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Spatial overlap patterns between Baltic larval cod and its prey obtained from drift model studies

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Abstract

Recruitment success of marine fish stocks can to a large degree be related to the feeding success of their early life stages, i.e. larvae and juveniles. Temporal mis-match between the occurrence of larvae and their prey potentially affects the spatial overlap and thus the contact rates between predator and prey. This might have important consequences for growth and survival. We performed a case study investigating the influence of the circulation on the overlap of Baltic cod larvae with their prey. A three-dimensional hydrodynamic model was used to analyse spatio-temporally resolving drift patterns of larval Baltic cod. A coefficient of overlap between modelled larval and idealized prey distributions indicated the probability of predator-prey overlap, dependent on the hatching time of cod larvae. By performing model runs for the years 1979-1998 we have been investigating the intra- and interannual variability in the potential spatial overlap between predator and prey. Assuming uniform prey distributions, we generally found the overlap to decrease since the mid 1980s, however being maximal variable during the 1990s. Seasonally highest overlap occurred in summer and lowest at the end of the cod spawning season. Horizontal variable prey distributions generally resulted in decreased overlap coefficients. Finally, we have related variations in overlap patterns to the variability of Baltic cod recruitment success.

Keywords: Baltic Sea, Drift model, Spatial overlap, Baltic cod

Introduction

Recruitment success of marine fish stocks can to a large degree be related to the feeding success of their early life stages, i.e. larvae and juveniles (Mullin, 1993). The survival of fish larvae and juveniles depends on their ability to encounter, capture and ingest a sufficient quantity of appropriate prey in order to avoid starvation and assure growth. According to the “match-mismatch” hypothesis, variability in recruitment depends on the temporal match/mismatch of the annual reproductive cycle of fish and the prey of their larvae (Cushing, 1973). Differences in the match between larvae and their prey may thus generate variability in larval feeding success, including both interannual (Cushing 1996) as well as spatial variability. Thus, the transport of eggs and larvae into sub-optimal feeding environments may influence recruitment success (e.g. Sinclair, 1988; Heath and Gallego, 1988; Hinrichsen et al., 2002).

The deep water area off the island Bornholm (Baltic Sea) is the major spawning ground of Baltic cod (Fig. 1). Larval cod preys mainly on nauplii of the dominant calanoid copepods in the area, i.e. *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp. and *Centropages hamatus* (Voss et al., 2003). Based on long-term data sets (Möllmann et al., 2000), idealized spatio-temporal distributions of the seasonal nauplii abundance of the main copepod species can be constructed (Fig. 2). In deep water areas, where *P. elongatus* is most abundant due to its deeper vertical distribution compared with the other calanoid species (Möllmann and Köster, 2002), mean nauplii abundance strongly increases during late winter with peak abundance between April and May (Fig. 2a). In late summer and autumn, *P. elongatus* abundance decreases whereas the abundance of all other species peaks later in the year. Shallow areas on the margins of the deep basin show a similar temporal trend as the deep water areas, with the maximum of the “other” copepods in late summer being significantly higher than the *P. elongatus* maximum (Fig. 2b).

The described spatio-temporal variability in occurrence of food for larval cod indicates the possibility of a spatial mismatch between larval predators and their planktonic prey depending on the hatching time of larvae. It can be assumed that the degree of this spatial mismatch strongly depends on the intra- and inter-annual variability in circulation patterns. In the present study we thus use data on the location and timing of spawning of Baltic cod as input into a particle-tracking model (Hinrichsen et al., 1997). Utilizing currents from a three-dimensional circulation model of the Baltic Sea (Lehmann, 1995), cod larvae were tracked through space and time. Modelled distributions of larvae were then compared to assumed distributions of prey reflecting the spatio-

temporal variability in occurrence of copepod species. The utilization of an overlap coefficient (Horn, 1966) provided an integrative view, indicating the probability of the simultaneous spatial occurrence of larval cod and its prey.

Material and Methods

Hydrodynamic model and particle tracking

The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth et al., 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea can be found in Lehmann (1995) and (Lehmann and Hinrichsen, 2000a). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann et al. (2002). Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann, 1995; Hinrichsen et al., 1997; Lehmann and Hinrichsen, 2000a).

The model domain comprises the entire Baltic Sea including the Gulf of Bothnia, Gulf of Finland, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. The horizontal resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels is chosen to best account for the different sill depths in the Baltic. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a mean runoff database (Bergström and Carlsson, 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of 1 x 1 squares. Meteorological parameter, such as geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness and precipitation are stored with a temporal increment of 3 hours.

Simulated three-dimensional velocity fields were extracted (at a 6 hours interval) in order to develop a database for a Lagrangian particle tracking exercise for larval cod. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Vertical velocities were calculated from the divergence of the horizontal velocity fields. The drifters were allowed to leave the layers where they were launched. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced.

In order to establish a Lagrangian view of the simulated circulation, drifters can be placed in the modeled flow fields at every location within the model domain. Moreover, the initial launch positions can be chosen independently from the vertical resolution of the model's grid. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen et al., 1997).

First, the hydrodynamic model on Baltic cod larval drift has been utilized for the time period 1979 to 1998 in order to obtain means of intra-annual variability in distribution and transport patterns. In order to consider its seasonal variability in relation to spatial and temporal variations in larval transports a total of 720 Lagrangian drifters were released at depth between 25 and 35 m (depths at which feeding larvae occur after vertical feeding migration) on a regular spaced grid enclosed by the 60m isobath representing the main spawning area of the Bornholm Basin (Fig. 1). Drifters, at their release representing first feeding larvae, were inserted into the modelled flow fields at 10 days intervals and were tracked for certain time periods. The release dates commenced April 1st and ended September 20th, thereby encompassing the historic as well as the present main spawning period of eastern Baltic cod (Wieland et al., 2000).

Overlap calculation

Our main goal was to estimate the overlap between successively released batches of larval cod and their prey (Fig. 2). To determine how many larvae and prey were simultaneously present in the specified subareas of the Central Baltic Sea (Fig. 1), a coefficient of overlap (C) was calculated (Horn, 1966), which is 0 when there is no overlap, and 1 when two distributions are identical:

$$C = 2 \sum_{i=1}^n (A_i \times B_i) / \left(\sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2 \right)$$

where n is the number of statistical rectangles (Fig. 1) covering the main spawning area as well as the whole Bornholm Basin. The letter is known as the area of most likely larval and juvenile appearance (Hinrichsen et al., 2003). For our analysis, A and B are the proportions of larvae found in each rectangle at hatch (A) and after a given time period of larval drift (B), respectively. The

delayed time period at which final larval drift locations are calculated has also been defined as the time period of peak prey abundance. High values of this coefficient indicate retention of larvae in the region of initial larval release (water depth > 60 m). Low values indicate dispersal and hence transport of larvae out of the area where they originally hatched. According to the mean seasonal evolution of prey fields (Fig. 2), during spring and early summer retention in the deep area can be related to optimum encounter rates between predator and its predominant prey (*P. elongatus*), whereas low values might indicate low survival success and growth of larvae. On the other hand, a low spatial overlap coefficient obtained for the late spawning period (late summer and autumn) might lead to higher prey encounter only in shallower and coastal regions outside the main spawning area. Here, at this time of the year the abundances of “other” copepods are significantly higher than *P. elongatus* (Fig. 2b).

In order to analyse how geographically variable larval cod distributions impact the spatial overlap between larvae and its prey, we performed three case studies with different horizontal distributions of larvae; i.e. i) basin-wide (water depth > 60 m) mean abundance, as well as peak abundance ii) within the basin center area and iii) at the margin regions (approximately in the area of 60 to 80 m water depth) of the spawning area of cod (Fig. 3).

Results

Generally, results of the overlap probability between larval cod predators and their prey focused on the analysis of the within- and between year variation of larval drift. To obtain a general impression of the magnitude of the coefficient of overlap two contrasting examples are displayed in Fig. 4. The temporal evolution of the spatial overlap between prey and predator caused by a temporal delay in peak prey abundance is considered here. At the beginning of the spawning period in 1981 the probability of a high overlap between a predator cohort released as larval drifters at Julian day 111 and its larval drift endpoints obtained for specific drift periods remained high until Julian day 140. This indicates high retention of larvae in the spawning ground area (water depth > 60m). At this time of the spawning season of Baltic cod retention leads to a high overlap between predator and prey, which at this time of the year is most likely concentrated in the deep basin area (Fig. 2a). The opposite was observed for the early spawning period in 1995, when the spatial overlap was significantly lower compared to 1981. The coefficient rapidly decreased to values below 0.4 within

less than one week which can be related to strong dispersal and high transport of larvae out of the spawning ground caused by strong wind forcing.

Analyses of the intra- and inter-annual variability of the spatial overlap coefficient between initial larval release locations and its final larval drift endpoints, showed large differences if a drift period of 10 days was considered (Fig. 5). The coefficient of overlap ranged from 0.29 to 0.87 with the highest variability observed during the 1990s. The lowest value was obtained for autumn 1994 whereas the highest spatial overlap occurred in late spring 1995. Compared with the early 1980s, spatial overlap was lower since the mid 1980s, especially early and late in the spawning season. Only for the late 1980s and early 1990s, throughout the seasons, anomalously high coefficients of overlap were found. Generally, the overlap coefficient remained at a relatively high level during summer months. The latter is confirmed by seasonally averaged overlap coefficients obtained for the 20 years simulation period, (Fig. 6). If a delay of peak prey abundance of 10 days compared to the occurrence of larval cod has been considered, an uniform horizontal distribution of larvae resulted in higher spatial overlap in summer compared to spring and autumn. However, on average the overlap during the late spawning period was lowest. Assuming horizontal variability in prey abundance with maximum occurrence either in the center or at the margin areas of the basin yielded generally in a strong decrease in spatial overlap. However, during the early spawning period, larval growth, survival and subsequent recruitment benefits from retention. Hence, the highest survival rates of larvae could be expected if an uniform horizontal larval distribution is predominant. In contrast, optimal late spawners survivorship might result during periods of dispersal if larvae originally hatched at the margins of the spawning area.

Discussion

Hinrichsen et al. (2002) utilized a spatially-explicit coupled biophysical model to analyse the influence of abiotic and biotic environmental variability on the larval and juvenile survival success of Baltic cod. It turned out that variations of the feeding conditions (temporal and spatial variations of suitable prey availability) had a strong impact on survival of first feeding larval stages. Their study suggests that food limitation for first-feeding larvae during the last two decades was caused by a pronounced decline of the copepod *P. elongatus*, the main feeding component of larval cod. By the absence of this copepod, only larvae hatched at the outer edges of the Bornholm Basin at the end of the spawning period had higher survival probability, because of their short drift distances

towards the optimal feeding environments in more shallow coastal areas. In contrast, larvae hatched within the deep part of the Bornholm Basin required too much prey for survival along their drift routes in less favourable feeding conditions.

In our study, information on temporally and spatially resolved larval drift patterns can be applied for determining larval prey encounter, by coupling transport regimes to temporal and spatial differences of the feeding environment. From numerical simulations it appeared that variation in larval transport and hence horizontal distribution is mainly controlled by the local atmospheric conditions over the Baltic Sea (Hinrichsen et al., 2001; Hinrichsen et al., 2003). We investigated the influence of retention/dispersal of Baltic larval cod in the Bornholm Basin on the overlap with the prey, dependent on the time of hatching. High overlap values could be related to periods in which larvae are retained in the spawning ground, thereby suggesting beneficial feeding conditions with a positive effect on growth, survival and subsequent recruitment for spring and early summer spawners. Those time periods are characterized by weak wind forcing conditions and occur mainly in summer. On the other hand, relatively strong wind forcing results in a low spatial overlap and was found to be highest late in the cod spawning season. Thus, larvae hatched within the spawning area are transported to shallower or coastal areas and potentially could only contribute to recruitment if they are in contact with high food abundance late in the spawning season.

The coefficients of overlap have been calculated with respect to some simplifications. Detailed information on spatial and temporal variability in availability of larval cod and prey in combination with variation in ambient physical conditions was lacking. Although, transport patterns of water layers where post-yolk-sac larvae mainly occur (Grønkjær and Wieland, 1997) are relatively well known (Krauss and Brügge, 1991; Voss et al., 1999; Hinrichsen et al., 2003), validation of the modeling results is difficult. Transport patterns of larvae are influenced by the initial spawning location assumed here to be an even horizontal distribution, their initial vertical position in the water column and their behaviour. These processes and factors were not incorporated in our study. Furthermore, resolving the importance of co-occurrence of larvae and the peak abundance of their prey requires the analysis of growth characteristics of larvae and juveniles over the range of potential prey abundance available to them during the season. Grønkjær et al. (1997) clearly identified the importance of prey abundance for the successful growth of larval cod.

As obtained by a comparative analysis of simulated coefficients of spatial overlap and observed recruitment, temporal and their corresponding spatial mis-matches between predator and prey

potentially have an impact on the reproduction success of Baltic cod. Both, recruitment and the overlap coefficients calculated for the early and late spawning period showed general declining trends towards the end of the 1990s (Figs. 5 and 7), with extraordinary high values from 1979 to 1983. Accompanied with changes in the timing of spawning of Baltic cod (Wieland et al., 2000), the slight recovery of recruitment at the end of the 1990s (Fig. 7) might be due to a high spatial overlap between peak abundance of larvae and prey appearing late in the spawning in shallower and coastal areas of the basin. Please note that in the latter the high spatial overlap between predator and prey is represented by extremely low overlap coefficients between larval hatching locations and final larval drift endpoints.

Acknowledgements

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Figure captions

Fig. 1 Map of the Bornholm Basin (Baltic Sea) and statistical rectangles. Thick line represents the spawning area of Baltic cod

Fig. 2 Schematic of seasonal copepod abundances in the Central Baltic a) deep water areas, and b) shallow water areas

Fig. 3 Horizontal distribution patterns used for the calculation of the coefficients of overlap a) maximum abundance in the center area, and b) at the margins of the main spawning ground of Baltic cod

Fig. 4 Temporal evolution of the coefficients of spatial overlap a) May 1981, and b) May 1995

Fig. 5 Coefficients of overlap between larval cod and its potential prey (time lag 10 days)

Fig. 6 Seasonal averaged coefficients of overlap between larval cod and its potential prey (time lag 10 days) a) uniform even distribution, b) maximum distribution in the center, and c) at the margins of the cod spawning area

Fig. 7 Baltic cod recruitment obtained from Multi Species Virtual Population Analyses (MSVPA)

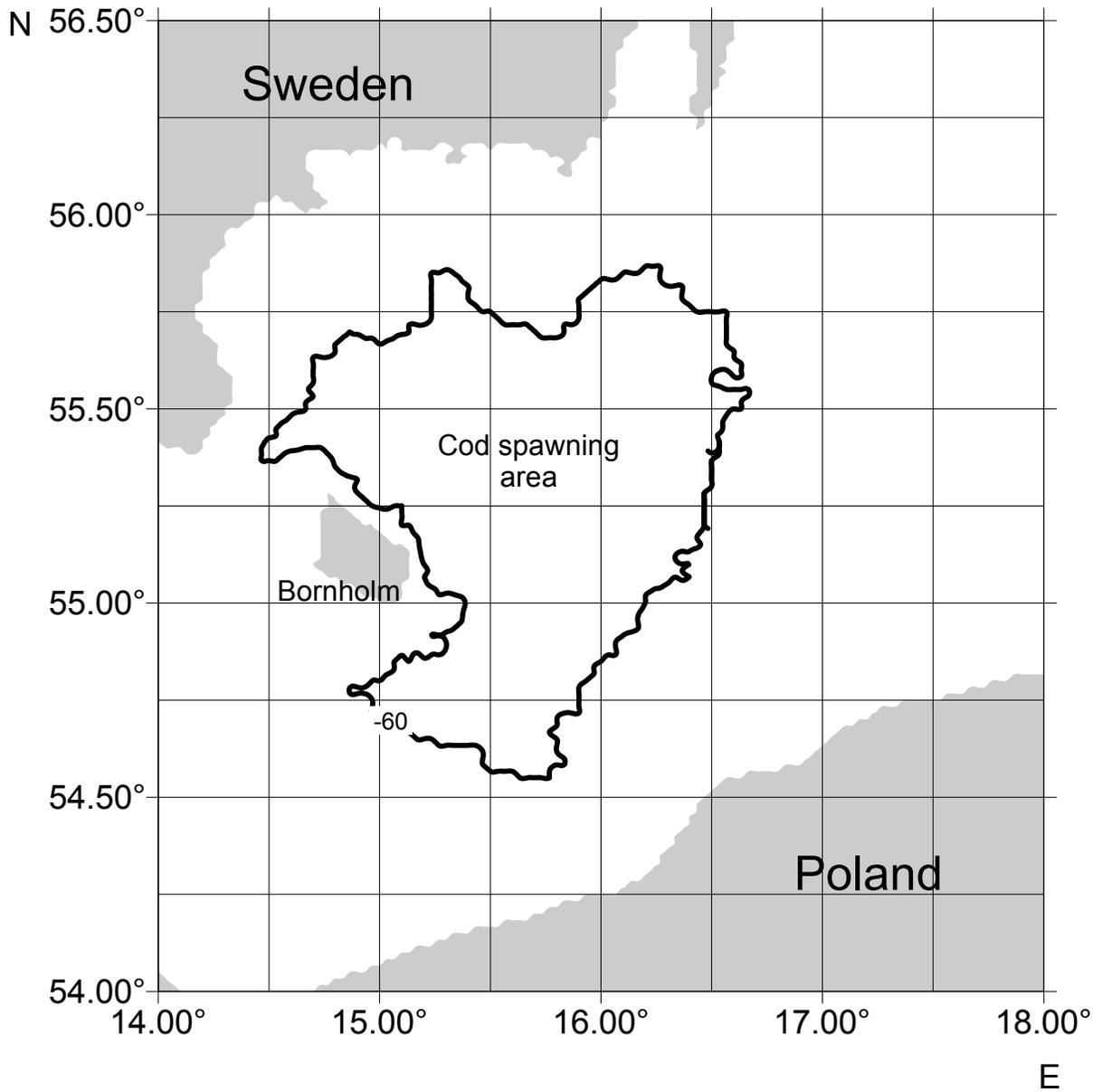
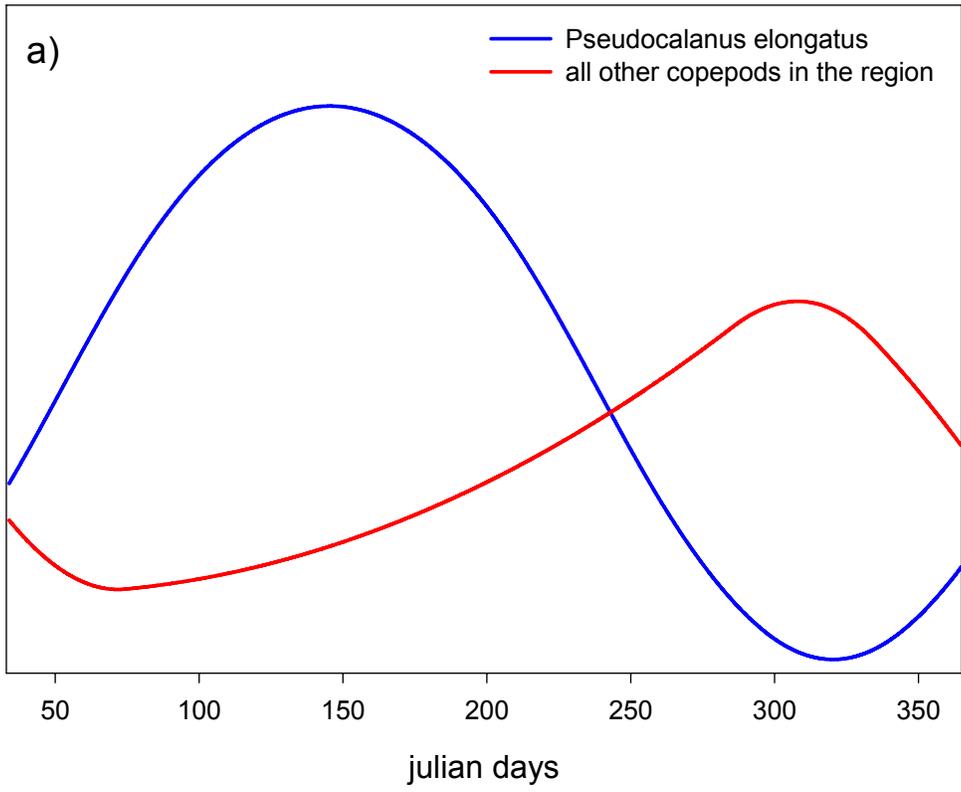


Fig. 1



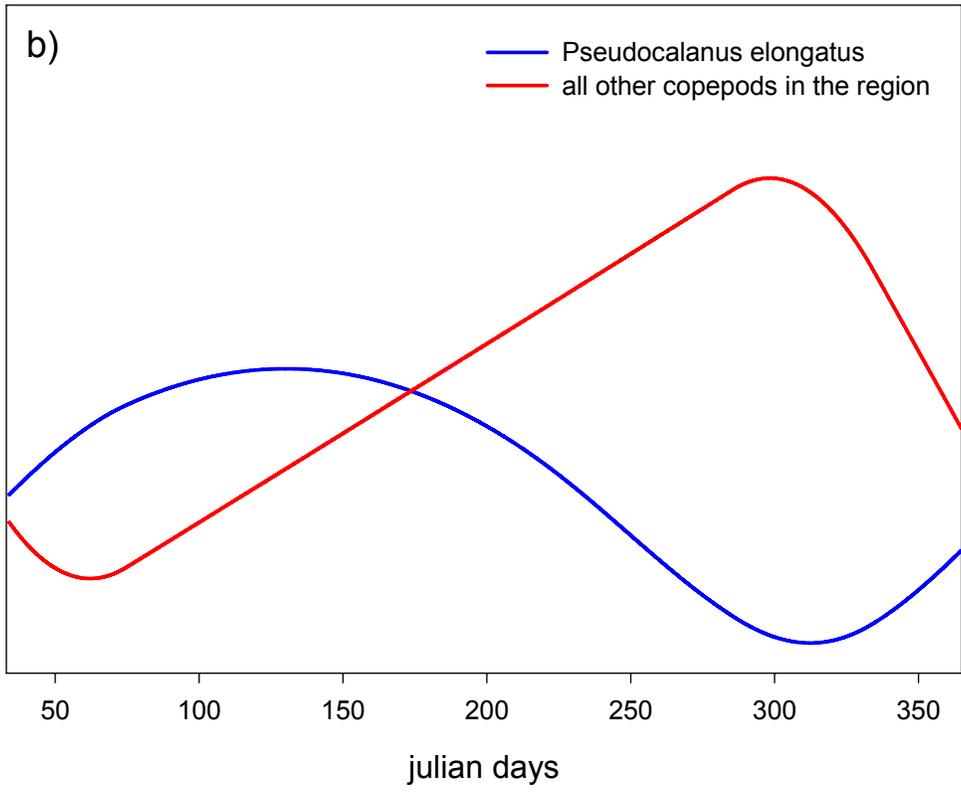


Fig. 2

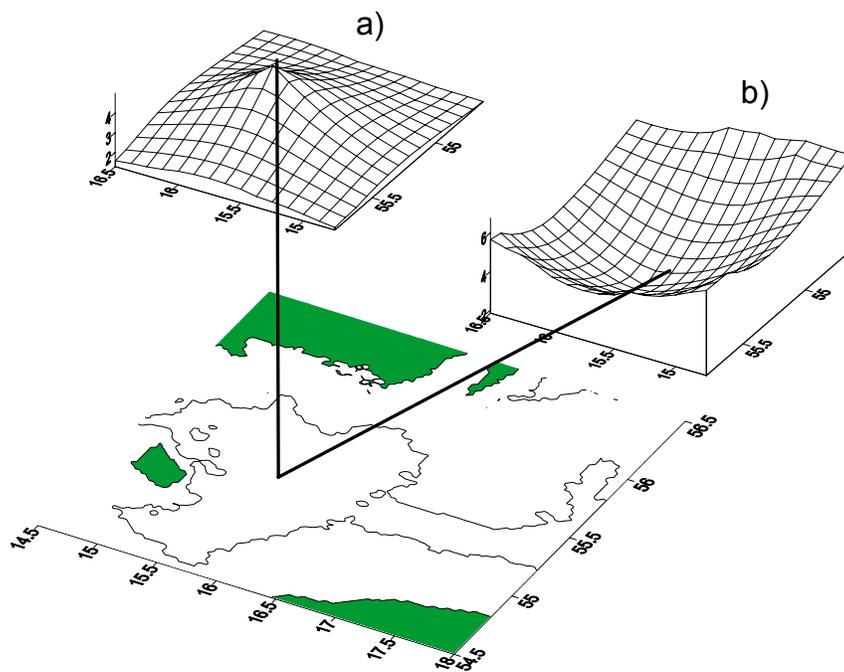


Fig. 3

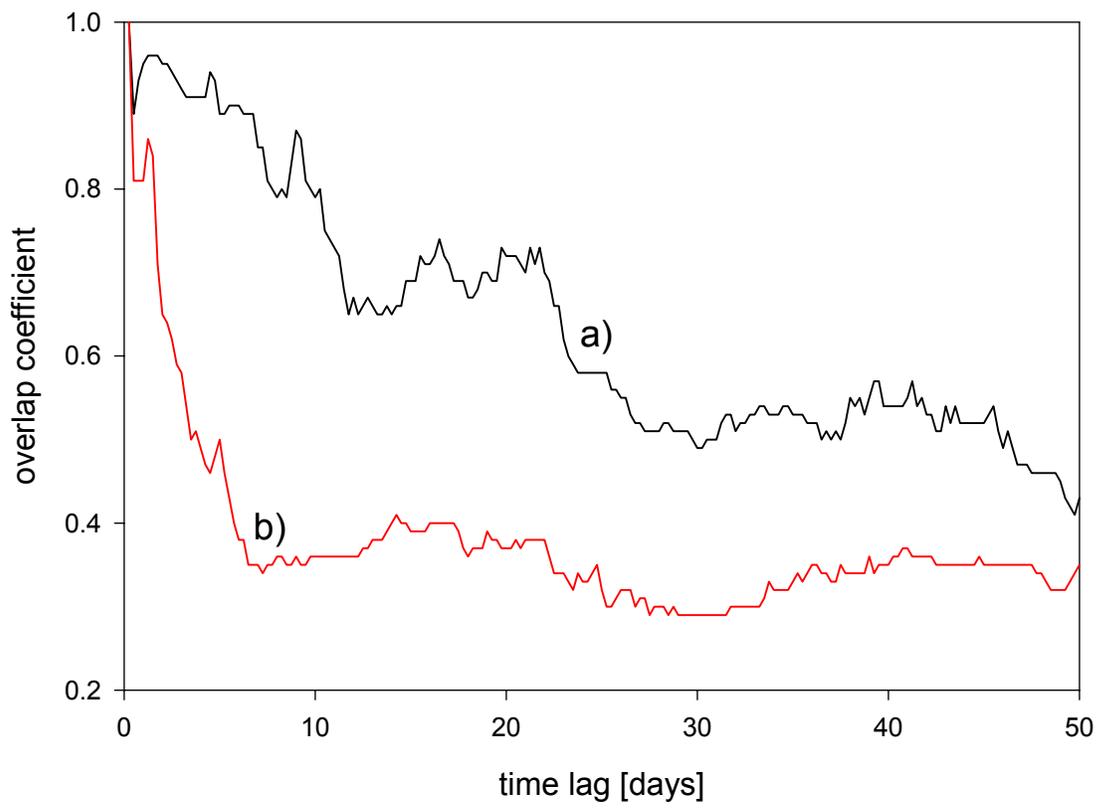


Fig. 4

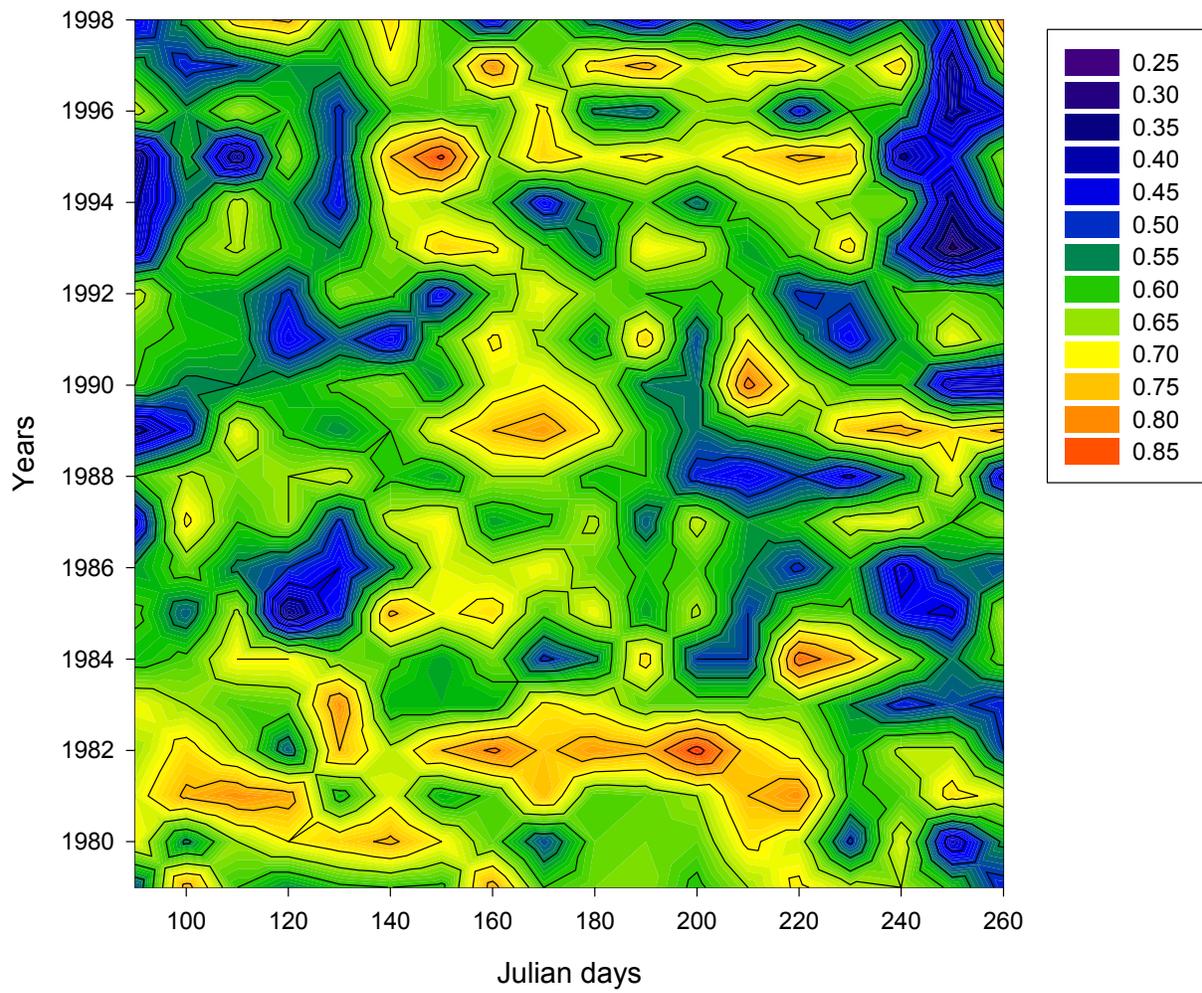


Fig 5

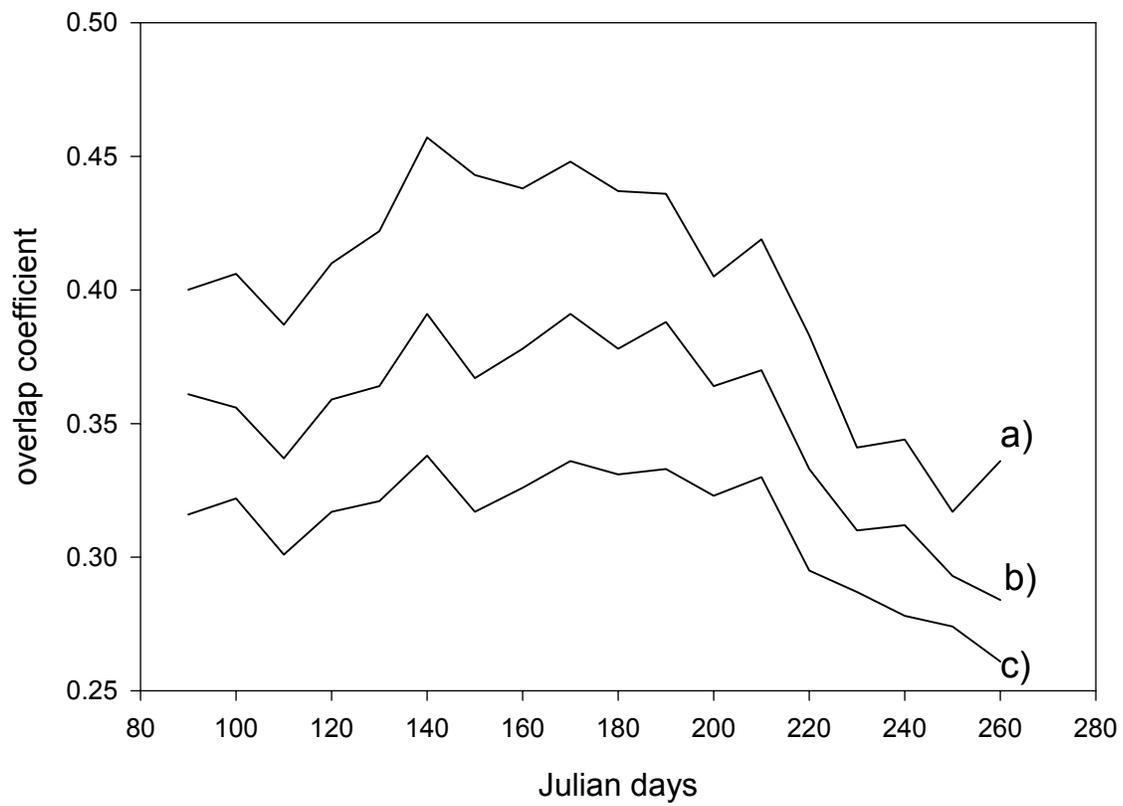


Fig. 6

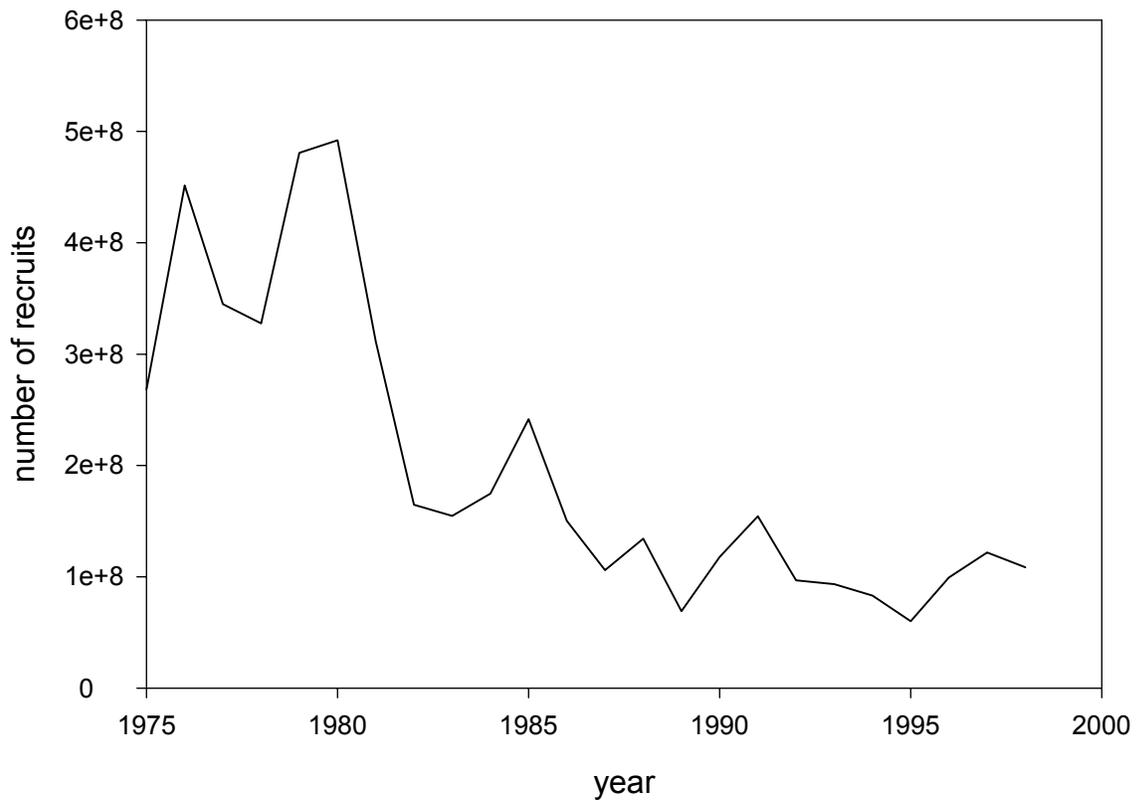


Fig. 7

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