the future. Second, the new model is applied to a case study for the globally-distributed copepod, *Pleuromamma xiphias,* to disentangle underlying drivers of genetic structure. We compare our model results to the observed spatial distribution of genetic variation across the Atlantic basin to assess model performance and gain insight into the functional traits that affect connectivity.

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Introduction

Holoplanktonic copepods are extremely abundant crustaceans that spend their entire lives in the pelagic realm and occur in all ocean basins around the world (Mauchline 1998). They are an important trophic link near the base of the marine food web, grazing directly on phytoplankton and microzooplankton (Calbet & Landry 1999), and copepods are in turn prey for micronekton and the larvae of pelagic fish. Their central position within the marine food web makes them extremely important in supporting higher trophic levels and commercially valuable pelagic fisheries (Landry et al. 2001; Lynch et al. 2001; Greene et al. 2003). Furthermore, they contribute significantly to carbon and nitrogen export to the deep ocean via excretion of dissolved organics, sinking fecal pellets, and vertical migration (Al-Mutairi & Landry 2001). Little is known about connectivity among populations of copepods, because patterns of dispersal are difficult to discern with extremely large populations and small individual body sizes. Extremely large populations make it difficult to determine population dynamics, and their small bodies cannot be tagged for in-situ tracking.

Estimates of connectivity among populations are necessary to determine effective management units for marine protected areas and fisheries, explain genetic variation across space, and predict adaptation potential and/or distribution shifts by populations that could cause dramatic effects to associated ecosystems. A mechanistic understanding of the factors that influence connectivity requires accurate estimates of the rate of exchange among geographically separated populations (Cowen et al. 2007; Cowen & Sponaugle 2009). Because holoplanktonic copepods spend their entire lives in the pelagic realm and are unable to swim horizontally against ocean currents, they have the potential for high dispersal (Peijnenburg & Goetze 2013). Genetic methods have been helpful for exploring connectivity among holoplanktonic populations. In principle, holoplanktonic populations should be exchanging migrants regularly and appear genetically homogenous both within and among ocean basins because of wind-driven mixing and the fact that there are relatively few land barriers across ocean basins (Palumbi 1994; Norris 2000). Contrary to this expectation, studies have found species-specific distribution patterns and intraspecific genetic structure among oceans and within basins and gyres that could not be explained by physical transport processes alone (e.g. Bucklin & Kocher 1996; Goetze 2005; Blanco-Bercial et al. 2011; Goetze 2011; Norton & Goetze 2013). Thus, it is likely that biological and behavioral factors play a significant role in shaping the connectivity among copepod populations and population structure within species. A number of studies in population connectivity have focused on meroplanktonic larvae (e.g., Paris et al. 2007; Cowen & Sponaugle 2009; Soria et al. 2012), while very few explore the connectivity of holoplanktonic populations (Blanco-Bercial et al. 2011). The studies that have explored the connectivity among holoplankton so far have addressed patterns at smaller regional scales; this thesis is the first mechanistic study that aims to understand how biological and behavioral traits affect the connectivity of holozooplankton across the Atlantic basin at broad spatial scales from 45°N to 45°S.

Biophysical interactions have been shown to greatly affect connectivity of meroplankton. Differences in life history traits such as growth, development, mortality, larval behavior including vertical migration, and pelagic larval duration (PLD) as well as the interaction of these traits and behaviors with environmental factors have been shown to significantly affect meroplankton dispersal (Cowen & Sponaugle 2009; Weersing & Toonen 2009; Gilbert et al. 2010; Kendall et al. 2013). For example, while the duration of time that larvae spend in the water column allows for high dispersal, it is not sufficient to estimate dispersal solely based on a constant PLD because PLD is influenced by environmental factors such as temperature and season, and varies by species and location (Cowen & Sponaugle 2009). In this study, PLD was not considered because holoplanktonic zooplankton do not settle. Instead, the effects of reproduction, development, mortality, and vertical migration on dispersal and connectivity was explored.

Holoplanktonic copepods are a diverse group with variable life history strategies, including reproduction, growth and development, mortality, and vertical migration behavior (Norris 2000; Campbell et al. 2001; Bunker & Hirst 2004; Palomares-Garcia et al. 2013). These biological and behavioral traits, referred to as functional traits in this study, have a strong link with environmental factors because copepods are ectotherms, meaning that they are unable to regulate their internal temperature. Therefore, ambient temperature has a significant effect on biological processes such as reproduction and development (Hirche et al. 1997; Campbell et al. 2001; Bunker & Hirst 2004). Laboratory experiments have shown that egg production rates increase with temperature and food concentrations across various copepod species (Hirche et al. 1997; Bunker & Hirst 2004). Regional modeling studies of holoplanktonic copepods have shown that biological and behavioral processes such as development, fecundity, mortality, and vertical migration can significantly affect spatio-temporal distribution and connectivity (Speirs et al. 2005; Paris et al. 2013; Record et al. 2013).

The probability of connectivity depends on population size. With a larger population size, the probability of survival and dispersal to new regions is higher than that of a smaller population. Therefore, connectivity patterns of copepods may vary with reproductive strategy since the number of eggs that are produced can differ by an order of magnitude (Bunker & Hirst 2004). Broadcast spawners lay their eggs directly into the water column and are able to produce a greater number of eggs than sac spawners, which carry their eggs in sacs attached to their bodies until the eggs are hatched (Bunker & Hirst 2004). They have smaller clutch sizes due to the limited space that is available in sac. However, mortality rates must be considered, because the evolutionary tradeoff for broadcast spawners is that their eggs have lower survivorship than those of sac spawners (Hirst & Kiørboe 2002). Developmental rate can also affect the survivorship and population size, such that faster developing species could in theory have a higher probability of survival by passing more quickly through the earlier high mortality life history stages and becoming reproducing adults (Hare & Cowen 1997; Cowen & Sponaugle 2009).

Ontogenetic and diel vertical migration are also common characteristics of zooplankton that can affect spatio-temporal distribution and connectivity because of variation in flow velocities at different depths (Cowen & Sponaugle 2009; Paris et al. 2013). Ontogenetic vertical migration (OVM) refers to the change in depth that some copepod species display as they moult from one developmental stage to the next (Ferrari 1985; Kobari & Ikeda 2001). Calanoid copepods have 12 developmental stages including six naupliar stages (N1-N6), five copepodite stages (C1-C5), and an adult stage (C6) (Allan 1976; Mauchline 1998). Typically in species that display OVM, adults are found deeper than eggs and juveniles. Shallower depths are favorable because of the greater abundance of phyotosynthesis and food availability, while deeper depths are favorable because of the lower number of predators. Some species of copepods display diel vertical migration (DVM), typically a daily ascent at dusk, and descent at dawn, at later developmental stages (Lampert 1989; Holliland et al. 2012). DVM allows zooplankton to feed during the night in the epipelagic zone, and avoid visual predators during the daytime (Zaret & Suffern 1976; Hays 1995; Hays 2003). The magnitude of DVM can vary from a few meters to hundreds of meters between species and developmental stages (Lampert 1989; Anderson et al. 2001).

Connectivity and rates of exchange can be explored through individual-based modeling (IBM), which tracks individuals through space and time. IBMs provide a powerful and effective tool to consolidate estimates of many environmentally dependent processes from field and laboratory experiments, while allowing for meaningful individual variability in responses (Paffenhöfer et al. 1995; Fiksen 2000; Neuheimer et al. 2010a; Richmond et al. 2013). IBMs can be used to assess our ability to explain variability in observations, identify knowledge gaps to direct future sampling and research, and make predictions about population and ecosystem dynamics in a changing climate. In particular, an IBM can be used to test which life history strategies and environmental parameters are driving population connectivity. In this study, various combinations of functional traits can be chosen in the IBM to represent different species of holoplanktonic copepods.

Recent studies have begun to investigate if higher mortality and lower rates of reproduction in equatorial regions can explain the observed equatorial dispersal barrier for holoplanktonic copepods (e.g. Norton 2013), however studies have yet to mechanistically link biological and environmental processes at the basin scale. Questions addressed by this study and their related hypotheses include:

1. Do modeled connectivity estimates differ between a physical transport only model and a model that includes environmentally dependent biological and behavioral traits such as vertical migration, development, reproduction, and mortality?
2. Which combination of biological or behavioral processes creates the largest number of significant changes in pathways?
    a. How do modeled connectivity estimates differ spatially across the Atlantic basin? Where do the differences occur, and are they gains or losses in connectivity?
3. How do modeled connectivity estimates of a target species, *Pleuromamma xiphias*, compare to observed spatial patterns of population structure and the distribution of genetic variation across these ocean regions? The null hypothesis is that modeled connectivity estimates will have no relationship with observed spatial patterns in pairwise F_{ST} values among sites or regions (data from Goetze et al. 2016).

The first objective of this study was to mechanistically link biological and behavioral processes to dispersal and connectivity among holoplanktonic populations. It is still unknown how environmentally forced biological processes influence connectivity across various species and locations, so this study should give insight into how the interaction of physical forces and biological processes could affect the connectivity of holoplankton at basin scales. The second objective was to create a biophysical model that is able to estimate connectivity for a variety of holoplanktonic taxa. Different types of holozooplankton, or copepod species, could be represented as trait-based functional groups to allow model results to be mechanistically linked to processes. The model created for this thesis is flexible and allows users to choose model species average depth, whether a model species is vertically migrating or non-migrating, has food-limited reproduction and development, etc. There are also options for choosing if fecundity and development are a function of temperature, or both temperature and food. Finally, the third objective was to test the accuracy of the biophysical model in a case study on the copepod *Pleuromamma xiphias,* for which genetic data was available. This study has the potential to disentangle the underlying drivers that influence connectivity across ocean basins and will produce testable hypotheses that can inform future research with regard to climate change and the potential for adaptation.

Methods

The biophysical model

The IBM tracks individual “compupods” (Maps et al. 2012), or electronically simulated copepods, as they are born, grow, develop, reproduce, move in space, and die. From this point hereafter, model-simulated copepods will be referred to as “compupods.” Biological processes, for example reproduction and development, were modeled based on laboratory and field data and were forced by associated environmental factors including advection, temperature, and food availability. Because holoplanktonic copepods are diverse and their life histories vary by species, variability in processes and strategies will be included via variability in process characterization; examples include ontogenetic vertical migration (OVM), diel vertical migration (DVM), and dependencies on temperature and food for reproduction and development.

Individual compupods were initialized across the Atlantic basin with forcing factors including abundance, advection, temperature, and food availability (Fig. 1). Temperature and physical forcing via 2D advection estimates for the model were obtained from the Simple Ocean Data Assimilation (SODA v2.2.4). SODA is a global oceanic reanalysis data set that provides monthly upper-ocean temperature, salinity, and advection data at a 0.25°x0.4°x40 level resolution for the years between 1871 and 2008 (Carton et al. 2000; Carton & Giese 2008). Although vertical advection estimates were available from SODA, they were not used because the estimates were relatively small compared to the vertical swimming speed of holoplanktonic copepods. Monthly data from SODA was temporally interpolated to obtain daily time-steps in the biophysical model. A daily time-step was chosen for this model since generation time and biological rates for most subtropical and tropical copepods are on the scale of days, and a finer temporal resolution would require an immense increase in model run time. The physical model was coupled with the biological model such that varying environmental temperature, food concentration and ocean currents forced the model processes, including the position of copepods, as well as rates of reproduction and development.

Average monthly chlorophyll-a concentrations (mg m^{-3}) for July 2002 – December 2014 were obtained from MODIS Aqua (Ocean Biology Processing Group 2003). Because the MODIS Aqua data covered a significantly shorter time period and different spatial grid than SODA, average chlorophyll-a concentrations were calculated for each calendar month and interpolated via inverse distance weighting to estimate concentration at locations on the SODA grid. Chlorophyll concentrations were used as a proxy for food availability, which has a positive correlation with rates of reproduction and development in copepods (Hirche & Kwasniewski 1997; Neuheimer et al. 2009). Food-dependency was included as a model choice because of the variation in responses to food limitation by species (Bunker & Hirst 2004).

Patterns of high abundance in the subtropical gyre and lower abundances at high latitudes and near the equator were observed on the AMT22 cruise for *Pleuromamma xiphias* (Goetze et al. 2016); therefore, the model was initialized with similar relative abundances distributed across the Atlantic basin in anticipation of the case study. Abundance varies across species through space and time, and the model can be adjusted to represent various distributions, although this was not done in this study.

The model was run for a simulation time of 30 years. A sensitivity analysis was run to assess the differences in connectivity for simulation times of 1, 5, 10, 15, 30, and

50 years. Sensitivity analyses were run by viewing connectivity and difference matrices for two simulations, and also by counting the number of origin-destination pairs with significant differences ($p<0.05$) from a general additive model (see statistical analysis below). 30-year simulations were used for experiments because there were no significant differences between connectivity results for 30 and 50-year simulations. Sensitivity of model results to modeled processes and parameterization was made to determine how connectivity changes among functional groups or copepod species.

The probability of connectivity among populations in Longhurst's biogeochemical provinces (Longhurst 2007) in the Atlantic basin was calculated after each model simulation (Fig. 2). Because of the difficulty in discerning latitudinal hemisphere of the equatorial Longhurst provinces, connectivity is discussed in this study with Longhurst provinces grouped into Northern Atlantic, Equatorial, and Southern Atlantic regions. The Northern Atlantic region consists of seven Longhurst provinces (Longhurst 2007) including the Gulf Stream (GFST), North Atlantic Subtropical Gyre West (NASTW), North Atlantic Subtropical Gyre East (NASTE), Mediterranean Sea (MEDI), Caribbean (CARB), North Atlantic Tropical Gyre (NATR), and Canary Current (CNRY). The Equatorial region consists of four Longhurst provinces: Guianas (GUIA), Western Tropical Atlantic (WTRA), Eastern Tropical Atlantic (ETRA), and Guinea Current (GUIN). The Southern region consists of four provinces: Brazil Current (BRAZ), South Atlantic Gyre (SATL), Benguela Current (BENG), and South Subtropical Convergence (SSTC). Results for the general model were in the form of 15x15 connectivity matrices, where the rows represent the Longhurst province of ancestral compupods, or origin, at model initialization and the columns represent the province of last position either due to death or end of simulation. Each box of the connectivity matrix represents a unique pathway that implies connectivity of a specific ancestral origin and destination.

Each connectivity matrix cell contains a “retention clock” (Fig. 3) (Defne et al. 2016), which visualizes how connectivity changes through time (i.e. over the 30 years). Viewing temporal changes in connectivity is especially important for holoplankton since they do no settle, and remain in the water column for their entire lives. Retention clocks are read clockwise, where 12:00 represents the connectivity at time = 0, and the end of simulation after one full rotation. Modeled connectivity was measured as a proportion calculated by dividing the total number of compupods in each matrix cell by the total number of live compupods from Longhurst region of ancestral origin at each time step. Because model simulations were all 30 years, and connectivity clocks have 17 slices each, the average connectivity for every ~1.8 years is shown in a pie chart slice. The change in color with clockwise rotation of the clock designates how the proportion of compupods that are retained in a particular Longhurst province is changing over time. The biophysical model used in this study was written in the R programming language (R Core Team 2014) with the following libraries: abind (Plate & Heiberger 2015), data.table (Dowle et al. 2014), doParallel (Revolution Analystics & Weston 2014a), dplyr (Wickham & Francois 2014), foreach (Revolution Analystics & Weston 2014b), ggplot, ncdf (Pierce 2014a), ncdf4 (Pierce 2014b), oce (Kelley & Richards 2016), plotrix (Lemon 2006), reshape (Wickham 2007), and sgeostat (Majure et al. 2013).

Experimental design

To assess the effect of various functional traits (Fig. 4), layers were added incrementally (Table 1) to the base model, which was a passive particle simulation. Functional traits that were modeled include ontogenetic vertical migration (OVM), diel vertical migration (DVM), temperature-dependent reproduction and development, and temperature and food dependent reproduction and development.

The base model simulated 13,000 passive particles at a constant depth of 200 m for 30-years. 13,000 particles were required to obtain connectivity across the majority of Longhurst regions, and increasing the number of particles did not improve resolution of the results. The depth of 200 m was chosen as an intermediate depth at which the primary daytime mode for *Pleuromamma xiphias* at stages C2-C6 has been approximately observed (Roe 1972; Ferrari 1985; Anderson et al. 2001) in anticipation of the case study. While depth distribution varies greatly by species, daytime depths of 200 m is not uncommon in other copepod species such as *Pleuromamma abdominalis*, *P. robusta*, *P. borealis*, *Scottocalanus securifrons*, *S. helenae*, *Scolecithricella ovate*, *S. vittata*, etc. (Roe 1972). Thus, the base model simulated a resident species at lower epipelagic/upper mesopelagic depths.

The first three experiments were chosen to assess how vertical distribution affects connectivity (Table 1). The models were similar to the base model, except that passive particles were distributed through a depth range of 50-500 m where they remained passive throughout model simulation at the depth initially assigned, so as to mimic depth distribution as a result of OVM for Experiment 1 (Table 2). For Experiment 2, DVM was modeled by switching ~25% of the compupods between depths of 50 m and 500 m with each time-step of one day, while the rest remained at 200 m. Only a quarter of the particles were chosen to switch depths, because copepods are only able to perform DVM at later developmental stages, including C4, C5, and adult stages. Although DVM is characterized by an ascent and descent within 24 hours, an approximation of switching between deep and shallow depths with each day was used because one day was the smallest time step obtained for model. Experiment 3 was a combination of Experiments 1 and 2, with compupods distributed across the depth range 50-500 m, and with some moving between depths of 50 and 500 m with each time-step. The depth range of 50-500 m was used as the generic depth range for OVM and DVM because it includes depths with a large range in temperature and flow velocity, and is a plausible depth range for OVM or DVM in holoplanktonic copepods (Roe 1972; Ferrari 1985; Anderson et al. 2001).

The next functional trait tested in Experiments 4, 5, and 6 was temperature-dependent development. Temperature-dependent development was added to the model by including development of compupods through 12 life history stages. Developmental rates could affect connectivity for species that display OVM because development into a new stage results in changes of depth, or vertical migration (Ferarri 1985; Anderson et al. 2001). Development was modeled using the Belehrádek function (Campbell et al. 2001), which assumes that stage duration is a function of temperature. The following equation was used (Campbell et al. 2001), where SD (stage duration, days) is dependent on a_i (a stage-dependent coefficient for stage *i,* days $°C^{2.05}$) (Table 3), and temperature (Temp, °C):

$$SD = a_i * (Temp + 9.11)^{-2.05}$$

In Experiments 7, 8, and 9, temperature and food dependent development was added as a model layer to assess how connectivity is affected when food is added into the model. Laboratory studies suggest that stage durations are affected by both temperature and food availability (e.g., Landry 1975; Campbell et al. 2001; Møller et al. 2012), and can be estimated with the following equation, where SD (stage duration, days) is a function of temperature (Temp, °C) and chlorophyll-a (Chla, mg m^{-3}):

$$SD = a_i * (Temp+9.11)^{-2.05} \times (17/(Chla*50 \text{ mg}^{-1} \text{ m}^{3})+1)$$

For all models including development, moult cycle fractions (MCF) were used for the accurate estimation of stage durations, with variations of temperature and food through time (Miller & Tande 1993; Gentleman & Neuheimer 2008; Neuheimer et al. 2010a). Using MCF allows for tracking of the proportion of development completed with each time-step in model simulations as compupods move through space and time. MCF = 0 when an individual moults into a new stage *i*, and is increased with each time-step. Therefore, the new MCF at time $t+\Delta t$ is (Gentleman & Neuheimer 2008):

$$MCF_{i,t+\Delta t} = MCF_{i,t} + \Delta t/SD_{i,t+\Delta t}$$

Once the MCF has reached or exceeded 1, individual copepods then develop into the next successive stage $i+1$, and MCF is set back to zero.

Reproduction and mortality were modeled in Experiments 10, 11, and 12. Reproduction was modeled with three variations, each of which depended on the number of adult females at every time-step: 1) uniform, where all female adults had 22 ± 8.9 eggs female^{-1} day^{-1} (Goetze et al. unpub, mean experimental egg production for *P. xiphias*), and 2) temperature and food dependent, with chlorophyll-a as a proxy for food converted to carbon with a 1:50 chlorophyll/carbon ratio (Hirche & Kwasniewski 1997; Neuheimer et al. 2010a). The following equation (Hirche et al. 1997; Neuheimer et al. 2010a) was used, where fecundity (Fecundity, eggs female^{-1} day^{-1}) is a function of temperature (Temp, °C) and chlorophyll-a concentration (Chla, mg m^{-3}):

$$\text{Fecundity} = (3.7\ {}^\circ\text{C}^{-1}\ \text{f}^{-1}\ \text{d}^{-1} * \text{Temp}) + (0.053\ \text{f}^{-1}\ \text{d}^{-1} * (\text{Chla} * 50\ \text{mg}^{-1}\ \text{m}^{3})) + (0.0066\ {}^\circ\text{C}^{-1}\ \text{f}^{-1}\ \text{d}^{-1} * (\text{Temp} * (\text{Chla} * 50\ \text{mg}^{-1}\ \text{m}^{3})))$$

Mortality was modeled in two ways. Linear mortality rates (m_1, day^{-1}) were stage-specific instantaneous rates obtained from Ohman et al. (2002), where ΔZ is the change in number of individuals at stage *i*, Z is the number of copepods currently in stage *i*, and Δt is the time step (days) (Table 4). In this formulation, mortality rates are constant over time.

$$\Delta Z = -m_1 Z \Delta t$$

A quadratic formula was used as the second option to represent density-dependent mortality (Gentleman & Neuheimer 2008). Mortality rate increases with compupod abundance, which could represent ecological effects of predation or cannibalism, where adult females eat their own eggs (Gentleman & Neuheimer 2008; Neuheimer et al. 2009).

Here, $m_2 = m_1$/aveNum, and aveNum is the running average abundance of individuals at stage *i*.

$$\Delta Z = -m_2 Z^2 \Delta t$$

Statistical analysis

Variation in connectivity estimates between two model runs was statistically modeled with the 'mgcv' library (Wood 2011) as a general additive model (GAM) assuming a beta distributed error (logit link) because connectivity was a proportion, which was beta distributed with values ranging between zero and one. Connectivity proportion was calculated as the number of migrants to each Longhurst region, given the origin of ancestor at model initialization. The following statistical formula was used where site-specific connectivity was the response, scenario (e.g. OVM versus OVM and temperature-dependent development) the predictor, and time was fitted with a smoother to allow for non-linearity in the relationship between connectivity and time:

$$\text{Connectivity} \sim \text{Scenario} + s(\text{Time})$$

Study region

The region of interest for this study includes the subtropical and tropical regions of the Atlantic basin, between 45°N and 45°S. Previous studies have shown that subpopulations and strong genetic structure of holoplanktonic copepods can occur at this spatial scale (Goetze 2011; Norton & Goetze 2013; Goetze et al. 2015). This region also covers the distributional range of *Pleuromamma xiphias* in the Atlantic Ocean, and our comparative genetic data from this species that was obtained on the Atlantic Meridional Transect cruise (AMT22).

Case study species: Pleuromamma xiphias

The target species for the case study was the abundant and cosmopolitan calanoid copepod, *Pleuromamma xiphias*. *Pleuromamma xiphias* is one of the largest-bodied species of the mesozooplankton (3.5-5.9 mm adult females), and this species displays both diel and ontogenetic vertical migration (Ferrari 1985; Goetze 2011). During the night, adults ascend to the upper 160 m of the water column, and during the day descend to depths between 400-1000 m (Roe 1972; Ferrari 1985; Goetze 2011, Goetze unpub). Both OVM and DVM were included in the *P. xiphias* model, with depths ranging between 50-1000 m, which is deeper than the range used for the general model. Using estimates from Ferrari (1985), compupods at earlier developmental stages were modeled to live at shallower depths than the later developmental stages. Only C4, C5, and adult copepods perform DVM (Ferrari 1985); therefore, the model reflected DVM by moving the C4, C5, and adult compupods between average stage-specific upper and lower depths with each daily time step. *Pleuromamma xiphias* are opportunistic feeders, switching between herbivorous and carnivorous diets (Schnetzer & Steinberg 2002), therefore the modeled chlorophyll-a may not be a very accurate estimate of food availability because of the ability of *P. xiphias* to switch to a carnivorous diet in regions with low-chlorophyll. For this reason, temperature-dependent development and reproduction with no food dependency were used to model *P. xiphias*. Scarce information is available for biological rates in *P. xiphias*, including egg production, growth, development, and mortality. We therefore model environmentally-dependent development rates for *P. xiphias* using scaled empirical estimates from another calanoid species that is also widely distributed and large-bodied (f.x. *Calanus finmarchicus* in Campbell et al. 2001). Scaled estimates for fecundity (eggs female^{-1} day^{-1}) of broadcast spawners from Bunker & Hirst (2004) was used for the reproductive rate of *P. xiphias*.

The 12 primary sites from which genetic data for *P. xiphias* were obtained on the Atlantic Meridional Transect cruise (AMT22) fall into four Longhurst provinces (Longhurst 2007): North Atlantic Subtropical Gyre East (NASTE), North Atlantic Tropical Gyre (NATR), South Atlantic Gyre (SATL), and South Subtropical Convergence (SSTC) (Fig. 5). For this case study, the Longhurst province "NASTE" is referred to as North Subtropical (N. Subtropical), "NATR" as North Tropical (N. Tropical), "SATL" as South Gyre (S. Gyre), and "SSTC" as South Convergence Zone (S. Convergence). Pairwise F_{ST} values for *P. xiphias* suggest that there should be little to no exchange of migrants across the equator, moderate mixing between North Subtropical and North Tropical, as well as between the South Gyre and the South Convergence Zone, and self-recruitment in all four provinces in which genetic data were collected (Goetze et al. 2016) (Fig. 5). We should expect to see persistence over time of a population in the equatorial regions because of the higher diversity and unique genotypes present only in this region (Goetze et al. 2016).

Results

Passive particle results

Passive particles showed high connectivity across the Northern Atlantic, Southern Atlantic, and Equatorial regions, but no particles had a destination in the SSTC province (Fig. 6). Particles were spread throughout all Longhurst provinces, with relatively high migration from the Northern to Equatorial region, and Equatorial to Northern and Southern regions, and self-retention in the equatorial regions. Relatively low self-retention was noted in the following Northern subtropical regions: GFST, NASTW, NASTE, MEDI, and CARB provinces. Low migration was also observed from the Southern to the Equatorial region. Without reproduction or mortality in the model, the number of particles remained constant unless particles were lost from being advected outside of the Atlantic basin, or into the continental margins. The long simulation time and lack of mortality allowed for high connectivity across the Atlantic basin, but no particles ended with the SSTC province as a destination.

Vertical migration (Experiments 1-3)

Differences between the base model and the vertical migration simulation results (Fig. 6, 7) were difficult to discern because of the large number of retention connectivity clocks and small pie sizes, with each pie representing the average connectivity every ~1.8 years. When compupods were distributed across the depth horizon 50-500 m to simulate ontogenetic vertical migration (OVM) in Experiment 1, GAM results showed that connectivity in 66% of the Longhurst origin-destination pairs were significantly different from the base model results ($p<0.05$) (Table 5), with a significant decrease in connectivity for 14 of 28 Northern Atlantic to Southern Atlantic pathways (Fig. 8). GAM results also showed that switching between shallow and deep depths to simulate diel vertical migration (DVM) in Experiment 2 resulted in significant differences for 46% of the Longhurst origin-destination pairs (Fig. 9). The combination of OVM and DVM for Experiment 3 resulted in significant differences for 64% of the origin-destination pairs, with a significant increase in connectivity for 16 of 28 pathways from the Northern basin to Equatorial regions (Fig. 10). Compared to the base model, all three vertical migration scenarios ended with slightly more gains than losses in connectivity with a general increase of connectivity from Northern Atlantic to Equatorial region, and loss of connectivity from the Northern to the Southern Atlantic (Table 5).

Temperature-dependent development (Experiments 4-6)

The addition of temperature-dependent development to the model resulted in significant differences ($p<0.05$) in 61-69% of the Longhurst origin-destination pairs with variation due to vertical migration settings (Table 5; Fig. 11-13). Over all experiments, the combination of temperature-dependent development with OVM in Experiment 4 caused the largest proportion of Longhurst origin-destination pairs to significantly differ, with slightly more losses (52.9%) than gains (47.1%) in connectivity (Fig. 11). The bulk of losses occurred in pathways with an Equatorial region destination. 51.6% of the pathways with an Equatorial destination had decreased connectivity. Experiments 5 and 6, which assessed effects of adding a layer of temperature-dependent development to DVM and OVM+DVM, respectively, resulted in more gains than losses in connectivity with no apparent spatial patterns among Northern, Equatorial, and Southern regions (Table 5).

Temperature and food dependent development (Experiments 7-9)

Temperature and food dependent development had a slightly smaller effect than temperature-dependent development on the proportion of Longhurst origin-destination pairs that were significantly different. 56-68% of Longhurst origin-destination pairs significantly differed, with variation due to vertical migration settings (Table 5; Fig. 14-16). Adding a layer of temperature and food dependent development to the OVM model for Experiment 7 resulted in the most significant differences, and more losses (44.7%) than gains (55.3%) in connectivity. Experiments 8 and 9 resulted in more gains than losses in connectivity. Adding temperature and food dependent development in Experiments 7 and 9, which both include OVM, caused significant losses in connectivity from the Northern Atlantic to the Equatorial region for greater than 50% of the pathways, and from the Southern Atlantic to the Equatorial region for greater than 40% of the pathways.

Reproduction and mortality (Experiments 10-13)

The model was extremely sensitive to changes in mortality rates when using linear mortality, and produced unstable populations. Populations either increased exponentially when mortality rates were less than reproduction rates, or were completely diminished when mortality rates were greater than reproduction rates. In most cases, South Atlantic population declined faster than the North Atlantic population. The model was able to reach steady state when using quadratic closure, density-dependent mortality. The resulting connectivity matrices had much less connectivity compared to passive particle runs without reproduction and mortality, as expected due to the shorter lifespan of the compupods, which on average was ~35 days (Fig. 17,18). Temperature and food dependent reproduction and density dependent mortality resulted in significant differences for 60-64% of the Longhurst origin-destination pairs, but more than 95% of these differences were decreases in connectivity (Table 5; Fig. 19,20). Reductions in connectivity occurred across the basin, except for in a few pathways with destinations in the NASTE and GUIN provinces.

Case study: Pleuromamma xiphias

In the passive particle simulation, particles were transported across the equator from the North Tropical province to the South Gyre, and no self-retention was noted in the North Subtropical province (Fig. 21). Particles that originated in the North Subtropical province were dispersed to the North Tropical province, while most of the particles that originated in the North Tropical province were retained or traveled to the South Gyre. Particles that originated in the South Gyre were retained for the entire simulation, and particles that originated in the South Convergence Zone were transported to the South Gyre. Connectivity clocks show that over a 30-year simulation, connectivity varies greatly over time. Over the entire simulation, persistent connectivity is only seen from the South Convergence Zone to the South Gyre, and persistent retention within the South Gyre.

When OVM was added to model, compupods were distributed through the reported depth range of 50-1000 m for *P. xiphias* (Roe 1972; Ferrari 1985; Goetze et al. unpub). The simulation resulted in retention in the North Subtropical province, no transfer from the North Tropical province to South Gyre, and an additional pathway for connectivity from North Tropical to North Subtropical province (Fig. 22). Simulation including DVM gave similar results to passive particle simulation with no retention in the North Subtropical province and transport from the North Tropical province to the South Gyre (Fig. 23).

Compared to OVM simulation with compupods vertically distributed between 50-1000 m (Fig. 22), the simulation including temperature-dependent development and OVM resulted in increased connectivity through time between the North Subtropical and North Tropical provinces (Fig. 24).

Setting all functional traits to model *P. xiphias*, including OVM, DVM, temperature-dependent reproduction and development, and density-dependent mortality, resulted in extremely limited connectivity (Fig. 25). The only pathways of connectivity were from the North Tropical to the North Subtropical province, from the South Convergence Zone to the South Gyre, and self-retention occurred only in the South Gyre. Populations did not appear to persist in these Longhurst provinces. In considering all 15 Longhurst provinces, the only persisting migration pathway was from the North Atlantic to the Equatorial Atlantic (Fig. 26). No migration occurred from the South Atlantic to the Equatorial Atlantic.

Discussion

Few studies have explored connectivity of holoplanktonic copepods, and none to date on a basin-wide scale possibly because of the difficulty with estimating connectivity of large populations of small organisms that do not settle. In contrast, the effect of biophysical factors on connectivity among benthic populations of vertebrates and invertebrates with meroplanktonic larvae has been studied extensively on regional scales (e.g., Paris et al. 2007; Cowen & Sponaugle 2009; Soria et al. 2012; Kendall et al. 2013). Because of the enormous biomass of holoplanktonic zooplankton and their important mid-trophic position in marine food webs, we should continue to investigate zooplankton population connectivity and ecology in order to better manage fisheries and predict effects of environmental shifts associated with climate change. It remains unknown how genetically distinct populations of holoplanktonic zooplankton in the open ocean are able to persist through time (Goetze et al. 2015). The combination of genetic studies and connectivity modeling can help to explain observed genetic patterns of various species by running simulations to generate possible pathways of dispersal. Biophysical modeling has the potential to disentangle the different biological and physical processes that affect connectivity, and to serve as an assessment of the empirical estimates derived from laboratory and field studies in order to better understand species-specific life history traits. Estimates of connectivity can also help to create hypotheses of adaptation potential. Theoretically, with increased connectivity, open populations should appear genetically homogeneous (Cowen & Sponaugle 2009). On the contrary, with lower connectivity or isolation, closed populations have the potential for genetic drift and differentiation (Cowen & Sponaugle 2009). Understanding the connectivity of holoplanktonic copepods can assist with determining where the borders of marine protected areas should be located.

This study demonstrates that environmentally driven biological processes have significant effects on the distribution and connectivity among marine populations within ocean basins. Modeled connectivity estimates between simulations that included biological and behavioral traits were significantly different ($p<0.05$) from simulations forced by physical transport alone. The combination of ontogenetic vertical migration (OVM) with temperature-development created the largest magnitude of connectivity changes, but was followed closely by when OVM was paired with temperature and food-dependent development, and when OVM alone was modeled. Using OVM and environmentally forced development in the model created differences in connectivity by changing the stage duration of individuals, and thereby changing the amount of time that compupods spend at various depths associated with developmental stage. Without reproduction and mortality in Experiments 4 and 7, which added a layer of environmentally forced development to the models, OVM only has effects near the beginning of the simulation while compupods are not adults. As time progresses, compupods in naupliar and copepodite stages move through the different depths associated with the developmental stages (Table 2), and the time it takes to become an adult depends on location because of varying temperatures (Fig. 27) and food concentrations across the basin. After all compupods have developed into adults in the 30-year simulation, compupods will all be at the deeper adult depth, but endpoints or destinations will differ because of the different pathways that were taken in the naupliar and copepodite stages. Advection estimates vary across 3D space (Fig. 28) and time, so the timing of development and vertical migration can have significant effects on connectivity, causing spatially patchy increases and decreases in connectivity. For example, adding OVM and temperature-dependent development to the model resulted in a reduction in connectivity for most provinces with an origin in the Northern Atlantic and a destination in the Equatorial regions, but some increases in connectivity also occurred (Fig. 11).

Having the ability to vertically migrate to a suitable habitat and depth at each developmental stage has the potential to drastically change connectivity because of the broadened depth distribution, which could increase or decrease horizontal transport of zooplankton because of variability in horizontal flow velocity with depth (Fig. 28). This could have evolutionary implications such that species that perform vertical migration might have a higher probability of survival with changing environmental factors because of their ability to disperse to more suitable habitats. The simulations in this study showed that vertical migration could significantly change connectivity in more than 40% of the dispersal pathways across the Atlantic.

Reproduction and mortality also caused significant changes in 60%-64% of the dispersal pathways of compupods. Adding the layer of reproduction and mortality to a model with OVM, diel vertical migration (DVM), temperature and food dependent development caused significant changes in 64% of the pathways in Experiment 13 (Table 5). Including reproduction and mortality in a model with environmentally forced development would cause changes in connectivity results because compupods in a location with warmer water would have shorter stage durations, which could increase connectivity due to the shorter duration in early high mortality stages, and reduction in time it takes to become a reproducing adult. The higher survivorship and increase in population can increase the probability of migration. In a location with cooler water, compupods would likely show reduced connectivity because of the longer stage durations.

The number of pathways that showed gains and losses in connectivity was similar when OVM, DVM, and development were added to model in Experiments 1-9 (Table 5). In contrast, connectivity was greatly reduced among different Atlantic basin regions when reproduction and mortality were included in the model for Experiments 12-13 because of their relatively short lifespans of compupods under these simulations. Prior to the layer of reproduction and mortality being added to the model, compupods were neither being added nor subtracted from the total population, and all compupods unrealistically lived for the entire simulation of 30 years. Despite lower connectivity with reproduction and mortality included in the model, compupods were able to disperse among the Northern, Equatorial, and Southern Atlantic regions. Models including reproduction and mortality resulted in patchy connectivity among all Northern Atlantic, Equatorial, and Southern Atlantic regions, but without a dispersal pathway from the Southern Atlantic to the Equatorial region when vertical migration was both included and excluded from model (Fig. 17,18). When vertical migration was included, no connectivity was noted from the Northern to the Southern Atlantic (Fig. 18). There appeared to be some dispersal from the South Atlantic to the North Atlantic in the Gulf Stream (GFST) and Northern Subtropical Western (NASTW) provinces, probably as a result of the strong western boundary currents. Although dispersal among the Northern Atlantic, Equatorial, and Southern Atlantic was noted with these simulations, only 2-6 pathways out of a total of 225 pathways appear to persist through the entire simulation. While the power of the statistical model is reduced with lower numbers of compupods, knowing that a pathway for migration is possible with biological and physical processes modeled suggests that there is potential for genetic changes within the population that receives the migrant. The significantly lowered connectivity resulting from the inclusion of reproduction and mortality in the IBM implies that variations in reproduction and morality can have tremendous impacts on dispersal and connectivity, and can be a strong driver of genetic structure in holoplanktonic copepod populations. This finding agrees with other meroplankton studies, which found that mortality, along with pelagic larval duration, the time larvae spend in the water column, have significant effects on connectivity because of changes in dispersal ability (Cowen & Sponaugle 2009; Kendall et al. 2013).

Case study: Pleuromamma xiphias

Genetic data for *P. xiphias* from Goetze et al. (2016) allowed for model assessment, and further confirmed the importance of OVM in influencing connectivity. While genetic data are able to give an estimate of genetic differentiation among sites, it does not give the direction of migration. This biophysical model allows us to assess direction (e.g. site 1 to site 2 vs. site 2 to site 1) and showed that modeling biological processes could create differences in connectivity pathway directions. It is apparent that physical transport alone is unable to explain the genetic structure that is observed in *P. xiphias* as there is moderate dispersal of particles across the equator from the North Tropical province to the South Gyre and no self-retention within the North Subtropical and this contradicts genetic differentiation estimates, which suggests no migration across the equator and self-retention in all four regions that genetic data was obtained from. The addition of OVM alone resulted in modeled connectivity closest to the expected pattern (via genetics) with no migration across the equator, and mixing between the North Subtropical and North Tropical provinces, as well as between the South Gyre and the South Convergence Zone (Fig. 22). This model was unable to explain how retention occurs in the South Convergence Zone; this might not be a weakness of the model, as few particles would be expected to be retained considering that no particles were retained in this region during passive particle runs for the general model (Fig. 6). The smaller latitudinal band and size of the South Convergence Zone province, and variability of currents in that region are factors that reduce retention (Fig. 5).

DVM had less of an effect on connectivity than OVM, and did not cease dispersal from the North Tropical province to the South Gyre (Fig. 23). A similar genetic break at the equator between North and South Atlantic populations was observed for the cosmopolitan holoplanktonic copepod species *Haloptilus longicornis*, which does not exhibit DVM (Norton & Goetze 2013). Therefore, DVM is probably not the main driver for the strong genetic break observed at the equator.

The four Longhurst provinces used in this case study, from which genetic data was obtained, were insufficient for capturing modeled large-scale migrations that occurred throughout the Atlantic basin among the other Longhurst provinces (Fig. 26). Considering connectivity among the 15 Atlantic Longhurst provinces, persistent connectivity was noted was from the Northern Atlantic to the Equatorial Atlantic, and no migration occurred from the South Gyre to the Equatorial Atlantic. These results agree with a recent study, which used single nucleotide polymorphism (SNP) loci from

Pleuromamma xiphias in the Atlantic (Van Woudenberg 2016). The study suggests range overlap between the North subtropical/temperate Atlantic and Equatorial Atlantic populations, and less overlap between the South Atlantic and Equatorial Atlantic populations (Van Woudenberg 2016). Therefore, the modeled higher connectivity between the North Atlantic and Equatorial Atlantic, and lower connectivity between the South Atlantic and Equatorial Atlantic are consistent with observed population ranges. This could explain the higher haplotype diversity found in the Equatorial Atlantic in Goetze et al. (2016), which might be the result of immigrant and resident populations co-occurring in the equatorial region.

Through this case study, the importance of looking at larger ocean regions rather than smaller Longhurst provinces for connectivity became apparent. Longhurst regions were created to designate unique biological, physical, and geochemical properties, and were used in this study as origins and destinations for compupods (Longhurst 2007). Longhurst provinces were used in this study as a starting point because of the absence of other biogeographic schemes. Future studies should assess how well Longhurst provinces are suited for basin-wide connectivity studies, and consider other methods to determine the borders of origin and destination regions.

An assumption of the model is that genetic differentiation may arise among populations within *P. xiphias* within a 30-year period, but timescales for genetic drift within *P. xiphias* is unknown. The absence of empirical estimates for the life history processes of *P. xiphia*s also required large assumptions in this model.

Besides feeding behavior and depth distribution, little is known about the life history of *P. xiphias*. Estimates of reproductive rates were obtained from Goetze et al.

(unpub), but egg production experiments were only conducted on specimens from the southern Atlantic Ocean. Extrapolation was required to assume the same pattern of egg production rates across the Northern Atlantic, which could have introduced uncertainty in model results. Given the influence of development on the results, the largest source of error in this model is likely due to not having estimates for the development rates of *P. xiphias*, because there were no reference rates for this species. Development rates were scaled from another species (*Calanus finmarchicus* in Campbell et al. 2001*)*, but it would be optimal to have species-specific developmental rates for future studies because of high model sensitivity to differences in development rates. In addition, estimates of how developmental rates might vary across the range would help assess adaptation potential among populations.

Some testable hypotheses and research questions resulting from this case study include: 1) How do abundance and distribution patterns of *P. xiphias* in the Atlantic Ocean vary with season and on decadal timescales? 2) How does genetic data vary across longitude? Are populations in Longhurst provinces at the same latitude genetically similar? 3) Are *P. xiphias* populations migrating from the South Atlantic to the North Atlantic as a result of the strong Western Boundary currents? In particular, are there migrants from the Southern Atlantic in the GFST and NASTW provinces? 4) How do egg production and development rates of *P. xiphias* vary across the entire Atlantic basin?

Model sensitivity and limitations

A sensitivity analysis found that the model was slightly sensitive to start year of simulation. 12% of the pathways showed a significant difference when the model was started in year 1970 rather than 1950. In future use, this model should be run with various start years to obtain average connectivity estimates. Model was not sensitive to changes in simulation length for simulation lengths greater than 15 years.

This model could be improved with the use of a shorter time-step. The common form of DVM involves two migrations within one day; therefore, the depth changes could not be resolved with one-day time-step in this study. A higher time resolution would also be useful for calculating more accurate rates of advection, reproduction, development, and mortality considering the relatively short lifespan of most holoplanktonic zooplankton. The power of the model was also reduced when mortality and reproduction were included because of the drop of abundance. Future studies should look into other methods for maintaining statistical power, such as analyzing absolute number rather than proportion of compupod migrations, or modeling mortality with environmental forcing (Neuheimer et al. 2010b), so that rates or reproduction and mortality are better balanced.

Future direction in exploring connectivity

The next steps for moving forward with the research on connectivity of holoplanktonic copepods are to obtain basin scale patterns of abundance and biogeography for various species. Due to the high variability in biological and behavioral traits among holoplanktonic copepod species, it would also be helpful to conduct studies that obtain species-specific genetic data and empirical estimates of abundance, fecundity, growth, development, and mortality across various cosmopolitan species latitudinal ranges. Obtaining physiological data across different temperatures or biogeochemical regions would allow for a better understanding of how the environment affects biological processes and connectivity. It would assist in testing and improving the general model created in this study, providing insight into which types of environments tend to contain holoplanktonic populations with adaptive traits, and highlighting the key drivers of connectivity for holoplanktonic copepods.

IBM's are very flexible and can be easily modified. The addition of other biological traits to the model would be beneficial for making more accurate species-specific connectivity estimates. An important trait to add is reproductive strategy, which has shown to greatly affect connectivity among broadcast and sac spawners because of the differences in dispersal ability (Weber et al. 2015). Other traits to consider including as model options are seasonal spawning and diapause. Lastly, expansion to a global spatial scale could be useful for understanding the drivers of connectivity among populations in different ocean basins (Goetze 2011).

Conclusion

This study has shown that environmentally forced biological and behavioral processes can greatly affect connectivity among plankton populations at basin scales in the Atlantic Ocean. Although all of the general model layers of DVM, OVM, development, reproduction and mortality caused significant changes in connectivity across the Atlantic basin, OVM paired with environmentally forced development created the most changes. The losses in connectivity as a result of adding the layer of OVM and development, and the layer with reproduction and mortality suggest that these traits are major drivers of the isolation of populations and genetic structure in holoplankton. Understanding the different pathways of dispersal for holoplanktonic copepods could help in understanding observed genetic variation over space and obtaining more accurate predictions of population distributions and connectivity under various climate scenarios. With concern about climate change today, there are an increasing number of stressors including global warming, increasing ocean temperatures, and changing weather patterns. Models, like the one created in this study, can be used to assess whether or not a specific species is capable of range shifts to more suitable regions (Beaugrand et al. 2009). Using environmentally forced parameters to assess connectivity is extremely important for the prediction of how holoplanktonic populations can be affected in the future.

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Tables

Table 1. Experimental design to compare functional traits of vertical migration, temperature-dependent development, temperature and food dependent development, reproduction and mortality.

Experiment #	Test
Vertical Migration	
1	Base model (passive particles at one depth (200 m) – physical transport only) vs. **Ontogenetic vertical migration (OVM)**
2	Base model vs. **Diel vertical migration (DVM)**
3	Base model vs. **OVM+DVM**
Temperature Dependent Development	
4	OVM vs. OVM with **temperature dependent development**
5	DVM vs. DVM with **temperature dependent development**
6	OVM+DVM vs. OVM+DVM with **temperature dependent development**
Temperature and Food Dependent Development	
7	OVM vs. OVM with **temperature and food dependent development**
8	DVM vs. DVM with **temperature and food dependent development**
9	OVM+DVM vs. OVM+DVM with **temperature and food dependent development**
Reproduction and Mortality	
10	OVM+DVM with temperature and food dependent development vs. OVM+DVM with temperature and food dependent development + **uniform reproduction + linear mortality**
11	OVM+DVM with temperature and food dependent development vs. OVM+DVM with temperature and food dependent development + **temperature and food dependent fecundity + linear mortality**
12	OVM+DVM with temperature and food dependent development vs. OVM+DVM with temperature and food dependent development + **temperature and food dependent fecundity + quadratic mortality**
13	Base model vs. No vertical migration + **temperature and food dependent development + temperature and food dependent fecundity + quadratic mortality**

Table 2. Depths (m) used to model ontogenetic vertical migration (OVM) in the general model and for the case study species *Pleuromamma xiphias*.

Stage	**General model depth (m)**	***P. xiphias* model depth (m)**	**Standard deviation**
Egg	parent depth	parent depth	0
N1	50	100	20
N2	100	100	20
N3	100	100	20
N4	100	100	20
N5	100	100	20
N6	100	150	20
C1	150	150	30
C2	200	300	30
C3	250	400	40
C4	300	400	45
C5	350	700	45
C6 (Adult)	500	1000	30

Table 3. Stage dependent coefficients, a (days °$C^{2.05}$), for Belehrádek stage duration function: Stage duration = a_i * (Temp+9.11)$^{-2.05}$. Stage duration (days) is the length of time that an individual spends at stage *i*. (from Campbell et al. 2001 and Gentleman & Neuheimer 2008)

***i* (Stage)**	**a_i**
Egg	595
N1	387
N2	583
N3	1387
N4	759
N5	715
N6	841
C1	966
C2	1137
C3	1429
C4	2166
C5	5916

Table 4. Stage-specific instantaneous mortality rates (days^{-1}, digitized from Ohman et al. 2002; Neuheimer et al. 2010a)

Stage	m
Egg	0.495
N1	0.495
N2	0.2156
N3	0.051
N4	0.0765
N5	0.1412
N6	0.14865
C1	0.1163
C2	0.06905
C3	0.06095
C4	0.06715
C5	0.05785
C6 (Adult)	0.05785

Table 5. General additive model (GAM) results. Total proportion of significant ($p<0.05$) origin-destination Longhurst province pairs, and the percentage of pathways with increased and decreased connectivity.

Experiment	Test	Proportion of significant Origin-Destination pairs	Percent with increased connectivity	Percent with decreased connectivity
1	Base model vs. **Ontogenetic vertical migration (OVM)**	0.66	56.1%	43.9%
2	Base model vs. **Diel vertical migration (DVM)**	0.46	58.3%	41.7%
3	Base model vs. **OVM+DVM**	0.64	55.9%	44.1%
4	OVM vs. OVM with **temperature dependent development**	0.69	47.1%	52.9%
5	DVM vs. DVM with **temperature dependent development**	0.61	55.8%	44.2%
6	OVM+DVM vs. OVM+DVM with **temperature dependent development**	0.64	61.4%	38.6%
7	OVM vs. OVM with **temperature and food dependent development**	0.68	44.7%	55.3%
8	DVM vs. DVM with **temperature and food dependent development**	0.56	49.6%	50.4%
9	OVM+DVM vs. OVM+DVM with **temperature and food dependent development**	0.64	59.0%	41.0%
10	OVM+DVM with temperature and food dependent development vs. OVM+DVM with temperature and food dependent development + **uniform reproduction + linear mortality**	Unstable population, simulation did not finish	N/A	N/A
11	OVM+DVM with temperature and food dependent development vs. OVM+DVM with temperature and food dependent development + **temperature and food dependent fecundity + linear mortality**	Unstable population, simulation did not finish	N/A	N/A
12	OVM+DVM with temperature and food dependent development vs. OVM+DVM with temperature and food dependent development + **temperature and food dependent fecundity + quadratic mortality**	0.64	2.2%	97.8%
13	Base model vs. No vertical migration + **temperature and food dependent development + temperature and food dependent fecundity + quadratic mortality**	0.6	3.7%	96.3%

Figures

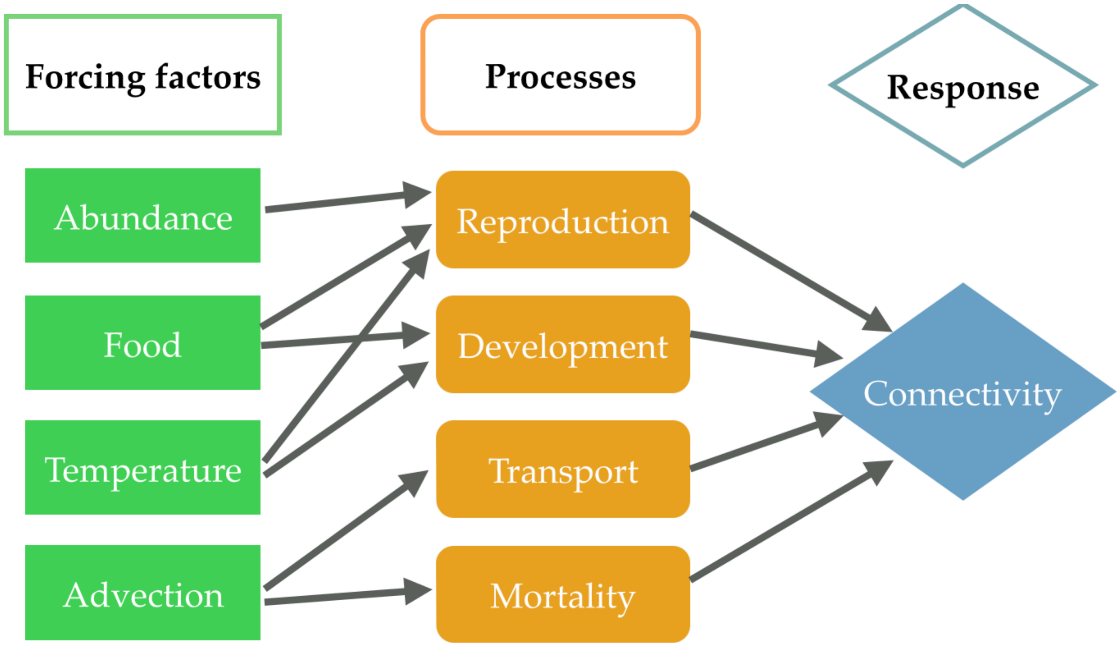


Figure 1. Flowchart for individual-based model (IBM) design including forcing factors, biological and behavioral process, and response.

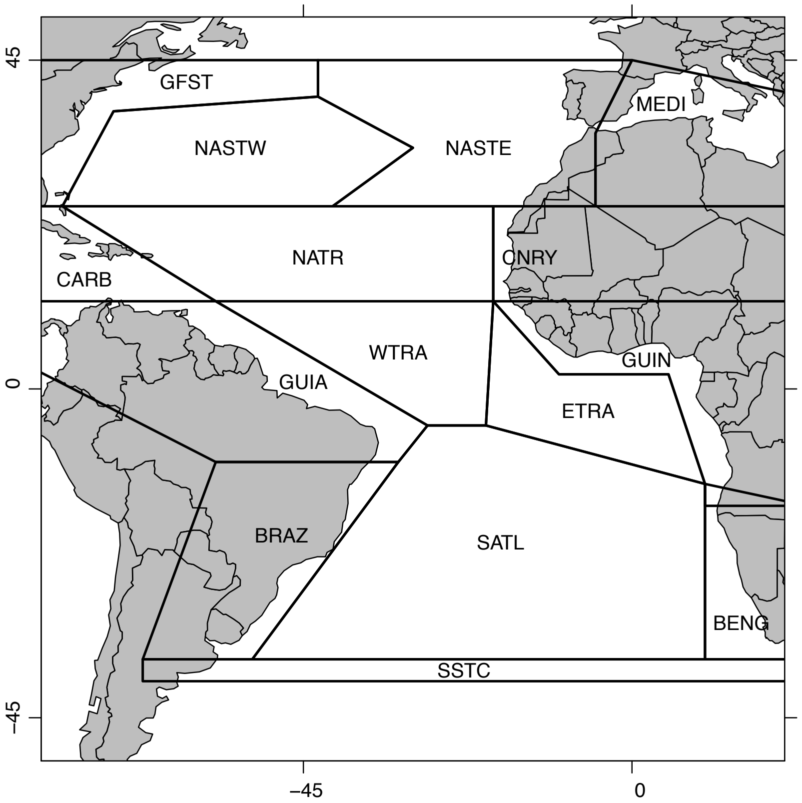


Figure 2. Longhurst's biogeochemical provinces across the Atlantic basin. Seven (#1-7) provinces are in the Northern Atlantic basin, four (#8-11) in the equatorial Atlantic, and four (#12-15) in the Southern Atlantic basin. 1) GFST = Gulf Stream; 2) NASTW = North Atlantic Subtropical Gyre (West), 3) NASTE = North Atlantic Subtropical Gyre (East), 4) MEDI = Mediterranean Sea, 5) CARB = Caribbean, 6) NATR = North Atlantic Tropical Gyre, 7) CNRY = Canary Current, 8) GUIA = Guianas, 9) WTRA = Western Tropical Atlantic, 10) ETRA = Eastern Tropical Atlantic, 11) GUIN = Guinea Current, 12) BRAZ = Brazil Current, 13) SATL = South Atlantic Gyre, 14) BENG = Benguela Current, 15) SSTC = South Subtropical Convergence (Longhurst, 2007)

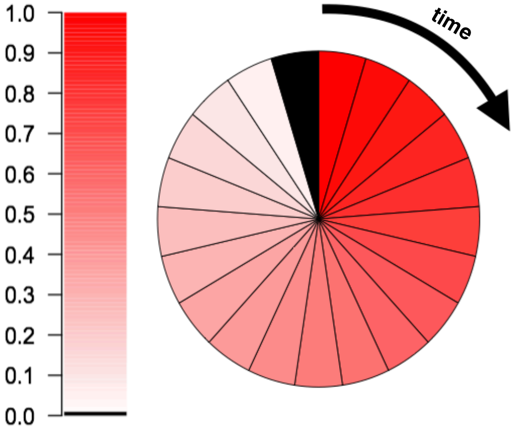


Figure 3. Example of a retention connectivity clock (Defne et al. 2016) to track changes in the proportion of compupod abundance over time. Color represents proportion retained, which in this example declines with time. Note black denotes no connectivity among origin-destination pair.

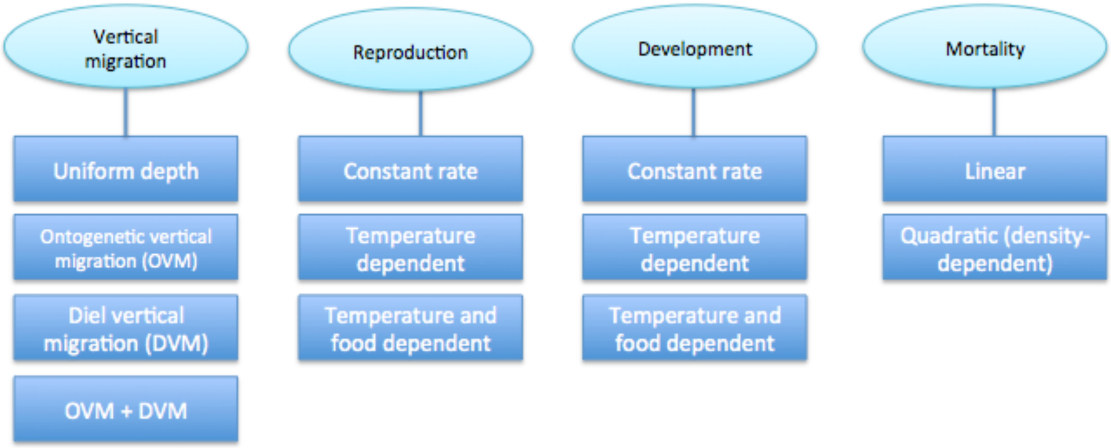


Figure 4. Model choices for the biological and behavioral functional traits including vertical migration, reproduction, and development.

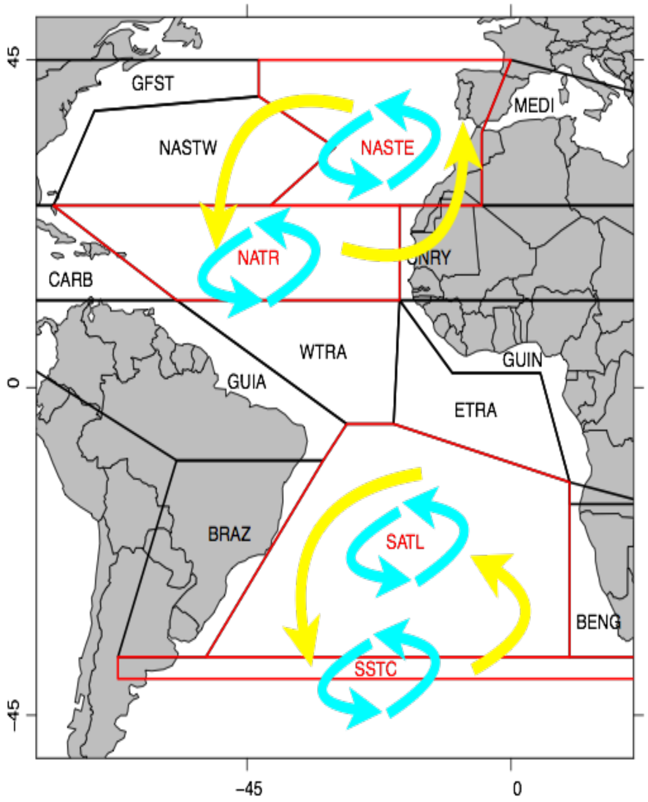


Figure 5. Expected connectivity for *Pleuromamma xiphias*. Provinces outlined in red are where genetic data for *P. xiphias* was available. Blue arrows represent self-recruitment, and yellow arrows represent exchange of migrants between regions. Here, we refer to Longhurst province (Longhurst 2007) “NASTE” as North Subtropical, “NATR” as North Tropical, “SATL” as South Gyre, and “SSTC” as South Convergence Zone.

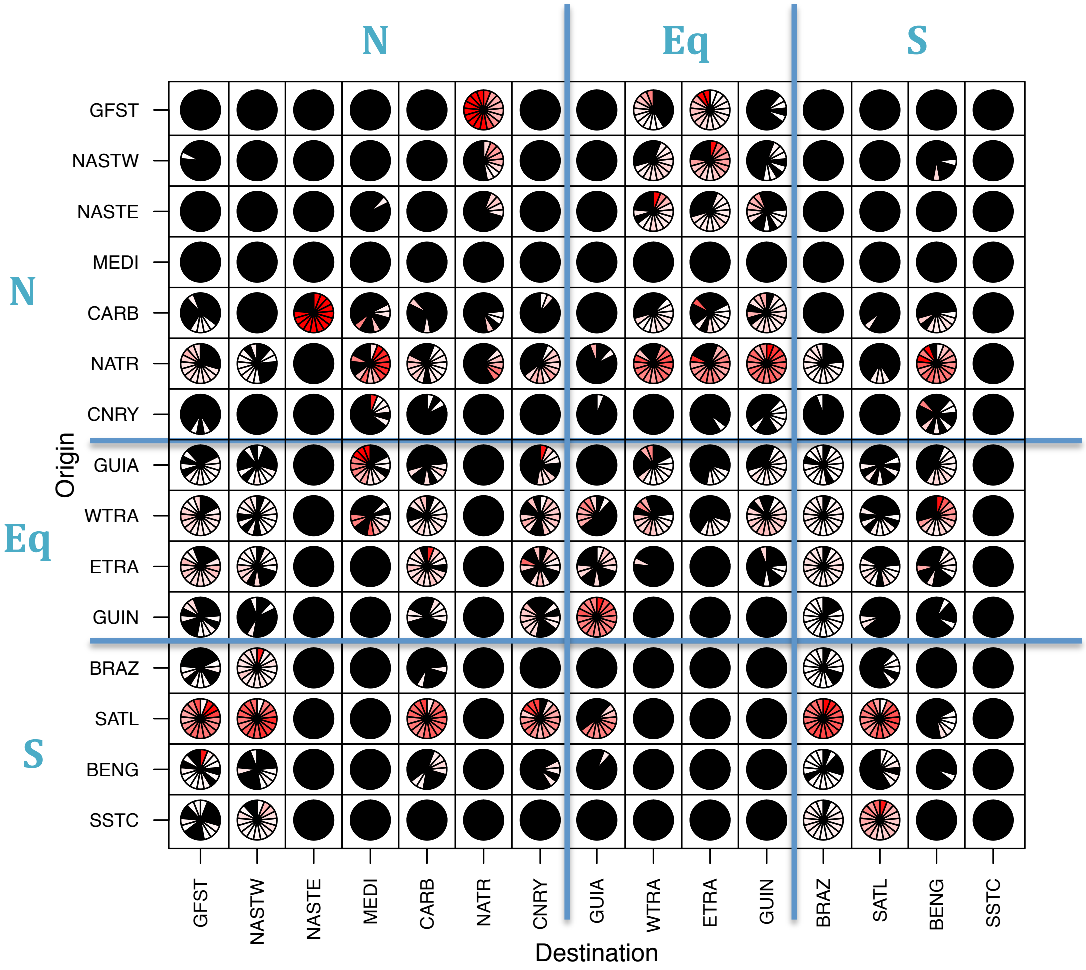


Figure 6. Modeled connectivity of passive particles among 15 Atlantic Longhurst regions for the base model. Simulation initialized with 13,000 particles, at depth 200m, over a 30-year time period. Average proportion of particles from originating Longhurst region (y-axis) and ending in destination region (x-axis) shown for every ~1.8 years in each slice of the pie charts. Longhurst regions as defined in Figure 2.

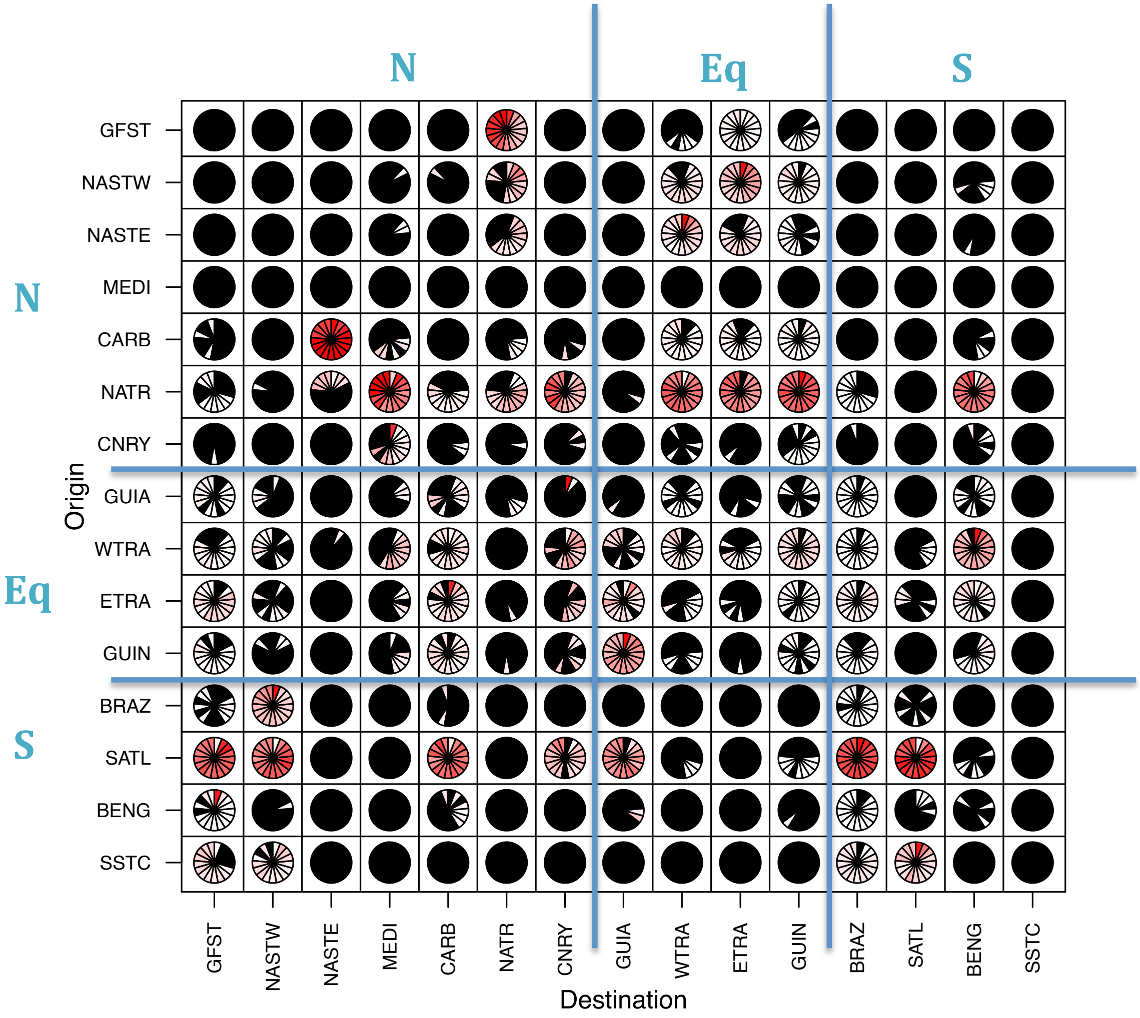


Figure 7. Modeled connectivity among 15 Atlantic Longhurst regions for Experiment 1. Compupods programmed with ontogenetic vertical migration (OVM) between depths of 50 m and 500 m. Simulation initialized with 13,000 compupods over a 30-year time period. Average proportion of particles from originating Longhurst region (y-axis) and ending in destination region (x-axis) shown for every ~1.8 years in each slice of the pie charts. Longhurst regions as defined in Figure 2.

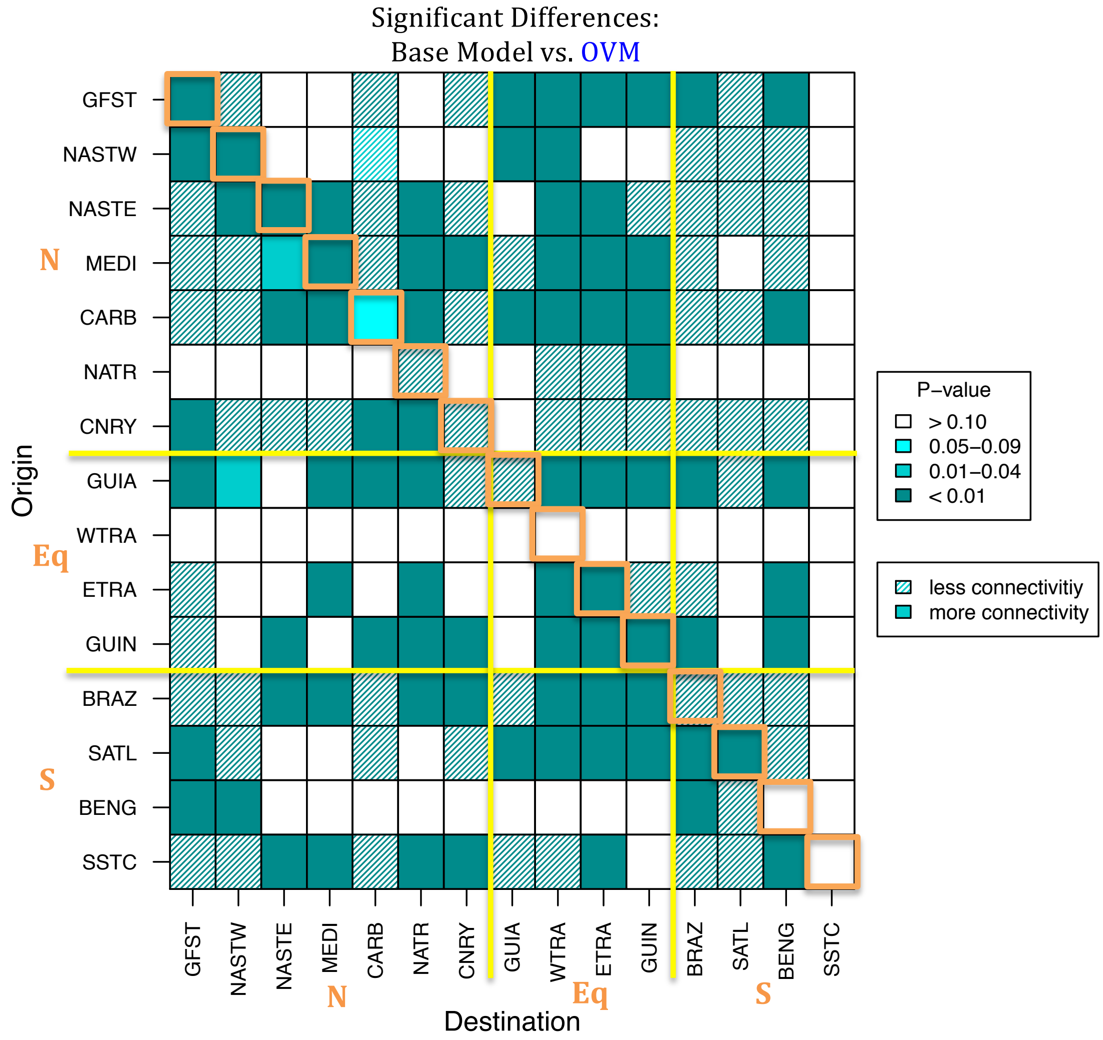


Figure 8. Experiment 1 significant differences in connectivity between passive particle simulation at depth 200 m (Fig. 5) and simulation including ontogenetic vertical migration (OVM) with depth range between 50 and 500 m (Fig. 6). Color of fill designates significance level, and hatched pattern versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under OVM scenario. Longhurst regions on x and y-axes as defined in Figure 2.

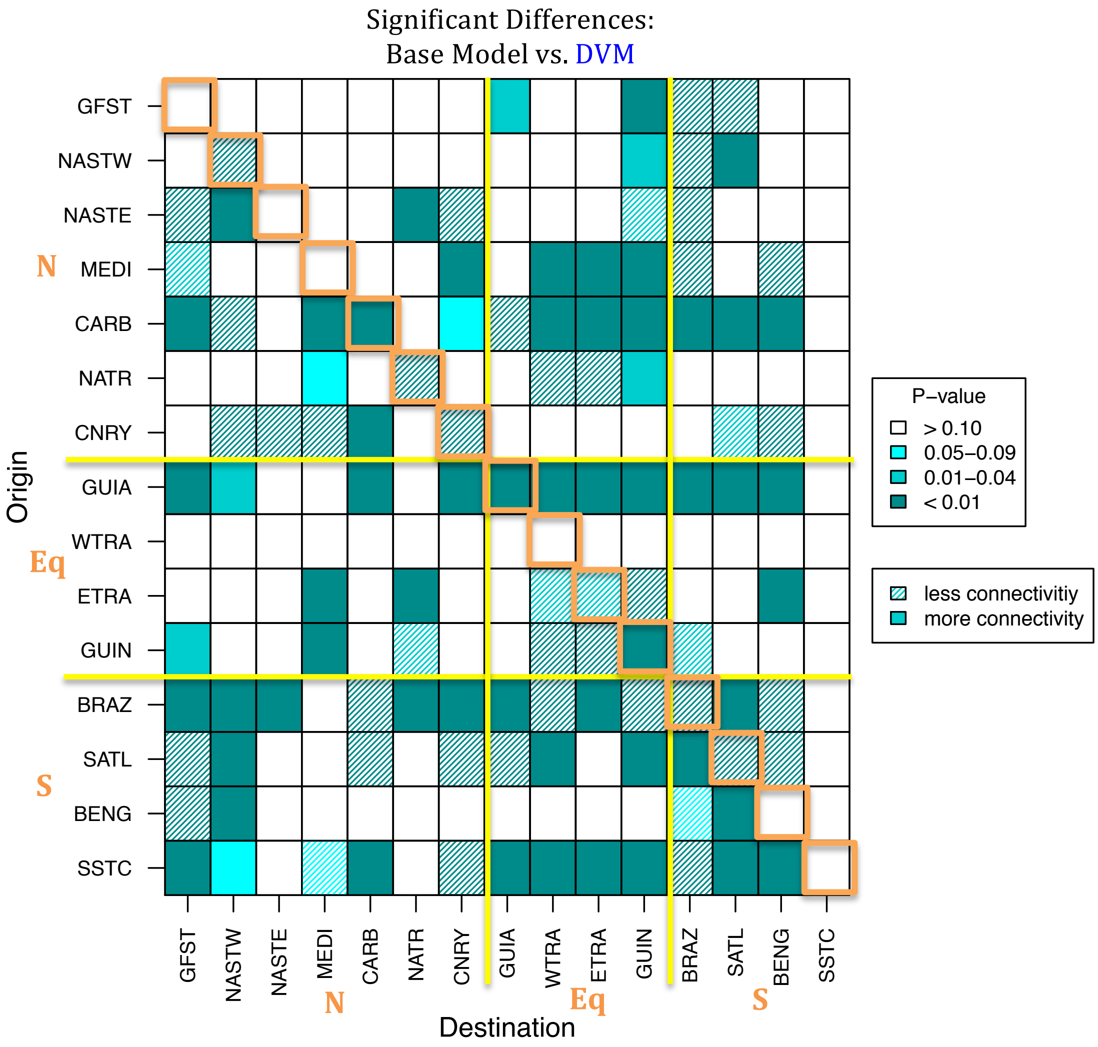


Figure 9. Experiment 2 significant differences in connectivity between passive particle simulation at depth 200 m and simulation including diel vertical migration (DVM) with depth range between 50 and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under DVM scenario. Longhurst regions on x and y-axes as defined in Figure 2.

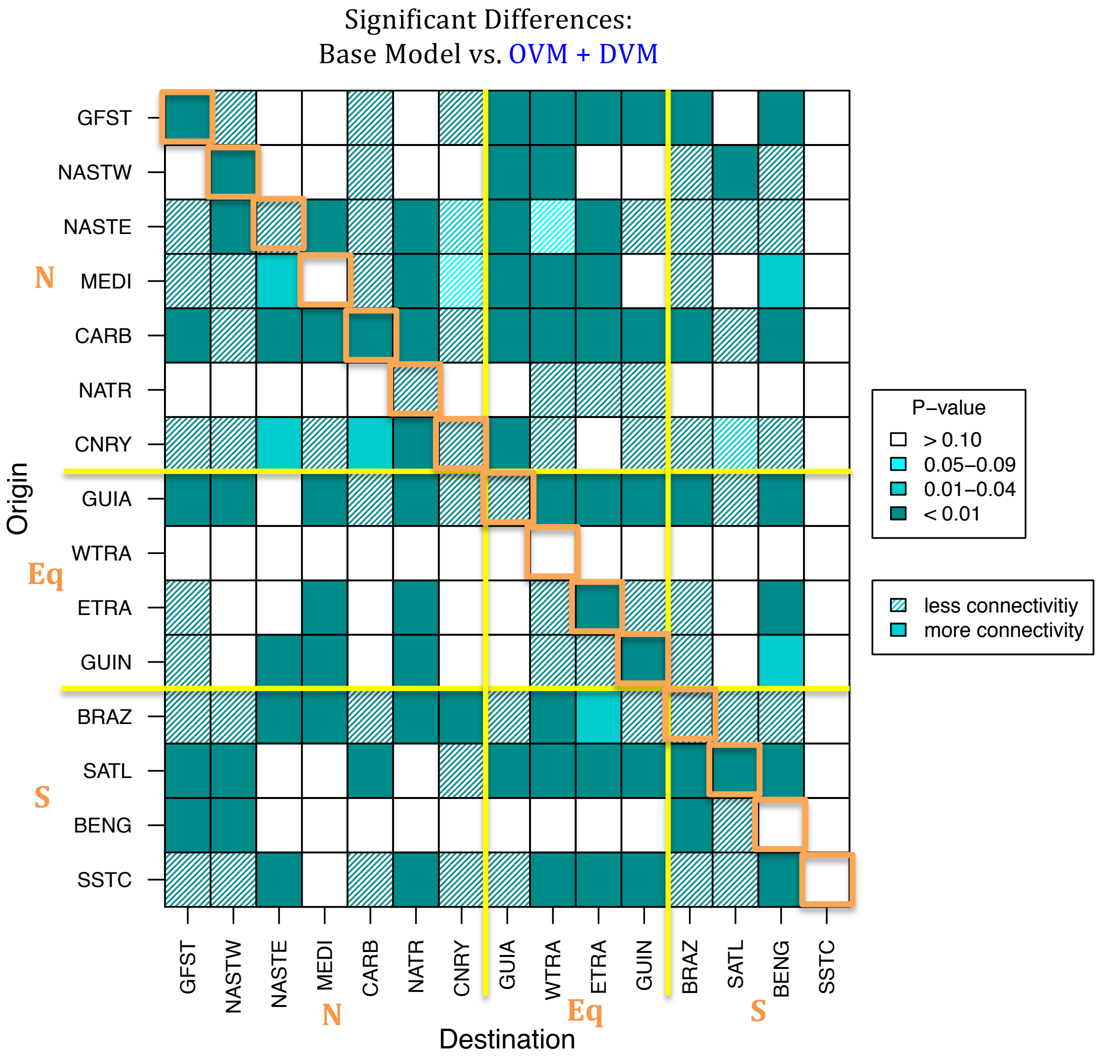


Figure 10. Experiment 3 significant differences in connectivity between passive particle simulation at depth 200 m and simulation including ontogenetic and diel vertical migration (OVM + DVM) with depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under OVM+DVM scenario. Longhurst regions on x and y-axes as defined in Figure 2.

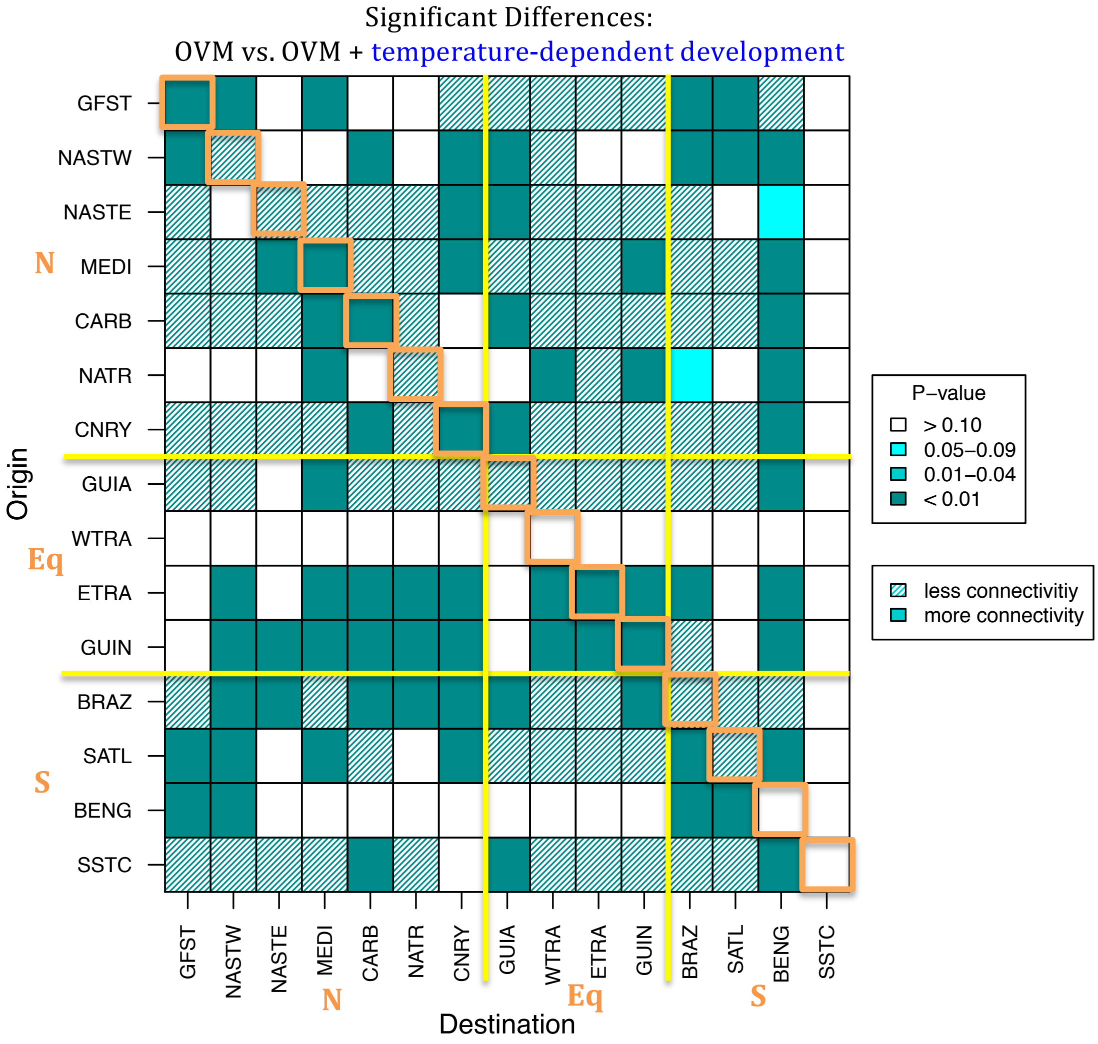


Figure 11. Experiment 4 significant differences in connectivity between simulation with ontogenetic vertical migration (OVM) and simulation including OVM with development forced by temperature. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under temperature-dependent development scenario. Longhurst regions on x and y-axes as defined in Figure 2.

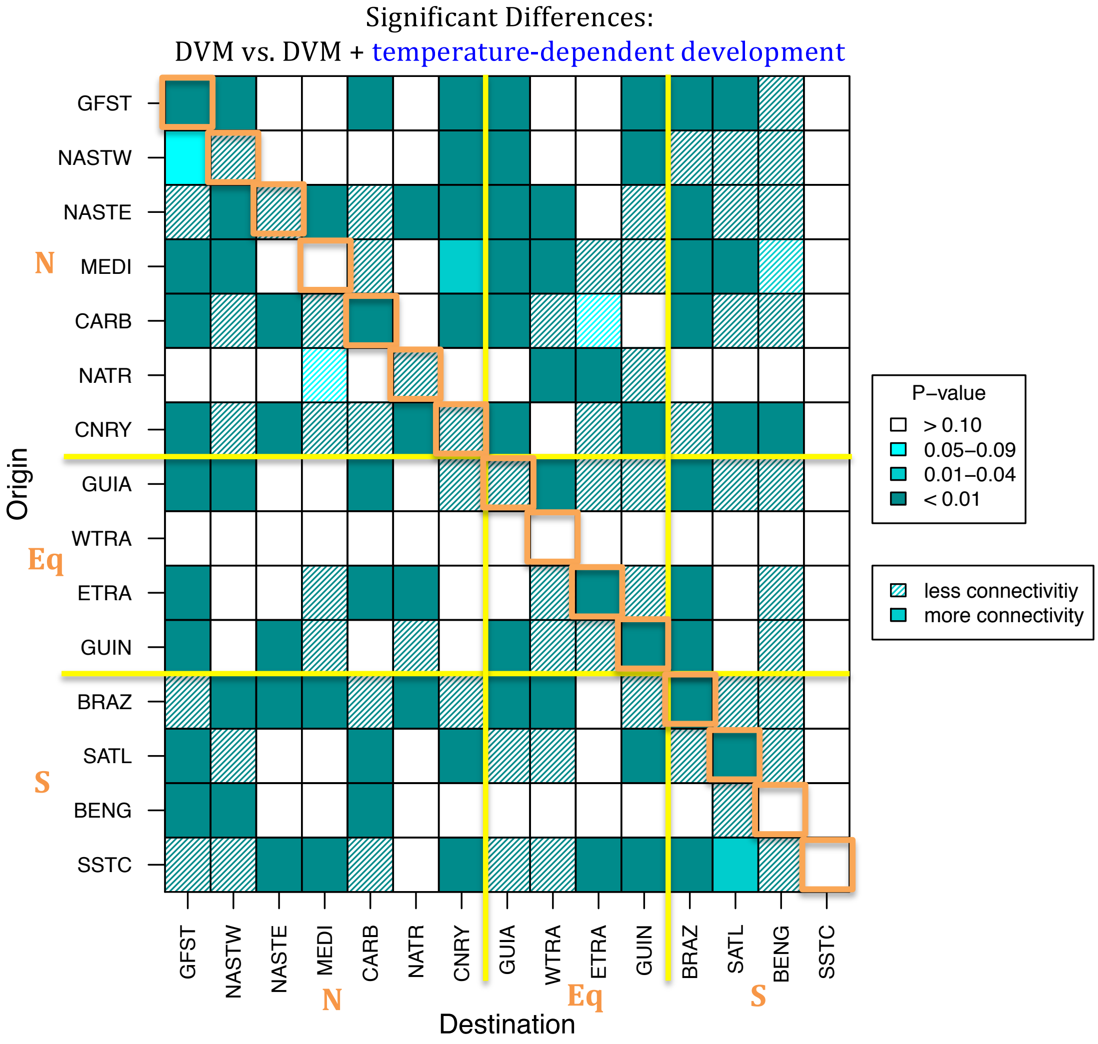


Figure 12. Experiment 5 significant differences in connectivity between simulation with diel vertical migration (DVM) and simulation including DVM with development forced by temperature. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under temperature-dependent development scenario. Longhurst regions on x and y-axes as defined in Figure 2.

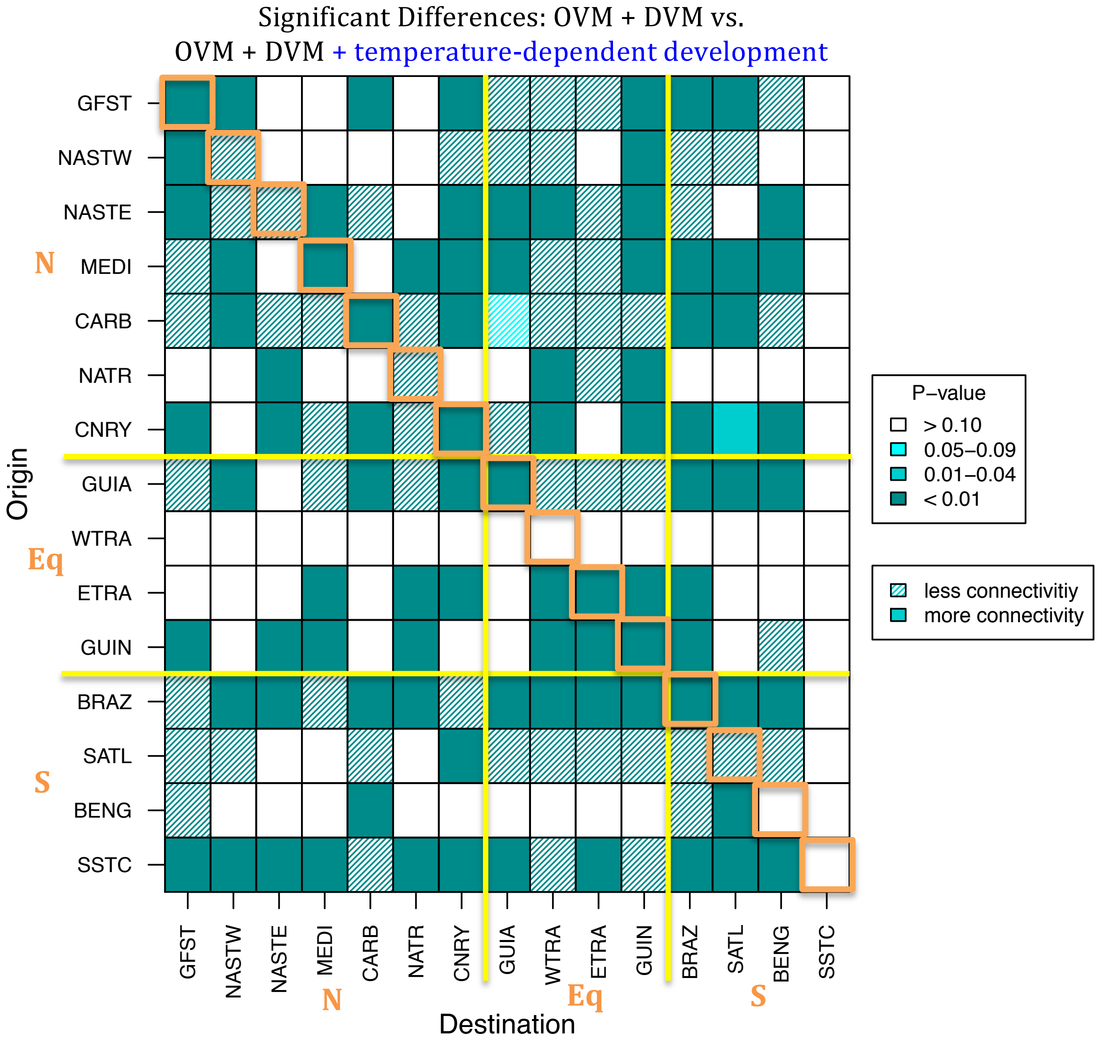


Figure 13. Experiment 6 significant differences in connectivity between simulation including ontogenetic and diel vertical migration (OVM + DVM) and simulation including OVM + DVM with development forced by temperature. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under temperature-dependent development scenario. Longhurst regions on x and y-axes as defined in Figure 2.

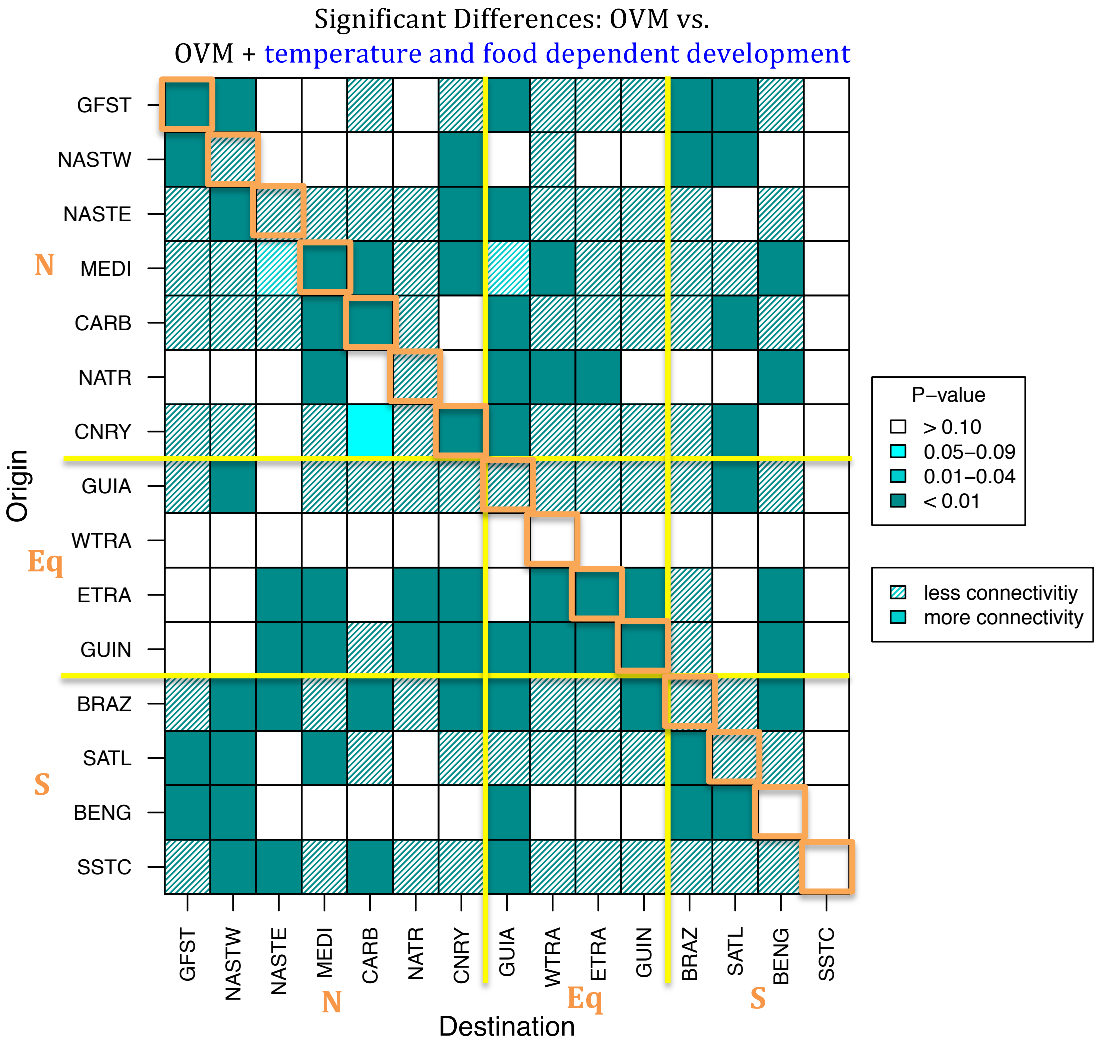


Figure 14. Experiment 7 significant differences in connectivity between simulation with ontogenetic vertical migration (OVM) and simulation including OVM with development forced by temperature and food. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under temperature and food dependent development scenario. Longhurst regions on x and y-axes as defined in Figure 2.

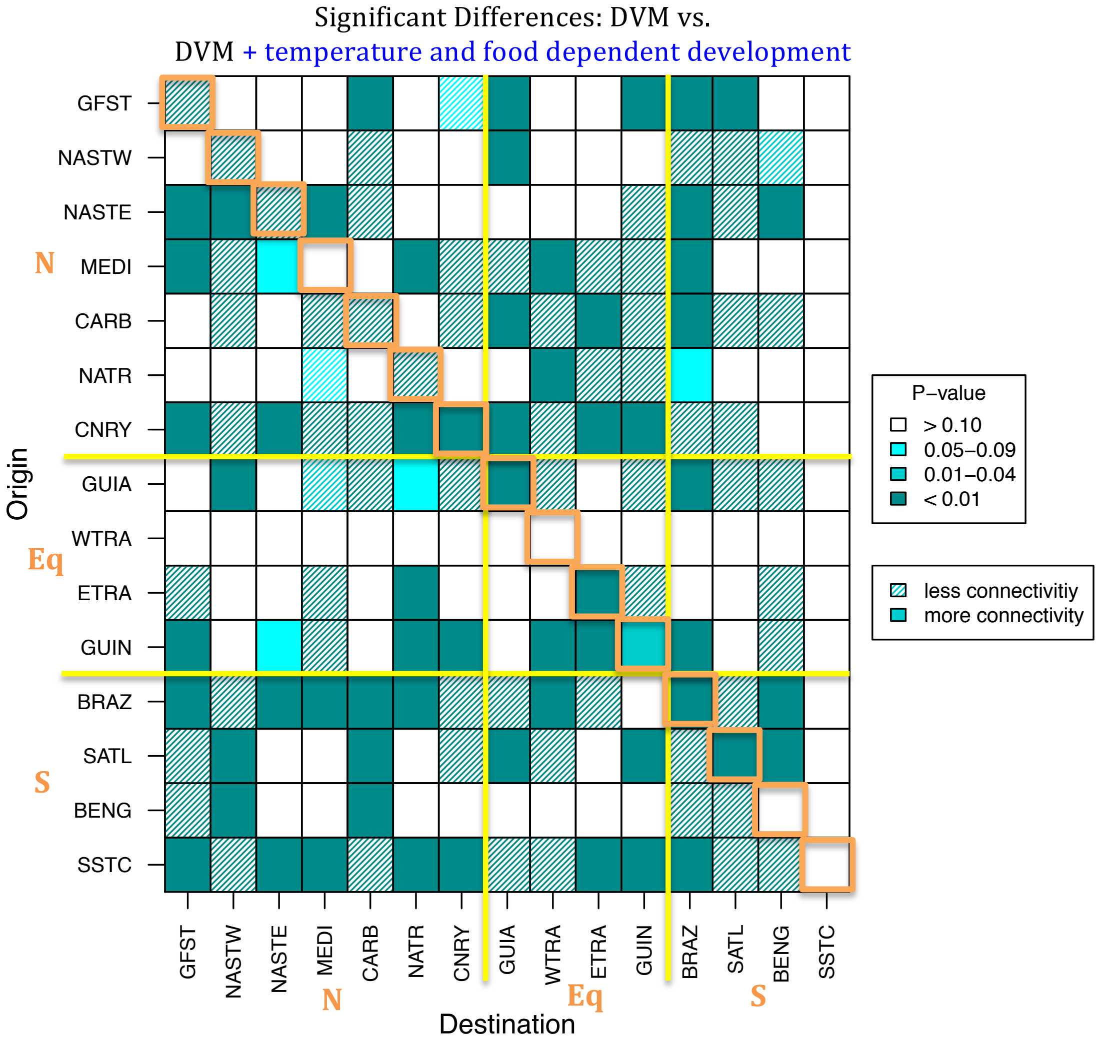


Figure 15. Experiment 8 significant differences in connectivity between simulation with diel vertical migration (DVM) and simulation including DVM with development forced by temperature and food. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under temperature and food dependent development scenario. Longhurst regions on x and y-axes as defined in Figure 2.

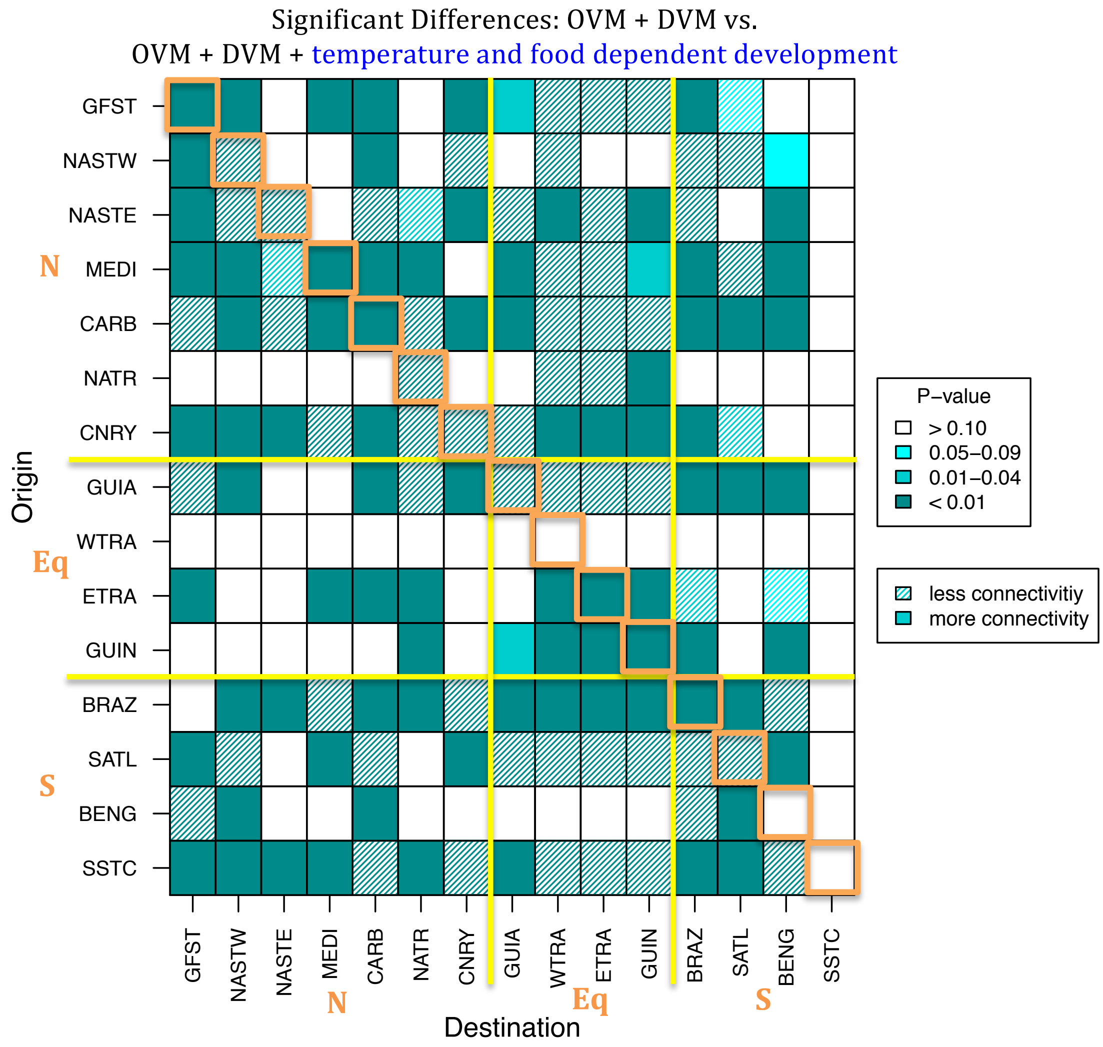


Figure 16. Experiment 9 significant differences in connectivity between simulation including ontogenetic and diel vertical migration (OVM + DVM) and simulation including OVM + DVM with development forced by temperature and food. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under temperature and food

dependent development scenario. Longhurst regions on x and y-axes as defined in Figure 2.

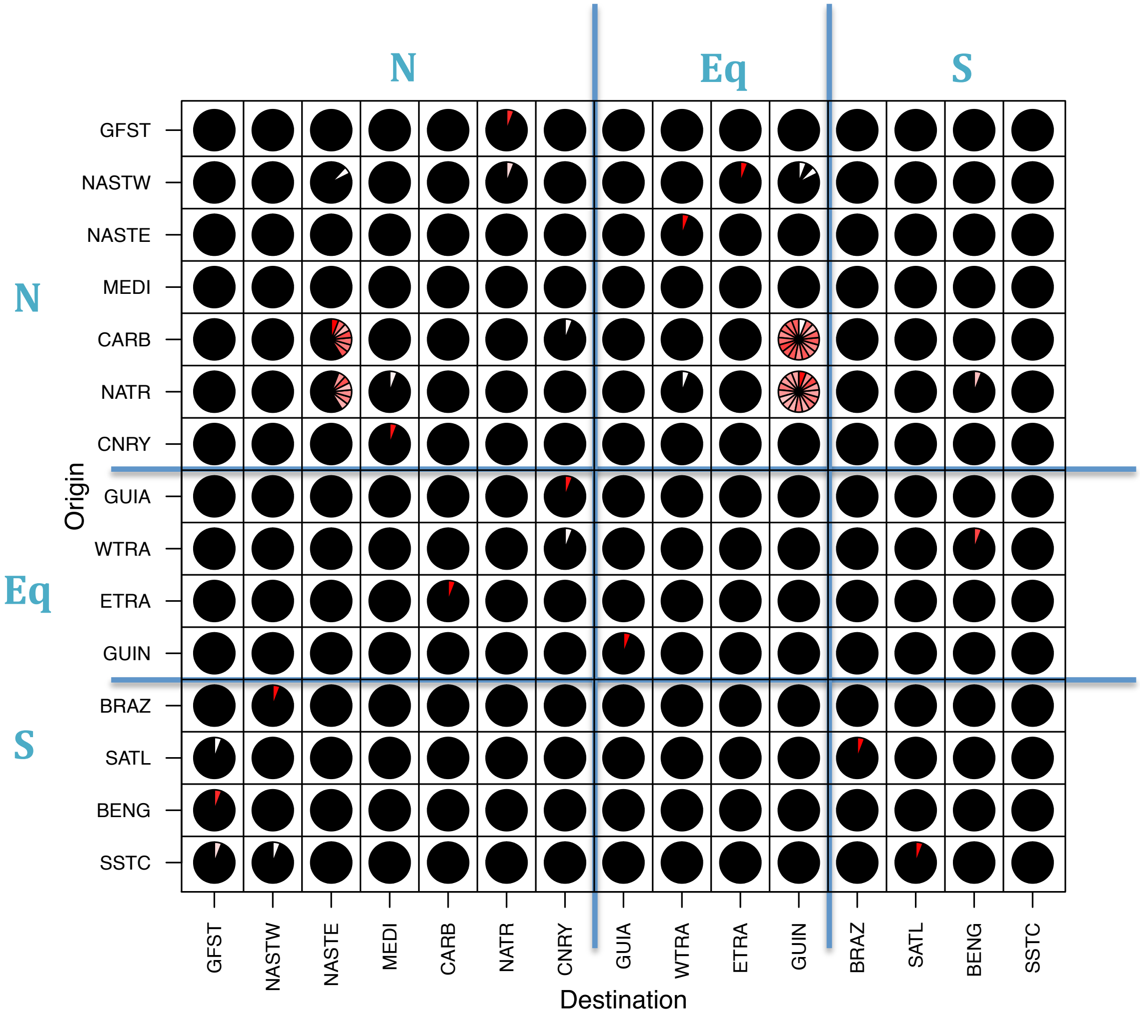


Figure 17. Modeled connectivity among 15 Atlantic Longhurst regions for Experiment 12. Compupods programmed at uniform depth of 200 m, reproduction and development forced by temperature and food, and density dependent mortality. Simulation initialized with 13,000 compupods over a 30-year time period. Average proportion of particles from originating Longhurst region (y-axis) and ending in destination region (x-axis) shown every ~1.8 years in each slice of the pie charts. Longhurst regions as defined in Figure 2.

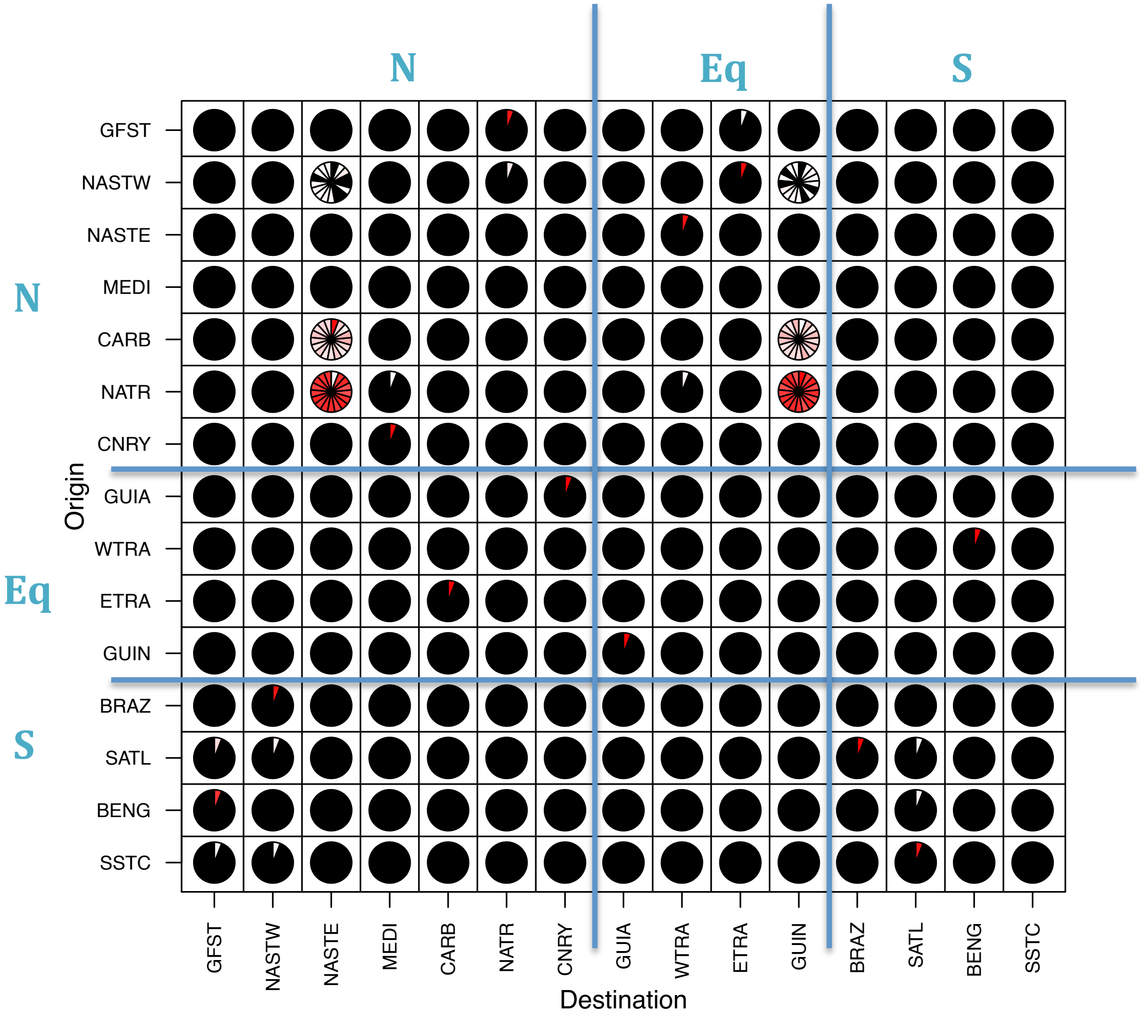


Figure 18. Modeled connectivity among 15 Atlantic Longhurst regions for Experiment 13. Compupods programmed with ontogenetic and diel vertical migration (OVM and DVM) between depths of 50 m and 500 m, reproduction and development forced by temperature and food, and density dependent mortality. Simulation initialized with 13,000 compupods over a 30-year time period. Average proportion of particles from originating Longhurst region (y-axis) and ending in destination region (x-axis) shown every ~1.8 years in each slice of the pie charts. Longhurst regions on x and y axis as defined in Figure 2.

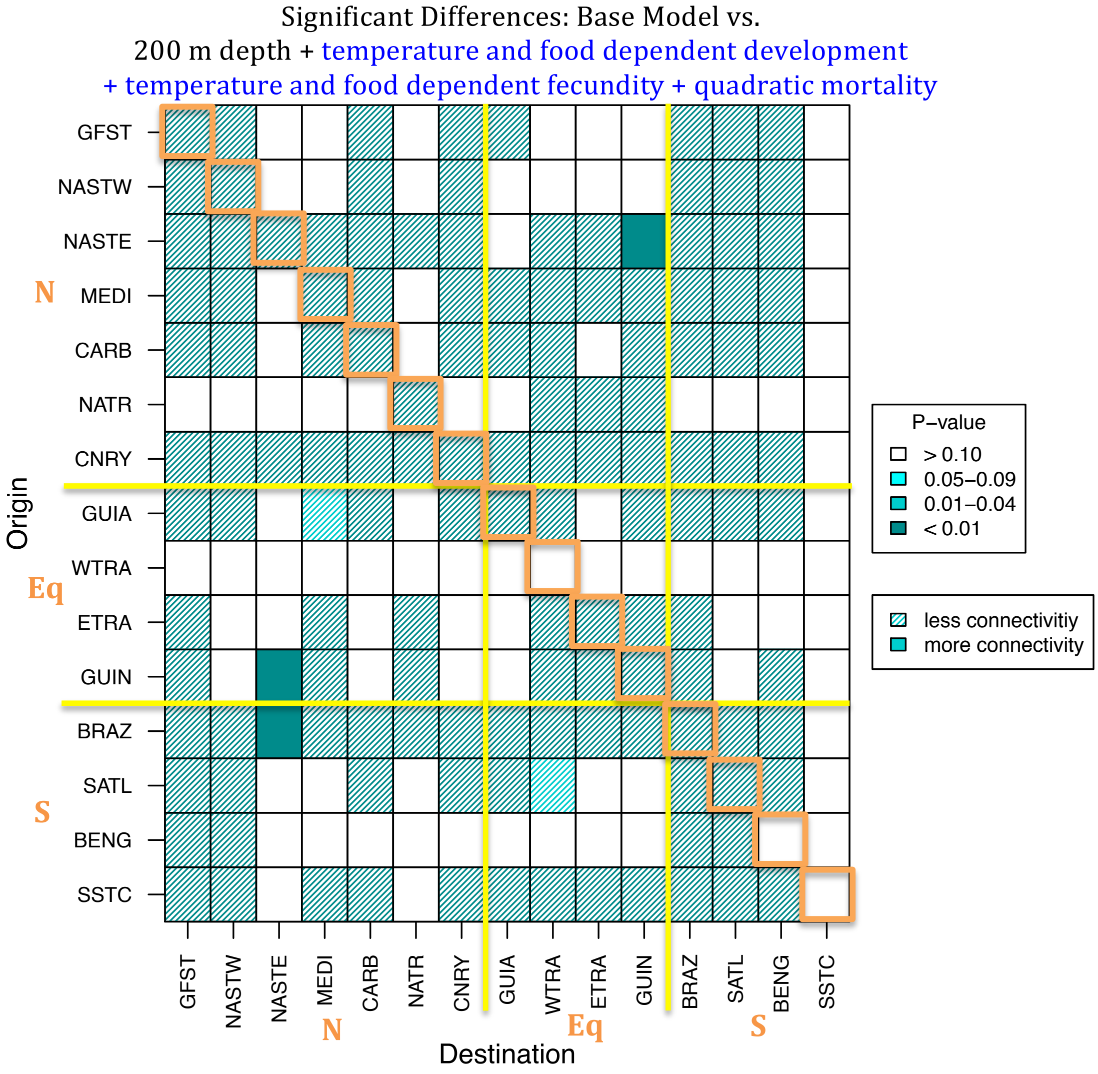
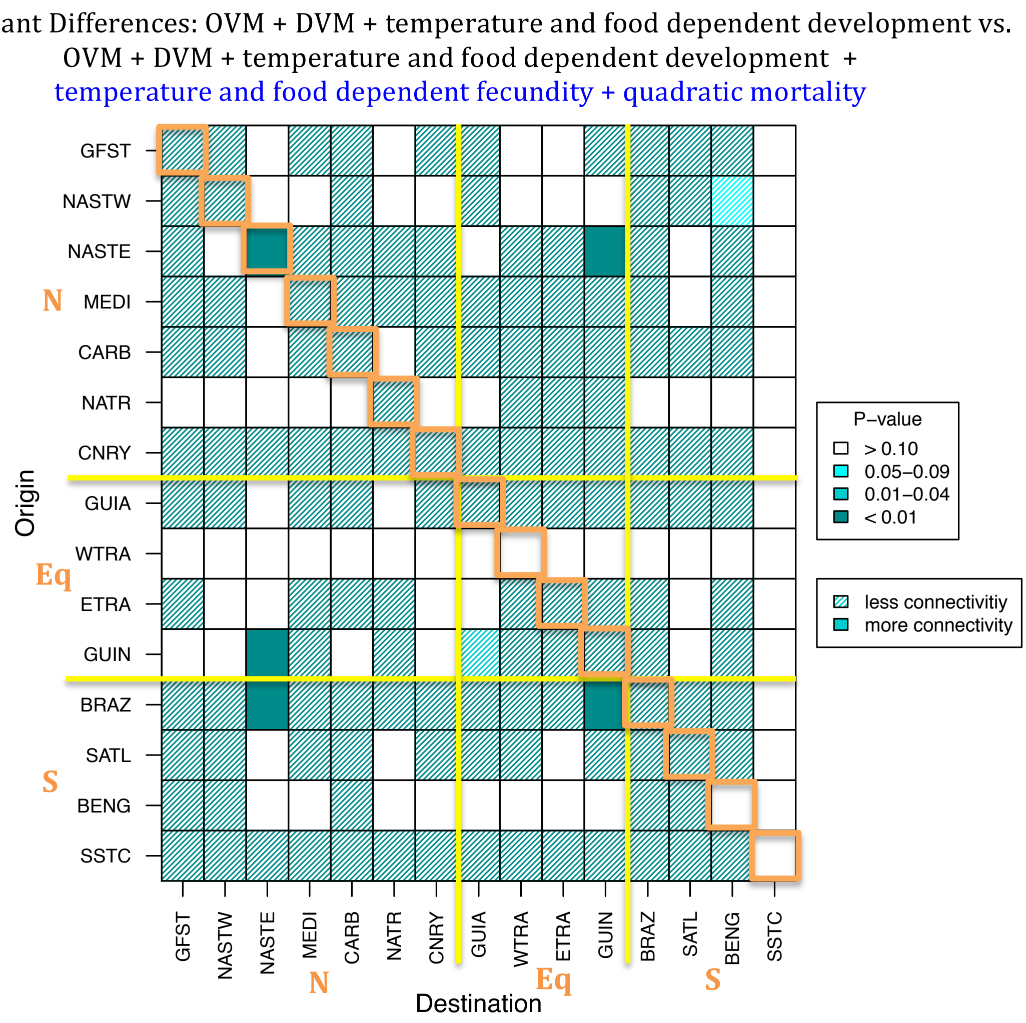


Figure 19. Experiment 12 significant differences in connectivity between passive particle simulation at uniform depth of 200 m and simulation including reproduction and development forced by temperature and food and density dependent mortality at uniform depth of 200 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more connections under reproduction, development and mortality scenario. Longhurst regions on x and y-axes as defined in Figure 2.



Significant Differences: OVM + DVM + temperature and food dependent development vs. OVM + DVM + temperature and food dependent development + temperature and food dependent fecundity + quadratic mortality

Figure 20. Experiment 13 significant differences in connectivity between simulation including ontogenetic and diel vertical migration (OVM + DVM) with development forced by temperature and food and simulation including OVM + DVM with reproduction and development forced by temperature and food, and density dependent mortality. Depth range between 50 m and 500 m. Colors designate significance level, and hatched versus filled boxes represent a decrease or increase of connectivity, respectively, and where increased connectivity means more

connections under reproduction and mortality scenario. Longhurst regions on x and y-axes as defined in Figure 2.

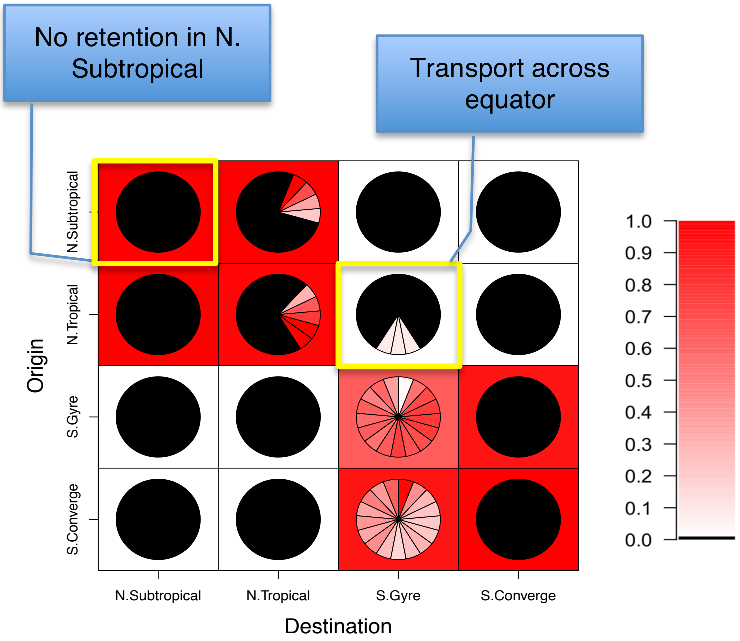


Figure 21. Modeled connectivity of passive particles at uniform depth of 200 m for comparison in case study species *Pleurommma xiphias*. Simulation initialized with 13,000 particles, and run for a 30-year time period. Background color represents the relative expected connectivity based on genetic results for the case study species *P. xiphias*. Connectivity clocks represent model results, with color representing the average proportion of compupods ending in a certain destination (x-axis), given originating region (y-axis) for every ~1.8 years in each slice of the pie charts.

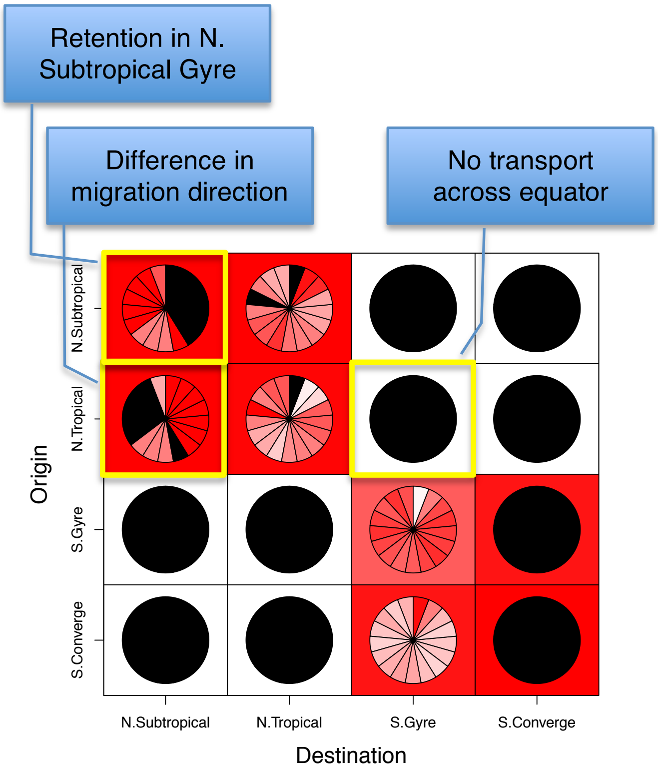


Figure 22. Modeled connectivity of compupods programmed with ontogenetic vertical migration and depth range of 50 m to 1000 m for comparison in case study species *Pleurommma xiphias*. Simulation initialized with 13,000 particles, and run for a 30-year time period. Background color represents the relative expected connectivity based on genetic results for the case study species *P. xiphias*. Connectivity clocks represent model results, with color representing the average proportion of compupods ending in a certain destination (x-axis), given originating region (y-axis) for every ~1.8 years in each slice of the pie charts.

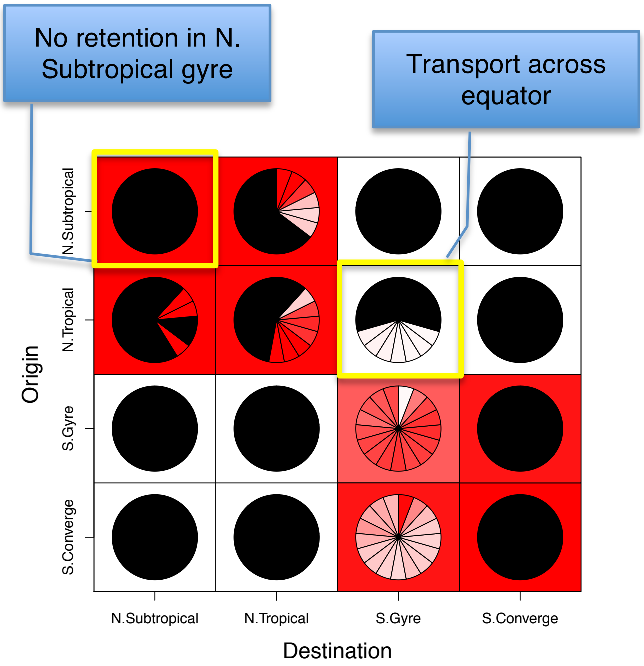


Figure 23. Modeled connectivity of compupods programmed with diel vertical migration and depth range of 50 m to 1000 m and development forced by temperature for comparison in case study species *Pleurommma xiphias*. Simulation initialized with 13,000 compupods, and run for a 30-year time period. Background color represents the relative expected connectivity based on genetic results for the case study species *P. xiphias*. Connectivity clocks represent model results, with color representing the average proportion of compupods ending in a certain destination (x-axis), given originating region (y-axis) for every ~1.8 years in each slice of the pie charts.

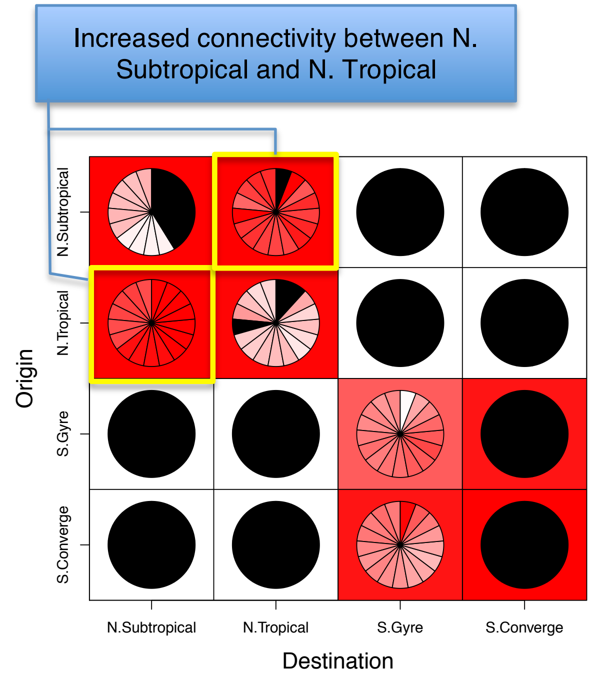


Figure 24. Modeled connectivity of compupods programmed with ontogenetic vertical migration and depth range of 50 m to 1000 m and development forced by temperature for comparison in case study species *Pleurommma xiphias*. Simulation initialized with 13,000 compupods, and run for a 30-year time period. Background color represents the relative expected connectivity based on genetic results for the case study species *P. xiphias*. Connectivity clocks represent model results, with color representing the average proportion of compupods ending in a certain destination (x-axis), given originating region (y-axis) for every ~1.8 years in each slice of the pie charts.

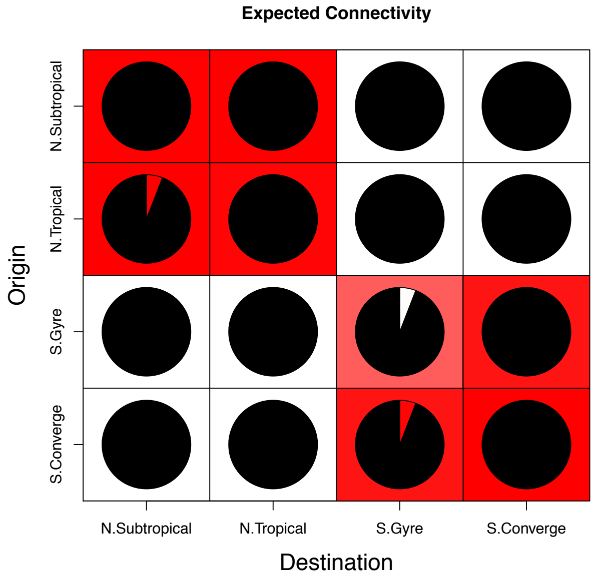


Figure 25. Modeled connectivity of compupods programmed with ontogenetic and diel vertical migration and depth range of 50 m to 1000 m, reproduction and development forced by temperature, and density dependent mortality for comparison in case study species *Pleurommma xiphias*. Simulation initialized with 13,000 compupods, and run for a 30-year time period. Background color represents the relative expected connectivity based on genetic results for the case study species *P. xiphias*. Connectivity clocks represent model results, with color representing the average proportion of compupods ending in a certain destination (x-axis), given originating region (y-axis) for every ~1.8 years in each slice of the pie charts.

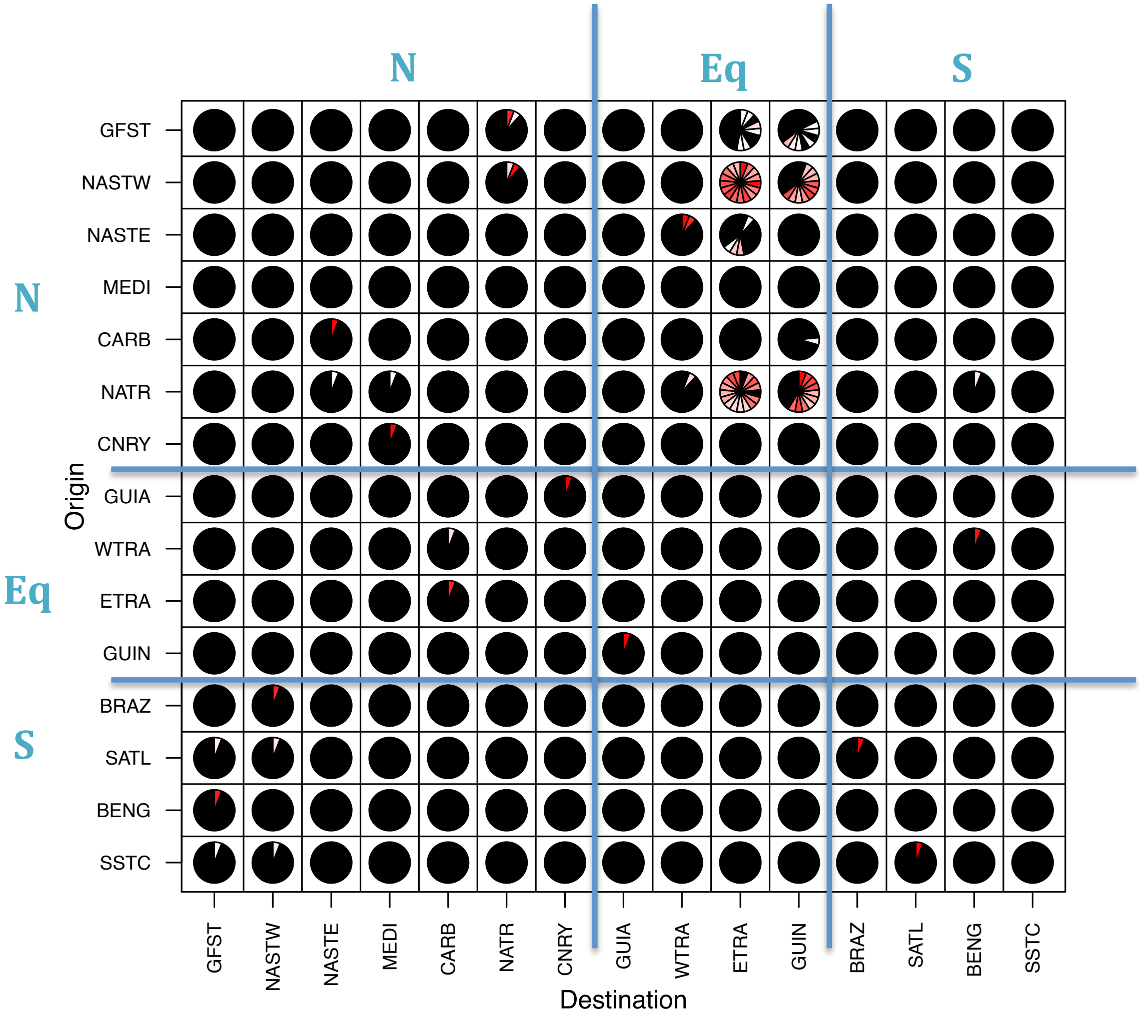


Figure 26. Modeled connectivity of compupods across 15 Longhurst regions programmed with ontogenetic and diel vertical migration and depth range of 50 m to 1000 m, reproduction and development forced by temperature, and density dependent mortality for comparison in case study species *Pleurommma xiphias*. Simulation initialized with 13,000 compupods, and run for a 30-year time period. Background color represents the relative expected connectivity based on genetic results for the case study species *P. xiphias*. Connectivity clocks represent model results, with color representing the average proportion of compupods ending in a certain

destination (x-axis), given originating region (y-axis) for every ~1.8 years in each slice of the pie charts. Longhurst regions as defined in Figure 2.

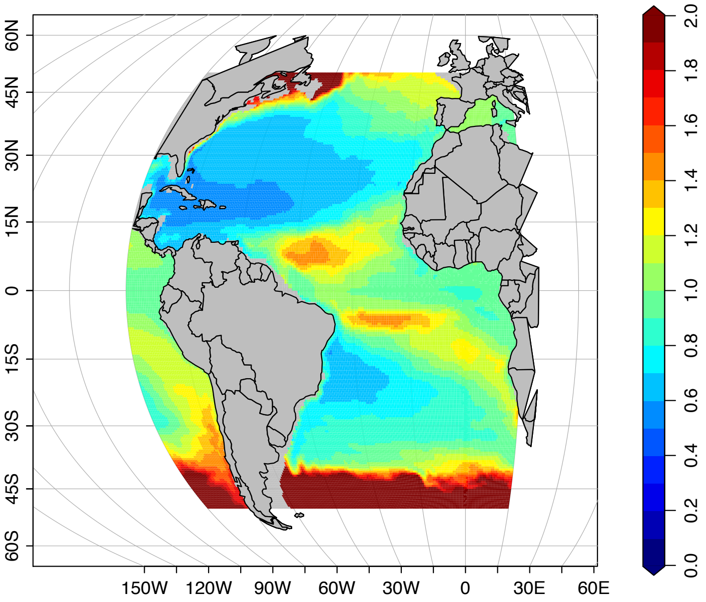
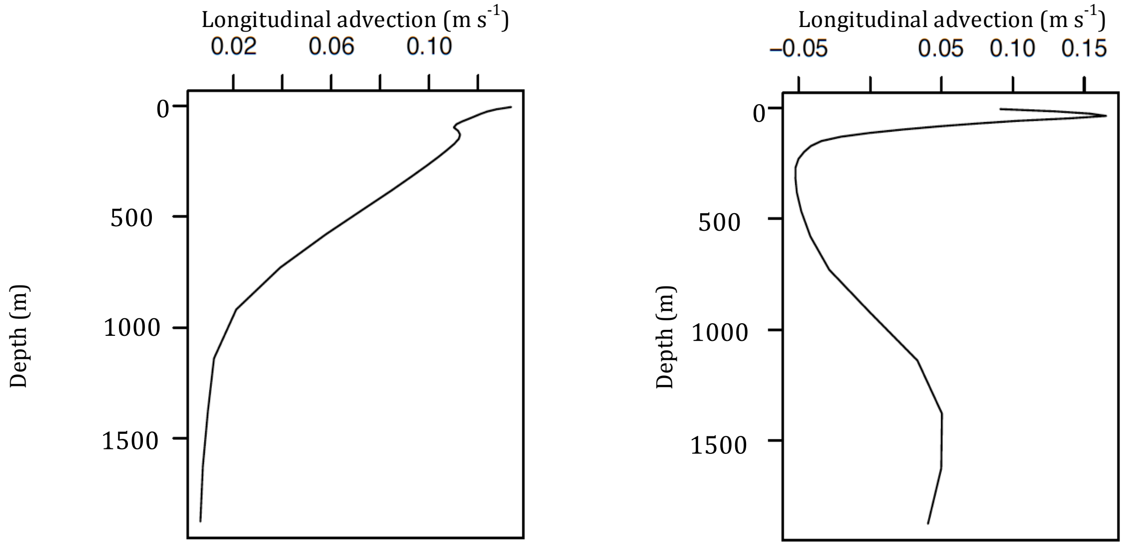
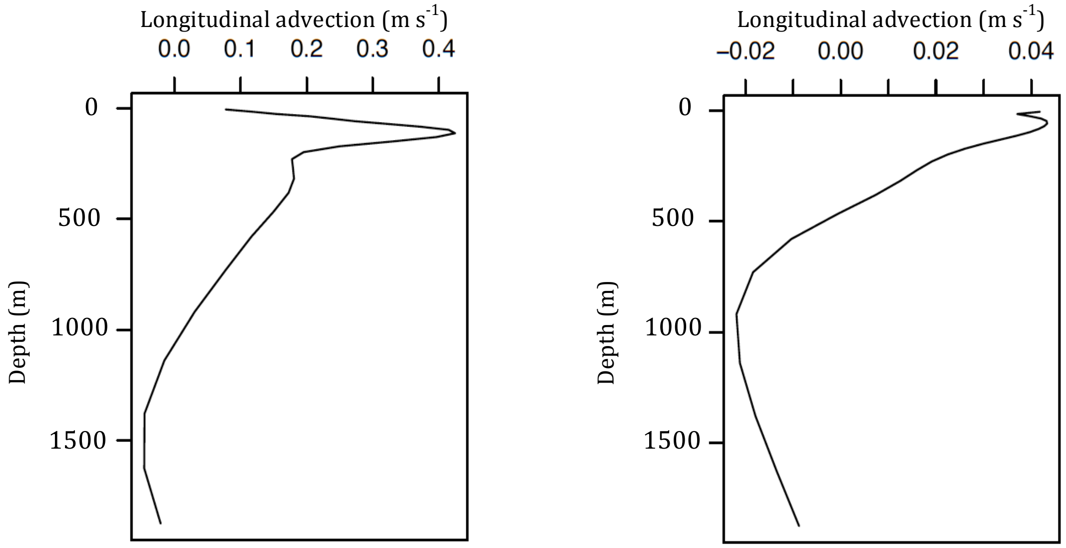


Figure 27. Stage duration (SD) of eggs across the Atlantic basin in January, using average monthly temperature to force development times. Color bar represents SD in days.



North Atlantic

South Equatorial Atlantic



North Equatorial Atlantic

South Atlantic

Figure 28. Variation of average longitudinal advection (m s^{-1}) in January for years 1871-2008 over depth and region, plotted using data from the Simple Ocean Data Assimilation (SODA).