Nephrops norvegicus in the Adriatic Sea: Connectivity modeling, essential fish habitats and management area network

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Abstract

Knowledge of connectivity among subpopulations is fundamental in the identification of the appropriate geographical scales for stock status evaluation and management, the identification of areas with greater retention rates, and space-based fisheries management. Here, an integration of hydrodynamic, biological and habitat models results is used to assess connectivity and support the definition of essential fish habitats (EFH) in the Adriatic Sea, with reference to *Nephrops norvegicus,* an

important benthic commercial resource, the recruitment of which is strongly related to larval dispersal from spawning to recruitment areas.

We explored oceanographic and biological connectivity in the Adriatic Sea under a wide and representative variety of oceanographic conditions (winter 2006-2012) by tracking 3D trajectories of larvae released from different areas. We used a Lagrangian model that features a specific larval behavior module with explicit dependence on environmental parameters (i.e., temperature and sediment type) and that is driven by high-resolution hydrodynamic and meteorological data.

The results were used to partition the area in which *Nephrops* was observed into 20 homogenous management subareas; to assess the connection between spawning, recruitment and harvesting grounds; and to identify potential subpopulation boundaries as well as the connectivity among the potential subpopulations.

The results suggest the presence of at least 3 distinct subpopulations, which need to be independently conserved, and confirms that the Jabuka-Pomo pit is the most important spawning area, but alone it cannot sustain *Nephrops* populations throughout the Adriatic Sea. The results also show that additional restricted areas should be established to sustain all subpopulations.

1. **Introduction**

The Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758; *Nephrops* hereon), is one of the most valuable species in Adriatic Sea fisheries. However, according to the recent assessments presented at the General Fisheries Commission for the Mediterranean, (GFCM, FAO, 2018) and carried out by the Scientific, Technical and Economic

Committee for Fisheries (STECF, 2018), in the last 10 years, the Adriatic *Nephrops* stock has been overexploited, the current fishing mortality is one and a half times the target, and the total Adriatic landings have decreased from approximately 3000 tonnes in 2006 to 1400 tonnes in 2017 (FAO, 2020). According to Carpi et al, 2017, several factors delayed the implementation of an effective management program for *Nephrops* in the Mediterranean, including a poor and delayed assessment of its distribution and density, and there is an urgent need to define and implement new effective measures to protect this resource.

A fisheries-restricted area was recently established in the Jabuka-Pomo pit, which is known as an important recruitment site (Bertrand et al. 2002, MEDISEH, 2013). This is in line with the Common Fisheries Policy (CFP) recommendation to identify no-fishing zones to preserve nurseries and juveniles. However, previous studies and assessments suggest that not all reserves and protection sites exhibit increases in target stock abundance (White et al., 2009), due to either poor enforcement or design processes that do not adequately account for key ecological factors (White et al., 2014). Both theoretical models and empirical assessments confirm that the spatial scale of dispersal, together with demographic and exploitation factors, is a key component for stock sustainability (White et al., 2011). In practice, it has been argued that the effects of closed areas are likely to depend on the particular circumstances of a fishery and the response of fishers and may not always be beneficial or reflect what was assessed based on data and models. Furthermore, it must be noted that in some cases, bioeconomic models are built assuming that larval dispersal is evenly distributed in space (Smith and Jensen 2008), thus missing a relevant feature of species connectivity and of the reciprocal relation among subareas.

In the Adriatic Sea, *Nephrops* are present in discontinuously distributed groups that have different densities and growth rates (Morello et al., 2007, Carpi et al., 2017, Angelini et al., 2020). The assessment of the connectivity among these subpopulations is fundamental for the accurate identification of the correct spatial scale for stock assessment and of marine management areas (MMAs) needed to support sustainable fisheries.

Connectivity models can provide helpful information to support the optimal design of reserve areas (Gerber et al., 2003, Kininmonth et al., 2011, Fogarty and Botsford,

2015, Balbar and Metaxas 2019), helping to minimize the economic costs of lost fishing grounds while protecting an adequate area of essential fish habitat (EFH), which can maintain sustainable population persistence. However, it is important to consider that during dispersal, larvae can undergo a number of biologically driven modifications, depending on their physiological characteristics and environmental conditions. Therefore, connectivity studies have to be performed with Lagrangian particle-tracking models able to quantitatively integrate the wide spatial and temporal variability in oceanographic processes with processes intrinsic to the biology of marine organisms, as already shown in previous studies addressing larval connectivity (Cowen et al., 2005, Gawarkiewicz et al., 2007, Werner et al., 2007), also over multiannual spawning seasons (Gargano et al., 2017, Rochette et al., 2012) and also adopting coupled Particle-Tracking- Individual-Based-Models to address the effect of migration behavior and of environmental parameters to planktonic larval duration and dispersal (Martha-Almeida et al., 2008, Bolle et al., 2009, Rochette et al., 2012, Meerhoff 2020). Here, the multiannual biophysical larval transport modeling approach was fully proved by a working example in which connectivity is assessed by the integration of hydrodynamic, biological, behavioral, and habitat models.

Here, a larval behavior and growth model was developed and integrated to a recently released three-dimensional Lagrangian particle-tracking model (Laurent et al., 2020), forced by output from a high-resolution modern finite-volume hydrodynamic model (Querin et al., 2016). The integrated larval + particle_tracking + hydrodynamic model has been used to explore and assess the connectivity of *Nephrops* in the Adriatic Sea for the period 2006-2012.

In detail, the aim of this manuscript are: i) to support the identification of management areas and of an essential fish habitat network for this species, ii) to explore connectivity among management areas and to assess the extent to which different subpopulations are connected or segregated, and iii) to discuss the current management of *Nephrops* exploitation in the Adriatic Sea, including the opportunity to assess and manage it as a single stock rather than multiple stocks. To achieve these goals we performed an ensemble of 558 simulations, which can be considered representative of a large variety of different oceanographic conditions. Each simulation returned a connectivity matrix, and statistics were calculated over the

whole set of simulations, providing i) the probability that a larva released from each release point settles in any arrival point, ii) the average connectivity time, and iii) the mortality. Several connectivity indexes were computed and mapped to identify the potential recruiting and spawning hotspots, and a cluster analysis on potential spawning sites was performed to support the identification of marine management areas (MMAs). Finally, connectivity was computed between spawning, nursery, and harvesting grounds and MMAs as well as between identified *Nephrops* (potential) subpopulations.

2. Materials and Methods

2.1 *Nephrops* in the Adriatic Sea

Nephrops is a bottom dwelling decapod crustacean, with a total body length among adult animals that varies between 8 cm and 24 cm (measured from tip of rostrum to end of telson) (Froglia and Gramitto, 1981). Its geographical distribution includes the Eastern Atlantic region, the western and central basins of the Mediterranean, the Adriatic Sea, the northern Aegean Sea, and the Marmara Sea (Farmer, 1975). *Nephrops* build complex burrows in muddy sediments, emerging from them with variable frequency, usually following diel and seasonal patterns, depending also on depth, season, animal size, sex, and reproductive status (Froglia, 1972; Chapman, 1980; Froglia and Gramitto, 1986; Tuck et al., 2000, Morello et al., 2007, 2009).

According to the information on the spatial distribution of the Adriatic *Nephrops* derived from the MEDITS survey carried out in the period 2002-2011 and from the results of the MEDISEH project (2013), in the Adriatic Sea, *Nephrops* has a discontinuous spatial distribution at depths between 40 m and 400 m, mainly in muddy (silty-clay) areas that are preferably medium-grained (~ 40% clay and silt) (Figure 1). Peak concentrations are observed at depths of approximately 70 m off Ancona, approximately 80-90 m in the Velebit Channel, and approximately 200 m in the Jabuka/Pomo pit (hereafter J/P pit) (Colloca et al., 2015). The data indicate several prevalent spawning grounds (indicated in yellow in Figure 1) and a main recruitment area in the J/P pit, which therefore is of particular interest, as it was identified as both

a recruitment area and a spawning ground. No survey data were available for the period considered for the eastern sector of the southern Adriatic Sea, but earlier studies reported the presence of *Nephrops* in some epibathial areas (Abellò et al., 2002).

Nephrops is generally characterized by spatially segregated populations, with little or no exchange between them (Bell et al., 2007). In particular, in the Adriatic Sea, *Nephrops* presents spatially different growth rates and sizes at first maturity.

The population connectivity between prevalent recruitment and spawning areas is not yet well understood, and several researchers argue that the J/P pit recruitment area, for reasons related to its geography, morphology and oceanography, is likely to be inhabited by a very dense "subpopulation" of smaller animals with slower growth rates; this area might be considered separate from other grounds, such as those off the eastern Italian coast south of Ancona (Froglia and Gramitto, 1981, 1988), northern Croatian channels (Vrgoč et al., 2004) and off the southern Croatian coast. This is also confirmed by a recent morphological study from Angelini et al. (2020), which highlights the presence of at least two distinct subpopulations in the J/P pit and off Ancona. However, genetic analyses have not revealed differences beyond the population level between these areas, thus suggesting that the differences are mainly due to different environmental conditions (Mantovani and Scali, 1992). A connectivity analysis based on larval dispersal, transformation and survival can be useful for understanding if and how much these populations are connected or segregated and if the assessment and management of *Nephrops* in the Adraitic Sea as a single or multiple stocks is appropriate.

Nephrops in the Adriatic Sea spawn once per year. Mating occurs in spring, and eggs are spawned in summer and incubated externally on the pleopods for 6 – 10 months depending on temperature and habitat (6 months is more likely in the Mediterranean; Farmer, 1974; Sardà, 1995). Soon after spawning, females carrying eggs tend to hide in their burrows until hatching occurs in late winter (Orsi Relini et al., 1998; Vrgoč et al., 2004; Bell et al. 2007).

The larval phase of *Nephrops* is pelagic and planktonic, and depending on temperature and environmental conditions, it can last between 3 (at 18°C) and 7 (at 8°C) weeks (Farmer, 1975; Orsi Relini et al., 1998; Dickey-Collas et al., 2000). Zoeal stages 1 and 2

are positively phototaxic, rising through the water column (Powell & Eriksson, 2013), with no independent horizontal movement (Hill, 1990). During zoeal stage 3, *Nephrops* move toward the bottom, where they stay until metamorphosis into the postlarval juvenile benthic stage; at this point, the larvae have some capability for horizontal movement (Hill, 1990; Powell & Eriksson, 2013). At the end of the pelagic larval period, *Nephrops* individuals metamorphose and settle on the sea floor, which needs to be fine sand-silt-clay sediments (grain size finer than 3 on Φ scale, see map and additional explanation in Supplemental materials) (Farmer, 1975; Chapman, 1980; Hill, 1990). The combination of favorable hydrodynamics and sediment conditions is thought to favor dense *Nephrops* populations in several hot spots, including the J/P pit (Bailey et al., 1995; Brown et al., 1995; Hill et al., 1996, 1997; Øresland, 1998).

2.2 Model setup

Simulations of larval growth, behavior and dispersion were performed using the LTRANS-Zlev Lagrangian particle-tracking model (Laurent et al., 2020) coupled with an MITgcm (Massachusetts Institute of Technology general circulation model, Marshall et al., 1997) ocean model implementation for the Adriatic Sea (Querin et al 2016).

The hydrodynamic simulation (currents and thermohaline properties) was run in non-hydrostatic mode and features 1/64° horizontal grid spacing, which corresponds to an average surface area of each element of the domain (i.e., each cell) of ~2.2 km². The vertical discretization consists of 60 unequally spaced z-levels, with decreasing resolution with depth, i.e., it is finest at the surface (1.5 m) and coarsest at the bottom (62 m at 1200 m depth). The adopted horizontal and vertical resolution allows for an accurate description of the connectivity processes in this basin. Following Querin et al. (2016), the southern open boundary conditions of the Adriatic model are provided by a simulation performed by a coarser (1/32°) resolution model run over the whole Adriatic-Ionian system, which in turn is forced at its boundaries (Sicily Strait and Cretan Passage) by the Copernicus Marine Environment Monitoring Service (CMEMS MED-physics, http://marine.copernicus.eu). The discharge rates of the main rivers flowing into the Adriatic Sea were defined using the dataset presented by Janeković et

al. (2014). The meteorological forcing fields (air temperature, humidity, winds, rain, and shortwave and longwave irradiance) were produced by the Regional Climate Modeling system (RegCM4).

LTRANS-Zlev is an offline particle-tracking model forced by 3D current, temperature, and density fields that is able to simulate (among other things) the complex behavior of planktonic larvae (Laurent et al, 2020). Based on general and site-specific information on the life cycle of *Nephrops*, adapting previous models already developed for the southern Portugal and Irish Sea stocks (Martha-Almeida et al., 2008, Phelps et al., 2015), LTRANS-Zlev was setup to simulate the larval phase from release to settlement. Larvae were advected using the 3D current fields and by superimposing upward and downward vertical migration due to positive or negative phototaxic behavior and diel migration. The effects of the subgrid horizontal turbulence were reproduced as a random walk diffusive process, with an intensity of 1 $m^2 s^{-1}$. The integration time step was 200 seconds. The simulation did not take into account larval stranding at the coast; therefore, when larvae reach the coastal boundary, they stay in the model domain. Conversely, larvae crossing the southern border exit the domain and are lost. Sea bottom suitability was introduced into the model by taking into account the temperature encountered by the larvae at settlement and sediment grain size.

Floating or sinking behavior is superimposed on vertical hydrodynamic transport based on larval size (total length). Larval growth, *Gr*,, is assumed to change through time as a linear function of local seawater temperature *T*, and since observed rates at 8 °C and 18 °C were 0.2 and 0.4 mm day^{-1}, respectively (Farmer, 1975; Orsi Relini et al., 1998; Dickey-Collas et al., 2000), it reads:

Gr=0.02**T +0.04   (Eq. 1)

Larvae grow to a critical size, after which settlement occurs. Accordingly, the time required for a larva to settle varies depending on the temperature exposure during its lifetime. In the first life stages, larvae released near the sea bed rise toward the surface and are transported by surface currents. They remain in the surface layer until they reach a critical size that allows them to sink down to the seabed. At this stage, they are transported by bottom currents and spend a variable amount of time searching for a suitable substrate for settlement (details below).

Spawning grounds are identified based on field data (MEDISEH and MEDITS) and are shown in Figure 1 (yellow areas). Based on biological information, spawning was simulated from 1st December to the start of march, for 93 days; new larvae are 6 mm long, and settlement occurs at the critical size of 14 mm (Powell and Eriksson, 2013). The larval dispersal behavior is represented in Figure 2 and summarized in Table 1. At the time of release, t_n^0, the 6 mm long larva is released from the bottom and is advected by the 3D current field. In this first life stage, larvae also have an upward vertical movement toward the surface (to simulate the positive phototaxic behavior), set to a velocity of 25 mm s^{-1} (Smith, 1987).

During the second life stage, between 6 and 14 mm long, when the larvae are at the surface, a diel migration pattern is introduced: larvae remain at depths of 5-10 m during the night and 0-30 m during the day. When larvae are outside their target layer, they move up or down with speeds of 25 mm s^{-1} and 9 mm s$^{-1,}$ respectively; when they are within their target layer, larvae move upward with a random velocity ranging (up and down) from 0 to +17 mm s^{-1}. The day and night diel migration was set in the model at the time when the downward shortwave solar radiation on the sea surface reached 50 W m^{-2}.

When a larva reaches 14 mm in length, it enters the third larval stage and starts swimming downward toward the seabed, with a velocity of 9 mm s^{-1}. Then, (stage four) the postlarvae remain in the 2 m thick layer above the seabed, where they are advected horizontally by the currents at 10% of the flow velocity, to account for the viscous effects of the boundary layer. During this period, they randomly move (upward or downward) with velocities between 0 and 9 mm s^{-1}, but if they rise above the bottom layer, the chances of swimming downward are increased from 50 to 80%, constraining the particle to return within 2 m from the sea bottom. Within 3 days from entering the fourth stage, the larva reaches an area of suitable sediment grain size (Φ > 3) and depth (> 20 m) where it settles (Figure 2a); otherwise, it dies (Figure 2b). If, at any instant during its pelagic state, the sea temperature at the position of the larva reaches a critical temperature (higher than 19°C), the larva dies (Powell and Eriksson, 2013) (Figure 2c).

The success in the settling of a generic larva is therefore calculated by the model as the combination of various constraints: a larva has to survive while growing to reach settling time/size, and at settling time, it has to be in an area having both adequate sediment composition and suitable sediment depth, with less than 3 days spent along the seabed. The final constraint is the maximum time a larva can live, set to 70 days.

2.3 Reference simulations

The simulation ensemble includes 558 simulations. Each simulation starts on a different day of the spawning period, lasts up to 70 days and is forced by oceanographic conditions provided by the hydrodynamic model forced by meteorological conditions. In each simulation, we tracked the trajectories of larvae released from each of the 15198 grid points within the spawning grounds, corresponding to the yellow areas in Figure 1. Larvae were released close to the seabed. The analysis was conducted over six years to capture the interannual oceanographic variability (Melaku Canu et al., 2015) during the spawning months.

2.4 Sensitivity simulations

Sensitivity analyses to tune three uncertain parameters were performed by running 8 additional simulation ensembles (each formed by 558 simulations covering the six years), varying the temperature tolerance between 16 and 19 °C, the searching time between 0 and 5 days, and the sediment grain size threshold for settling between 3 and 7 Φ.

2.5 Postprocessing

Each simulation returned a connectivity matrix between the 15198 releasing cells and 60143 settling cells, as detailed in the Supplemental materials (Eq. S17 and S18). The average over the 558 simulations allows the computation of the probability that a larva released in a given spot (R) settles in spot A. The simulations also return matrices of connectivity times, indicating how long it takes for a larva released from a given cell, in a given time, to reach its settling site, and mortality matrices.

Proper elaborations/aggregations of the connectivity matrices also return indexes for each of the *releasing* cells, which can be represented by maps. Each simulation returns a map that is representative of a specific period, and the average over the 558 maps produces settling index maps representative of the whole period covered by simulations, namely:

Potential spillover Index, PSOI, map, which describes the success of a release and is produced by calculating the percentage of successfully settled larvae released from each grid point (R), regardless of the settling point (as detailed in Supplemental materials, Eqs. S 7-S8, S11-S12), normalized by the maximum observed value. A *mortality* (or loss) map, computed as the percentage of the larvae released at each point that are lost or that die before settling, can be derived as 1-PSOI.

- *Dispersal Index*, DI, map which is the amplitude of the area connected with each spawning point R, and is computed for each cell R as the number of cells receiving one or more successful larvae from R, but which are more than 30 km from it (Supplemental materials, Eq. S 20), normalized by the total number of released particles per cell.

Similarly, indexes can be computed for each *settling* site, also represented as maps, such as:

- *Density-kernel index*, DKI, map of successful arrival, produced by tracking how many larvae settle at each point *A* (acceptor), regardless of their origin (Supplemental materials, Eq. S 9-10, S13-14), normalized by the maximum observed value.

- *Convergence Index*, CI, map which measures the number of cells contributing to the settlement in each settling point A, considering only the cells that are more than 30 km from the acceptor cell, by normalizing the total number of release cells. (Supplemental materials, Eq. S 22).

A buffer zone of 30 km was introduced in the calculation of *the convergence and dispersal* matrices to exclude all settling occurring in the surroundings of the source/sink cell from the computation. The *PSOI* and *DKI* maps do not overlap spatially, since we simulate a potential spillover occurring only from the areas shown

in Figure 1B, identified as the area of persistence of *Nephrops* in the Adriatic Sea, while settlement can occur anywhere in the domain.

The *PSOI* and *DKI* are normalized over the maximum observed values. Normalized standard deviations for the two indexes were also computed to highlight their variability.

Identification of management subareas and connectivity among them

Management subareas have been identified by i) identifying the spawning areas from MEDITS and MEDISEH observations and conclusions, ii) performing a cluster analysis on the average connectivity matrix to partition the spawning areas in several subareas, which can be used to identify potential management subareas, iii) computing settling indexes for these areas, and iv) the connectivity between them.

A cluster analysis of the spawning sites has been performed by using a K-means relocative-iterative algorithm, implemented as in Rodriguez and Laio (2014), which selects cluster centers among the points having a higher density than their neighbors and a relatively large distance from points with higher densities. The clustering algorithm has been applied by evaluating the distances between the release positions in the arrival-cell connectivity space , i.e. the difference in the spatial distribution of successfully settled particles. Consequently, the distance between two release points, $R_1 = (i^{R1}, j^{R1})$ and $R_2 = (i^{R2}, j^{R2})$, is computed by $D(R_1, R_2) = \sqrt{\sum (N_{Aj}^{R1} - N_{Aj}^{R2})}$, where N_{Aj}^{Ri} is the number of particles released in cell i that successfully settled in cell j, and nA is the number of arrival cells. A distance cutoff of 70 (particles) was used, and the original algorithm was slightly modified, adding a density cutoff of 1.2, so that the number of cluster centers could be increased without selecting as centers the points with insufficient density in the arrival-cell connectivity space.

Several clustering have been performed, by considering classifications with a number of groups ranging from 8 to 25, and the best classification (based on an expert judgment of the geographical division emerging from the classification) was retained for potential use in management subarea delineation.

The connectivity among the clusters (i.e., MMAs) was then computed by producing and analyzing a new aggregated connectivity map, obtained by averaging over the points in each cluster and normalizing fluxes by the number of larvae settled in a given cluster. The R igraph package (https://cran.r-project.org/web/packages/igraph/citation.html) was used to graphically illustrate the number and strength of connections between the MMAs.

3. Results

3.1 Settling times

Larval growth and settlement depend on environmental parameters. In our reference ensemble of simulations, the settling time varies between 53 and 70 days (the maximum duration of the simulation), according to the daily evolution of the environmental temperature and the time required to find suitable sediment conditions.

3.2 Larval mortality

Based on the average output, derived by averaging over all 558 simulations, 74% of the released larvae settle inside a suitable area of the model domain. Almost half of them (37% of the total released larvae) settle inside one of the cells included in the release area (yellow areas in Figure 1), and a little less (39% of total) settle in other areas in the domain. Among the remaining 26% of the larvae, 3% are lost from the model boundary, 8% die from settling in unsuitable sites, and 12% find suitable conditions too late.

The sensitivity of mortality was addressed by changing the uncertain parameters *searching time* and *temperature limitation*. The analysis indicates that by varying the searching time between 0 and 5 days (i.e., up to 60% more than the reference value (3 days)), settling success can be increased or decreased by only 1-5%. The model response is more sensitive to the temperature limit, which, if decreased by 1 or 2°C

(i.e. approximately 5% of the reference value (19°C)), can induce a 5 or 10% change (decrease) in mortality.

3.3 Spillover and dispersal

The PSOI index shown in the map of Figure 3A shows the spillover potential of the release areas, indicating the areas where larval release is potentially much more successful than other areas. The inspection of the map reveals that the larvae released from the areas located in the central basin, including the J/P pit, and the area off Puglia and along the Albanian coast, present higher potential for successful settling than those released in other areas. The standard deviation of the PSOI (Figure 3B) computed over the whole simulation set provides additional information regarding where and how the PSOI index varies in time, thus indicating the areas where the PSOI value is almost constant through time (i.e., has a low standard deviation) and areas where the PSOI variability through time is high.

The results show that the recently established fishery-restricted area (FRA), shown by the dashed black line in Figure 3, presents high PSOI values and low variability, supporting the conclusion that larvae released from this area consistently have successful settling probabilities higher than those realized from many other areas. However, similar or even higher PSOI values can be observed for other areas, including a substantially larger part of the J/P pit, the southeastern Adriatic sites, and the southern Adriatic area close to the southern Adriatic pit. PSOI variability is low in all of these areas.

In contrast, lower PSOI values are computed for the Kvarner coast (Croatia, in the northeastern part of the basin), but in this case, the standard deviation is higher, suggesting that during a specific time of the year, or under specific oceanographic conditions, this area also has good spillover potential

The Dispersal Index DI (Figure 4A) shows similar findings, summarizing the number of settling sites reached from each spawning site, and represents the extent of the influence of each spawning site over the whole domain.

3.4 Density kernel and convergence

The DKI map (Figure 5A) indicates that some areas have a higher recruitment potential than others, either because of the flow regime, which delivers more larvae to specific places, or environmental conditions. The map shows that the largest fractions of successful settlement occur in the central part of the basin, with peaks in the central part of the J/P pit and along the central and southern parts of the Italian coast of the Adriatic Sea. Moreover, the CI map, (Figure 4B) shows that the number of cells from which these areas receive larvae is larger than the number of cells contributing to other settling sites, i.e. they receive larvae from a higher number of cells compared to others areas.

The analysis of the standard deviation associated with the DK indicates (Figure 5B) that the recruitment potential in the J/P pit is persistently high under the whole range of environmental conditions.

High DKI values are also observed in the Kvarner area, but only in some patchy hotspots and, as evidenced by the higher DKI standard deviation, only for some periods. Furthermore, the convergence index map highlights that this area receives successful settlers from only a modest number of spawning sites, suggesting that it is somehow isolated from the rest of the basin, needs to be self-sustaining, and is potentially more vulnerable to a decline in spawning stocks.

The analysis confirms that the FRA in the central Adriatic Sea includes areas that are important as both spawning and recruitment sites; therefore, this FRA is an essential habitat for *Nephrops*, but the larger area around the FRA shares similar properties.

3.5 Management subareas

The results of the cluster analysis on the connectivity matrix produced a classification of spawning points that –when mapped into geographical space– returns a subdivision of the spawning area into reasonably 'compact' areas. Different cluster analyses

produced slightly different results but globally supported the identification of a clear and common division. Taking into consideration geographical and bathymetric constraints as well as the need to have easily recognizable boundaries among areas, we chose to retain the result of the classification with 20 clusters as a network of 20 management areas, presented in Figure 6. In agreement with the procedure followed to identify them, these are areas in which observations showed that there are a good number of adults and spawning sites. Furthermore, the larvae released from the points within a given MMA will follow similar trajectories and end up more or less at the same points, whereas larvae released from points belonging to different MMAs will generally follow different trajectories and settle in different areas. Area and average connectvity indexes for each MMA are given in Table 2.

3.6 Connectivity

The aggregated connectivity matrices for the MMAs represented in Figure 6 were computed and then were used to assess and visualize the properties of the different areas and their reciprocal relationships. The connectivity among the MMAs can be assessed using the normalized larval fluxes and their intensity, as presented in the heatmap table of Figure 7 and in the graph of Figure 8. Fluxes are normalised, with the number of larvae settled in each MMA. Therefore they return the information from a 'receiver' perspective, namely, they indicate which area contributes to settling in each MMA and to what extent (percentage). The arrows depict the connections among the subareas, and the intensity of the larval fluxes is expressed by the arrow thickness.

MMA_1 is largely self-sustaining and received some larvae from only the Kvarner area (MMA_2). Areas 3, 4, 5, and 6 (in Kvarner Bay and the Velebeit Channel) are interconnected, with a roughly anticlockwise larval flux; however, while approximately half of the production of areas 5 and 6 is self-sustained, MMA_4 relies significantly on settlement from MMA_5 and MMA_6, and MMA_3 relies almost completely on its neighborhood.

The set of MMAs in the central Adriatic Sea (i.e., those around the J/P pit (MMAs 7 to 12)) have asymmetric relationships: there is a coastal northward larval stream from MMA_19 to MMAs 20, 8, and 7. MMA_7 sends some larvae further north and some

west, toward the center of the basin. The very central MMA_10, which has high PSOI and DKI values, does not receive large contributions from other areas but sustains itself and is the only large contributor to MMAs 11 and 12 and the main contributor to MMA_9. The population of MMA_9, which contributes poorly to other areas, also depends on fluxes from MMA_7. The coastal area south of Ancona, MMA_13, is poorly connected to the J/P pit since it receives modest amounts of larvae from other areas and is sustained mainly by areas 16 and 17, which are to its south. The coastal area close to Ancona, MMA_15, does not receive contributions; instead, this area sustains itself and area 14, which is just south of it. The southern region (18) is self-sustaining and–likely through the circulation of the South Adriatic Gyre–also sends larvae to area 19, which in turn sustains area 20.

4. Discussion

Nephrops populations in the Adriatic Sea are facing a decline due to overfishing (Carpi et al., 2017), and there is a need for (and a lack of) quantitative methods and tools to support their management. Assessing the extent to which the benefits of closing an area to fisheries are reflected outside the protected area is crucial but also challenging and needs the integrated support of field data and different types of models. A great effort was made in the framework of the MEDITS survey program to produce basic information on the distribution of *Nephrops* in the Mediterranean Sea, including the Adriatic Sea, through systematic bottom trawl surveys. However, due to their nature, surveys are hampered by limitations such as space and time discontinuities and difficulties in detecting exchanges of larvae (Cowen and Sponaugle, 2009), which, for benthic species, are the predominant dispersal stage. In addition, owing to the temporal variation in *Nephrops* emergence behavior, bottom trawl surveys are not always the best tool for quantifying this species. Information on larval connectivity is particularly relevant for assessing the population dynamics of benthic sedentary species, such as *Nephrops*, and connectivity matrices are valuable for identifying MMAs, assessing the connections between them, and providing inputs for spatial population dynamics (Russo et al., 2019).

Here, we used a large number of simulations, representative of meteorological and oceanographic conditions over six years, which were characterized by a wide

variability. Therefore, the model results provide robust statistics of *Nephrops* larval connectivity in the northern and central Adriatic Sea. The inclusion of a larval behavior model dependent on environmental parameters, namely, temperature and sediment size, despite introducing additional variability, allowed us to represent the influence of the spatial/temporal environmental variability on recruitment dynamics in a more realistic way.

The quantitative results obtained allowed the identification of zones with high potential for spillover, i.e., areas that, if protected, could contribute in a very positive way to the maintenance of the *Nephrops* stock and to the sustainable management of the *Nephrops* fishery. Together with information on adult *Nephrops* presence and the trajectories of successful larval settlement, this allows the provision of advice on the definition of a network of MMAs. The PSOI and DK maps (Figures 3 and 4) integrate the outputs of the whole simulation set and highlight the existence of hotspots for both potential spillover and settling/accumulation. A visual comparison of the figures suggests that areas that have a high PSOI also released larvae that spread over a large fraction of the domain and supports the conclusion that these areas can be identified as particularly relevant marine management areas. Additionally, in this case, the J/P pit FRA presents high values, but not the highest, and the analysis of these indexes supports the conclusion that the southeastern Adriatic spawning area is a very relevant MMA that is able to spread larvae over a large area, whereas larvae produced in the northeastern part of the basin are poorly spread outside the production area. In the same figures, the standard deviation maps associated with each descriptor indicate that the potential spillover hotspots are very persistent, while the potential recruitment hotspots appear to be more variable. These results underline the importance of the wider J/P pit area and southeastern area (MMA 19) as essential fish habitats due to their spillover potential. Moreover, to a lesser extent, the J/P pit area is shown as an area of relatively high settlement.

The divergence index (DI) and the convergence index (CI) (Figure 5) identify for each point of the domain the number of different connections with other points of the domain as producers (DI) and as receivers (CI). This information is especially useful when dealing with genetic factors and allows the identification of areas that are 'segregated' as receivers, as 'producers' or as both, and that, therefore, need some

kind of autonomous management. The results show that the Kvarner region is segregated as both a receiver and producer, indicating that it should be managed separately from the rest of the Adriatic Sea.

The clusterization of the global PSOI map returns a subdivision of the potential spawning areas into 20 MMAs. The classification groups together points that have similar spawning performances, i.e., points within a group of released larvae that follow similar trajectories and have similar probabilities to successfully settle the same areas. Being performed from a 'donor' (i.e., spawning) perspective, this analysis returns information useful for conservation, i.e., on the area to be protected to maximize larval spreading (and settling) throughout the basin. Ideally, it is not necessary to protect all of the points in a given MMA, since they all provide similar contributions, but it would be optimal to protect at least a fraction from each of the MMAs. The fraction of MMA to be protected might be chosen by selecting the points with the highest PSOI and/or DI values within the MMAs.

These unambiguous results provide valuable information for the management of the Adriatic Norway lobster stocks and quantitatively confirm the scientific soundness of the recently established fishery-restricted area in the J/P pit, since it is indeed composed of points with good spawning performances (high PSOI and DI values) selected from fractions of different MMAS and, therefore, has potential to sustain part of the Adriatic *Nephrops* population. However, the results show that other areas should also be protected to sustain the remaining parts of the population.

The connectivity fluxes among the network of 20 MMAS, being computed from the 'receiver' perspective (i.e., which MMA contributes to sustaining the population of a given MMA), also provide useful information on conservation priorities as well as on segregation/connectivity between potential *Nephrops* subpopulations contained in different MMAs.

The MMAs are connected through the main pathway of the Adriatic Sea general circulation (Artegiani et al. 1996), with a coastal larvae stream northward along the Croatian coast and southward along the Italian coast and some recirculation in the South Adriatic Gyre. Inside the J/P pit area, the core of MMA-10, which sustains itself and the areas south and west of it, plays an important role as a producer. Conversely, a negligible connection is observed between the J/P pit area and the area off Ancona,

which reinforces the conclusion of a morphological study (Angelini et al., 2020) highlighting the presence of distinct subpopulations in these areas, calls for further genetic studies to clarify the reciprocal influence of environmental conditions and population connectivity on the observed phenotypic diversity, and stresses the need for proper assessment and management of *Nephrops* populations in those areas. The area along the northern Croatian coast also appears to be isolated and self-sustaining, with some internal heterogeneity reflected by the subdivision into several MMAs, among which areas 5 and 6 appear to have higher spawning potential. The area off the Po River also seems to be self-sustaining and isolated.

The connectivity results (PSOI maps) also identified a few areas as good receivers, such as the coastal zone north of the Gargano Peninsula (south of MMA 13); according to experimental observations, these areas do not support stable populations. This is probably due to additional factors leading to low settlement and growth of the species. These additional factors are not yet considered in the model, although they might be incorporated into it if they are recognized and properly quantified by the scientific community. The analysis of uncertainty in the larval behavior model, addressing *temperature tolerance* and *searching time*, highlights the sensitivity of *Nephrops* to the *temperature tolerance* parameter, suggesting the need for specific experimental observations to provide an even more robust model parameterization. This analysis also points to the need for specific studies to assess the possible effects of winter marine heat waves associated with projected climate change on larval mortality and recruitment (Melaku Canu et al., 2010, Galli et al., 2018) and in support of the development of adaptive and mitigating management strategies (IPCC, 2014). However, we must clarify that herein, we computed only the mortality due to temperature tolerance and sediment settling suitability and that the total larval mortality, considering disease, starvation, and predation, could be higher (up to 90%, as reported in Martha-Almeida 2008). Our results for mortality should therefore be used as relative and not absolute values. Similarly, we opted for nondimensional kernel outputs to focus on the relative index instead of giving absolute values of settling density, which would need a synoptic validation dataset that is not available.

Despite the limitations listed above, the connectivity outputs can be taken as a robust indication of the relative values of spillover and settling for *Nephrops* in the Adriatic

Sea. These results not only provide further evidence of the importance of the J/P pit as an EFH and support the establishment of an FRA in this area but also support the conclusion that the J/P pit, Ancona and the Kvarner regions host distinct subpopulations, which might benefit from the establishment of additional, smaller and potentially nonpermanent, fishery-restricted areas. Also worthy of attention is the finding that the larvae produced in the central southeastern areas are spread widely in the basin, while those produced in the northeastern area are poorly spread outside their production zone. The results of the present study comprise a significant step forward in understanding the distribution of essential fish habitats in the Adriatic Sea and fully support the conclusion that treating and assessing the *Nephrops* population at a GSA level (GFCM Geographical Sub Area) or joint GSA levels could lead to an inaccurate and imprecise evaluation of the status of this resource.

Finally, while the present work aimed to provide an in-depth analysis of a specific (ecologically and economically relevant) case study, it also provides some insight from a methodological perspective. In fact, it offers one of the first, and possibly most comprehensive, working example of actual full integration among: a truly 3D advanced hydrodynamic model, a biological model of larvae growth and survival as a function of environmental variables, a phototaxic behavioral model, and an habitat suitability sediment model. In this context, results confirm and highlight the possibility and the importance of moving from passive particle tracking experiments to novel approaches able to incorporate biological and environmental influence in connectivity studies, as well as the importance of of running ensemble simulations large enough to incorporate meteorological and oceanographic variability.

Author contribution

EBM, CF, GS, SA, and NV provided data and biological information on the species and its management. CL, DMC and CS designed the larval model, the simulations, and the post processing analysis, and CL implemented them. SQ provided the modeled hydrodynamic data. All the authors discussed the results. DMC wrote the paper with contributions from all the authors.

Data Availability Statement

The data used in this work will be provided upon request.

Conflict of Interest Statement

The authors have no conflict of interests to declare.

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| Larval life stage	Larval size	Larval activity	Vertical active velocity
One	> 6 mm	Positive phototaxic. From the bottom to the target layer	Upward: 25 mm s^{-1}
Two	6-14 mm	Positive phototaxic Diel migration Target layer: Night: 5-10 m Day: 0-30 m ,day	Out of target layer: Upward : 25 mm s^{-1} Downward : 9 mm s^{-1} Inside the target layer: Up and down, random: 0-17 mm s^{-1}
Three	> 14 mm	Negative phototaxic From the top to the bottom	Downward: 9 mm s^{-1}
Four	> 14 mm (3-5 days max)	Searching Target layer: 0-2 m above the bottom	Above the target layer: Downward : 9 mm s^{-1}. Inside the target layer: Up and down, random: 0-17 mm s^{-1}

Table 1. Larval behaviour at different life stages.

MMA	Area	DKI	DKI_StD	PSOI	PSOI_StD	CI	DI
1	1362.9	10.1	8.6	57.5	10.9	2.8	37.4
2	962.6	48.3	40.6	33.2	15.2	4.6	18.0
3	231.1	41.3	27.0	37.3	18.1	4.6	10.5
4	614.1	44.4	36.6	57.5	18.2	4.4	10.1
5	803.1	27.7	21.8	55.4	19.1	2.8	11.4
6	922.0	45.1	29.4	55.8	19.7	5.8	13.0
7	2866.9	55.0	25.9	83.0	10.3	14.3	52.4
8	1716.0	51.5	25.4	90.2	8.5	14.3	54.3
9	1375.7	66.0	24.2	89.9	7.5	18.4	60.7
10	3459.4	70.5	30.5	92.7	5.1	18.8	63.5
11	1969.2	62.4	22.0	88.7	8.9	18.6	59.4
12	990.4	66.7	28.9	89.3	5.8	19.3	62.8
13	2874.0	61.0	23.7	78.7	14.2	18.0	50.4
14	895.6	43.8	14.6	76.0	12.5	14.3	50.7
15	4010.6	30.2	14.4	69.6	12.8	8.6	45.5
16	2291.5	36.3	18.7	70.2	13.0	11.6	41.2
17	915.9	25.4	14.6	60.9	14.2	8.7	33.2
18	4137.5	14.0	7.9	81.6	8.7	4.8	63.8
19	1235.1	13.2	6.9	92.3	5.3	4.5	68.8
20	2944.6	30.4	16.1	94.8	3.6	9.2	58.3

Table 2 Area and connectivity indexes for the 20 MMAs
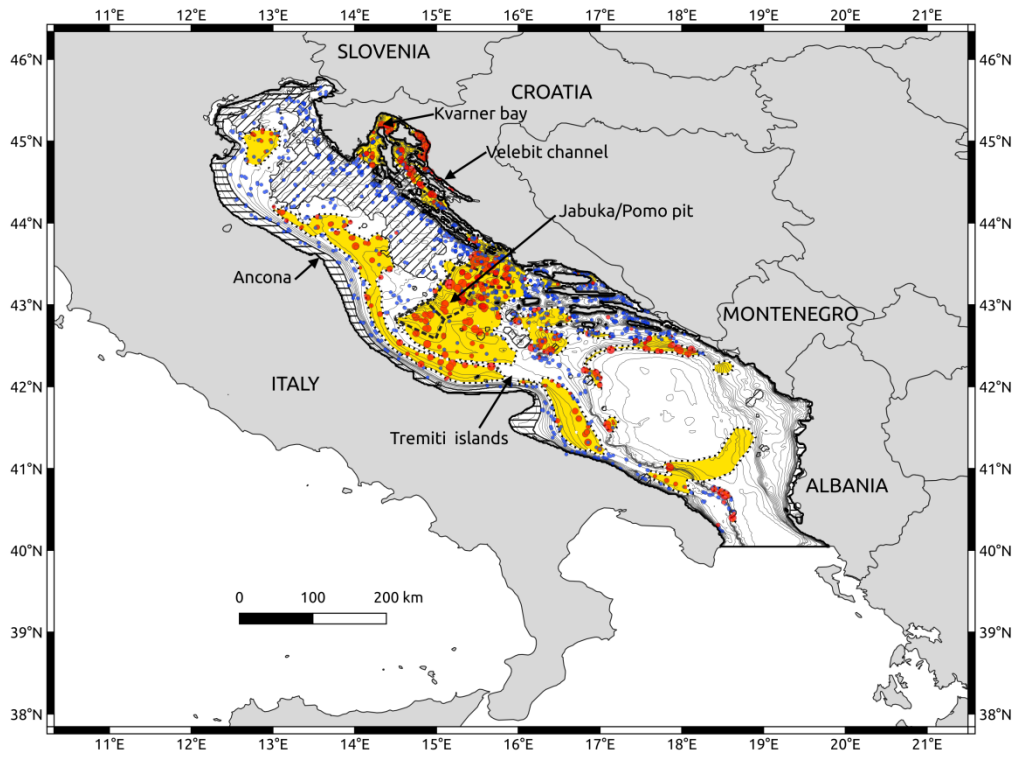
fog_12522_f1.tiff
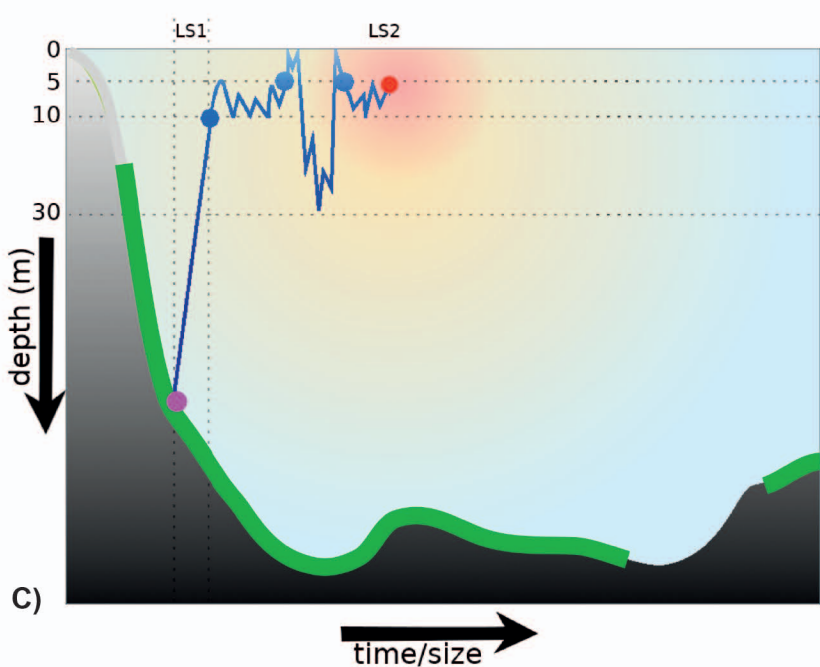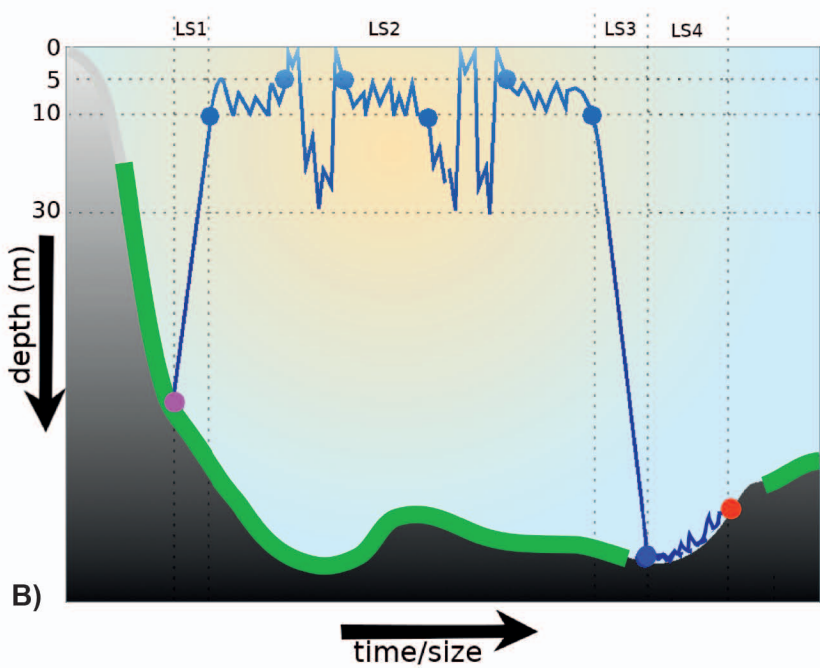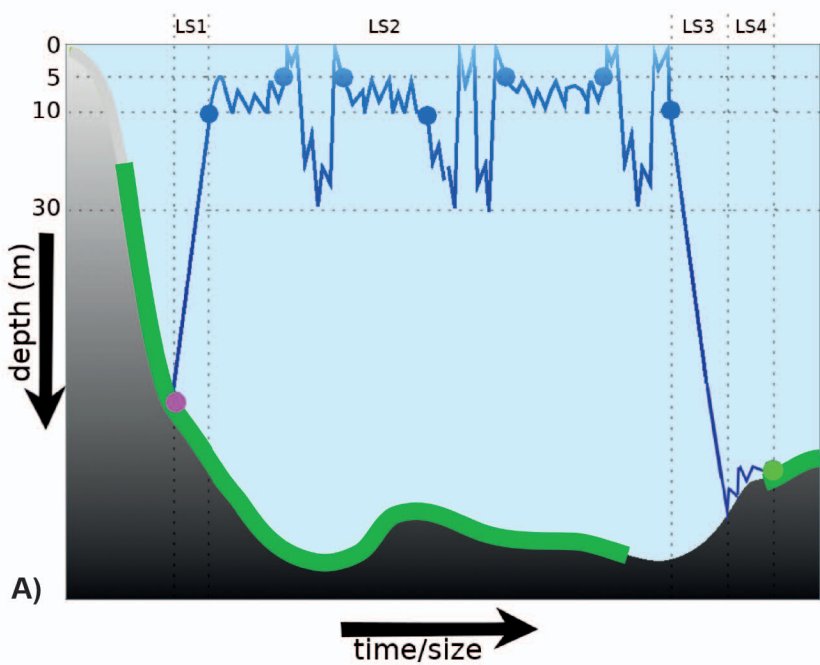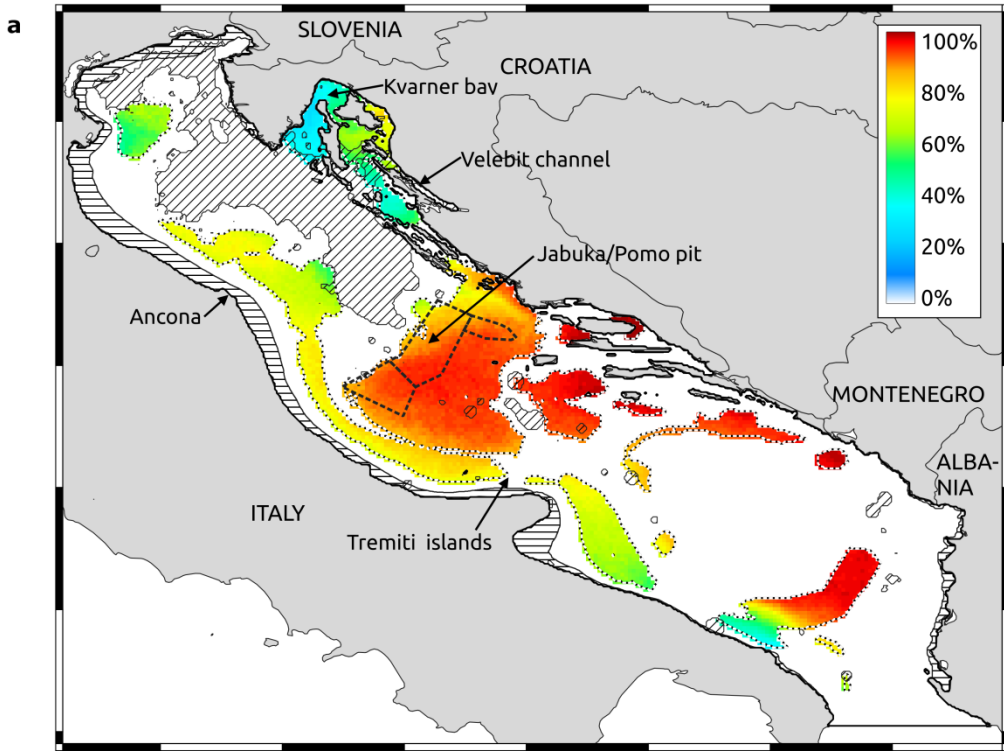
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fog_12522_f3b.tif

fog_12522_f4a.tif

fog_12522_f4b.tif

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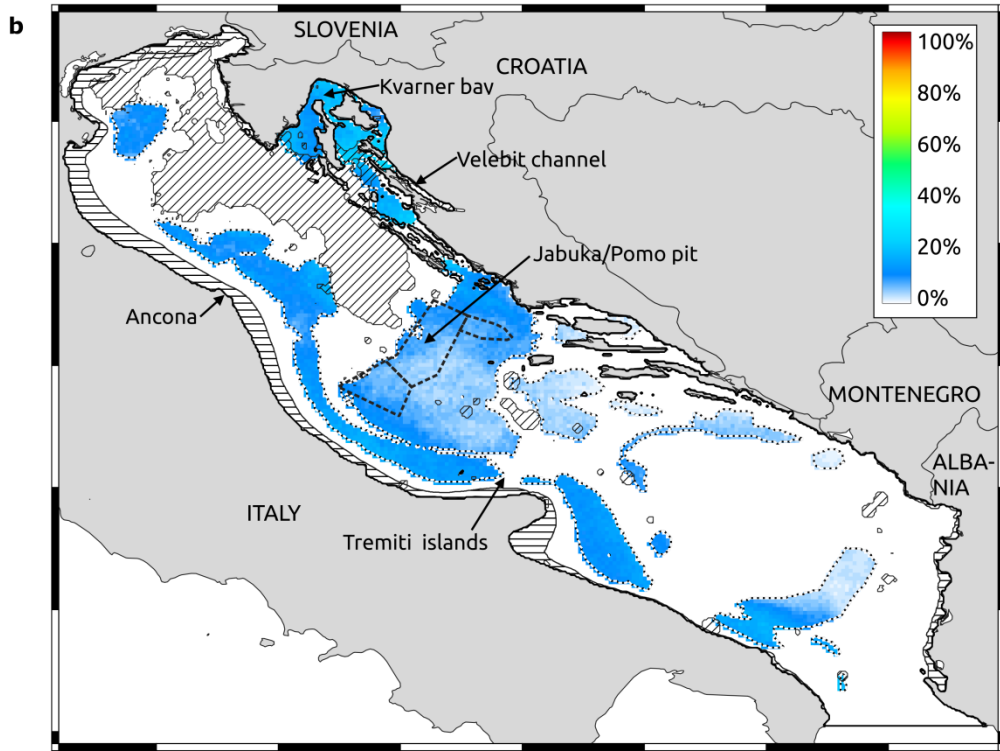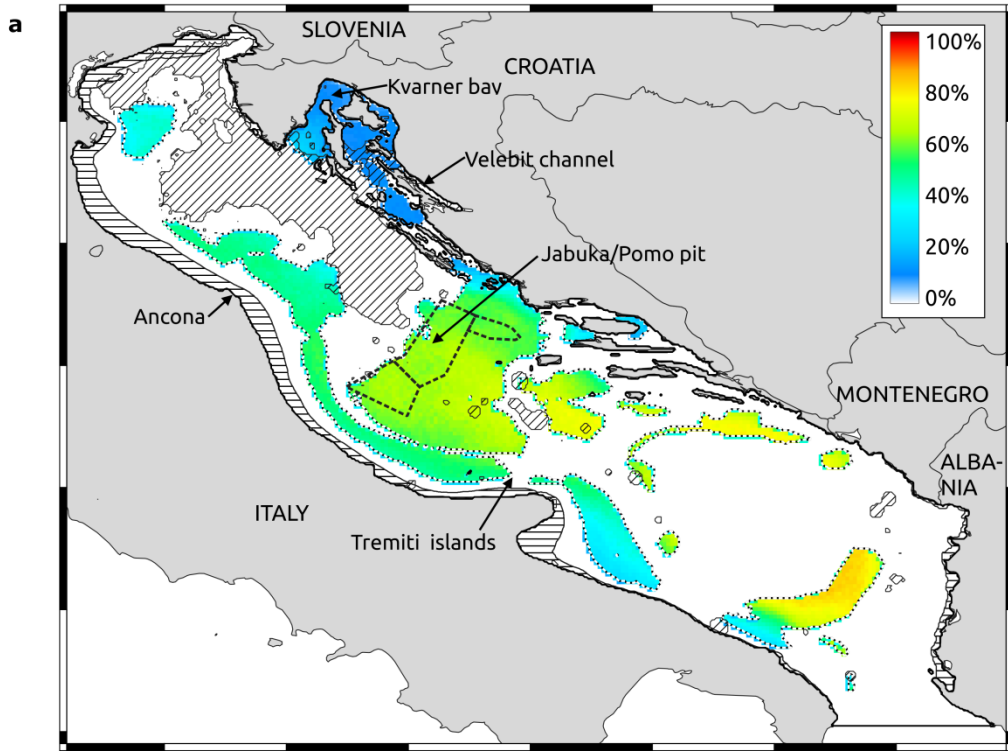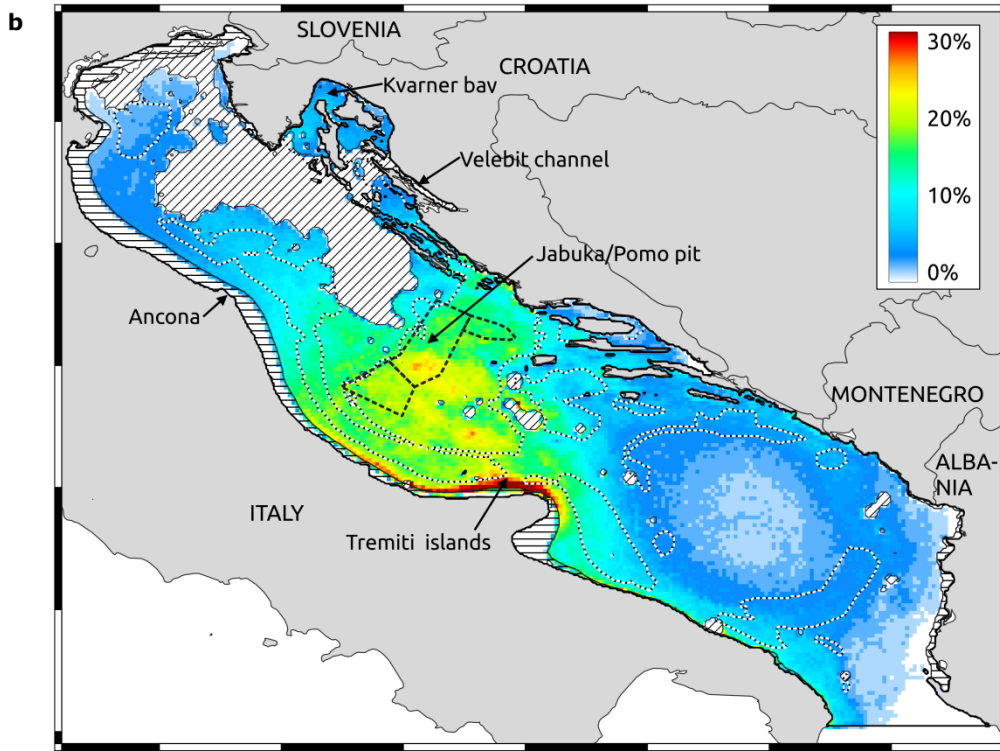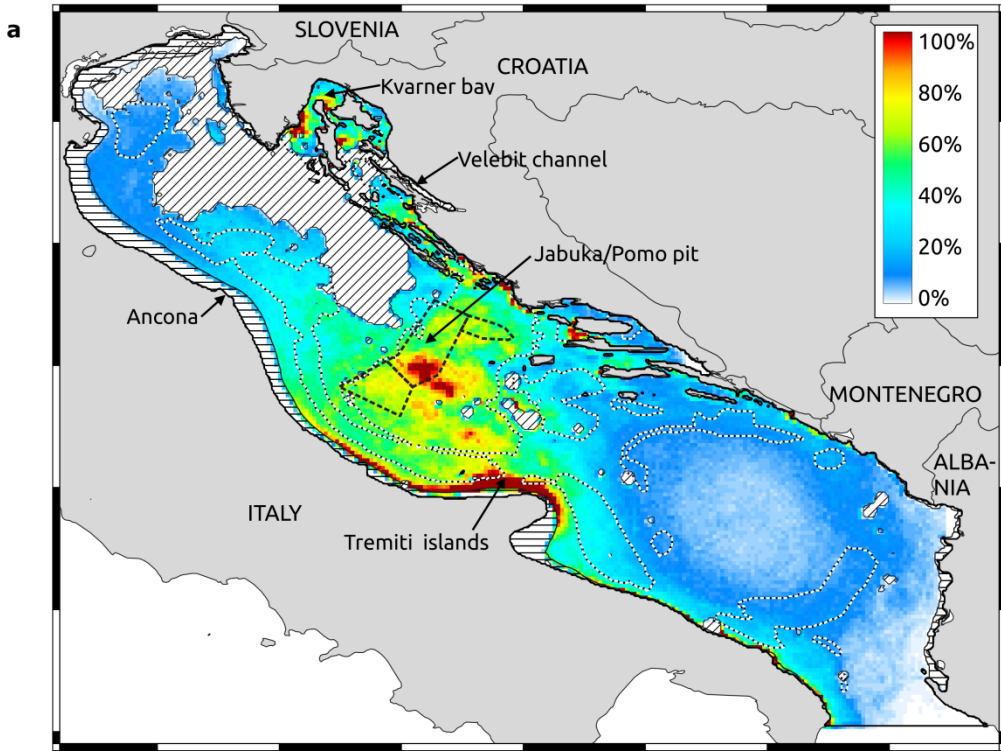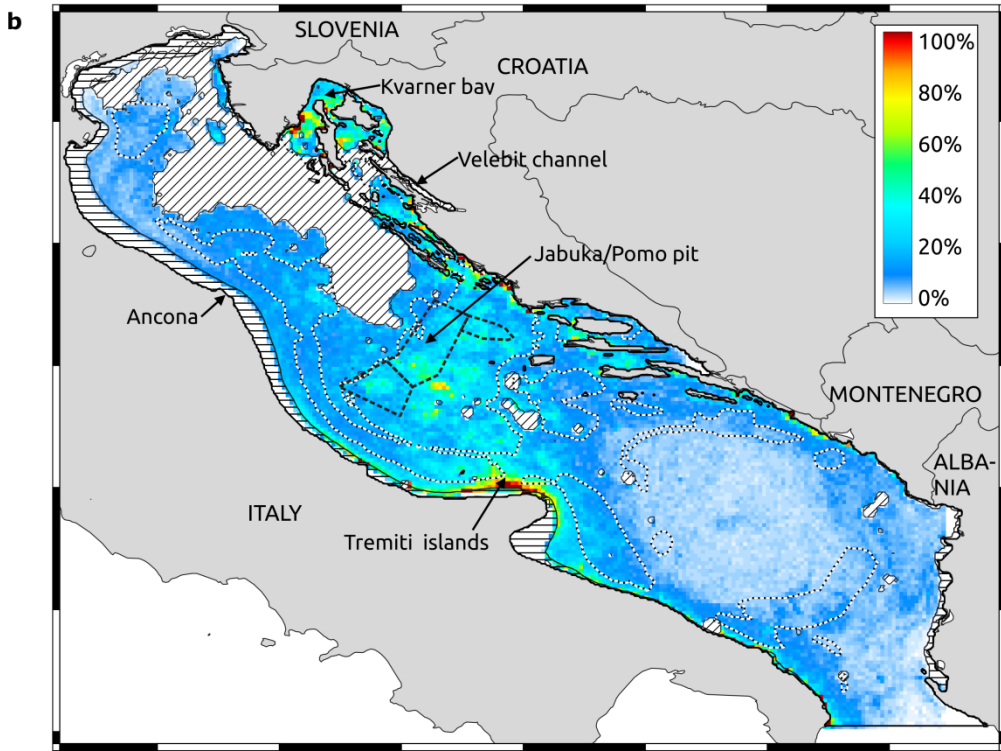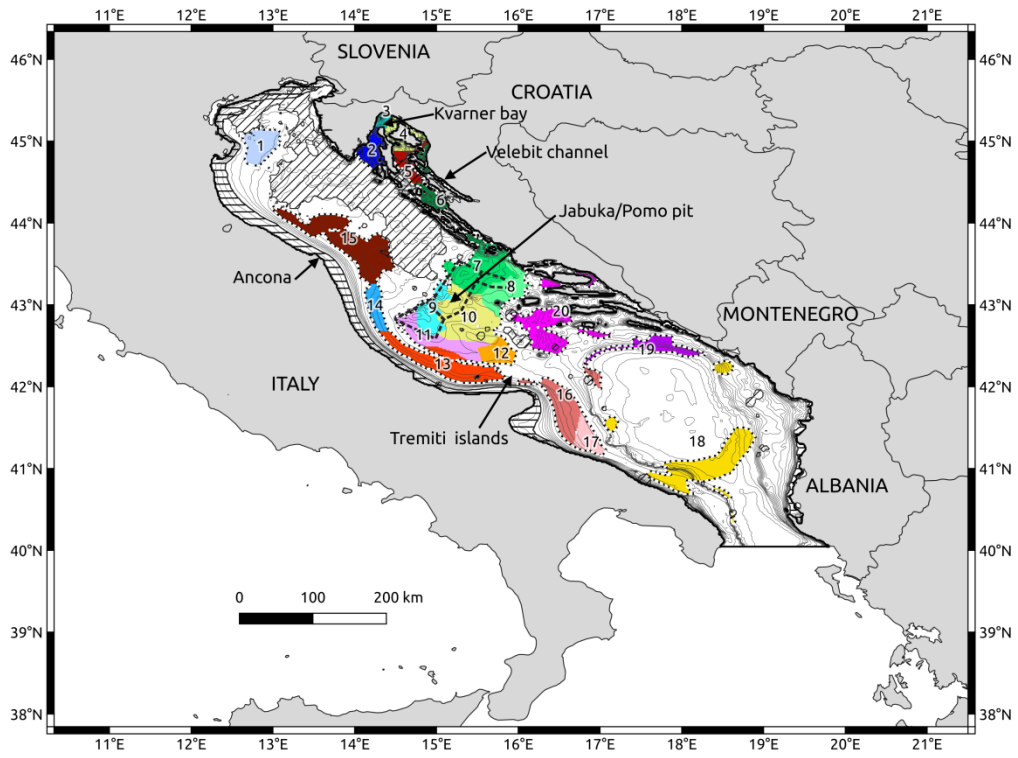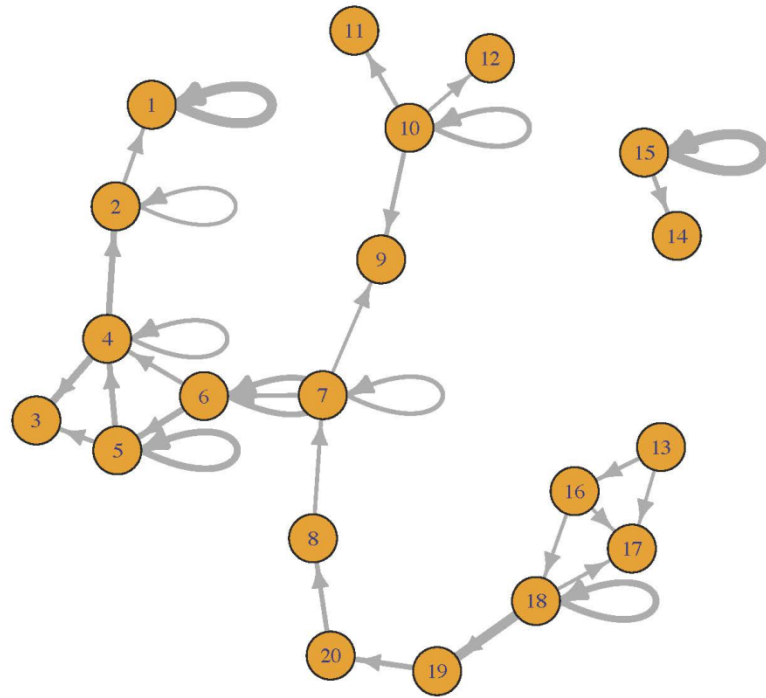
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fog_12522_f6.tiff

RELATIVE VALUES

	Settlement Area 1	Settlement Area 2	Settlement Area 3	Settlement Area 4	Settlement Area 5	Settlement Area 6	Settlement Area 7	Settlement Area 8	Settlement Area 9	Settlement Area 10	Settlement Area 11	Settlement Area 12	Settlement Area 13	Settlement Area 14	Settlement Area 15	Settlement Area 16	Settlement Area 17	Settlement Area 18	Settlement Area 19	Settlement Area 20
Release Area 20	0.00	0.00	0.00	0.00	0.00	0.05	0.19	0.32	0.07	0.09	0.07	0.12	0.04	0.02	0.01	0.08	0.07	0.02	0.04	0.37
Release Area 19	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.01	0.01	0.01	0.03	0.01	0.00	0.00	0.08	0.13	0.12	0.08	0.12
Release Area 18	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.01	0.01	0.01	0.03	0.02	0.00	0.00	0.12	0.22	0.46	0.69	0.14
Release Area 17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.09	0.08	0.01
Release Area 16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.01	0.00	0.00	0.12	0.23	0.22	0.08	0.02
Release Area 15	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03	0.02	0.09	0.28	0.72	0.03	0.00	0.00	0.00	0.00
Release Area 14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.03	0.02	0.05	0.10	0.03	0.04	0.02	0.00	0.00	0.01
Release Area 13	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.05	0.04	0.13	0.17	0.19	0.03	0.00	0.27	0.20	0.06	0.02	0.05
Release Area 12	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.03	0.04	0.07	0.11	0.06	0.01	0.00	0.08	0.04	0.01	0.00	0.05
Release Area 11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.10	0.11	0.15	0.16	0.17	0.06	0.01	0.08	0.03	0.01	0.00	0.04
Release Area 10	0.00	0.00	0.00	0.00	0.00	0.01	0.15	0.18	0.30	0.35	0.26	0.20	0.19	0.16	0.03	0.06	0.02	0.00	0.00	0.08
Release Area 9	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.03	0.12	0.11	0.10	0.06	0.09	0.11	0.02	0.02	0.00	0.00	0.00	0.01
Release Area 8	0.00	0.00	0.00	0.00	0.00	0.12	0.26	0.20	0.09	0.08	0.04	0.02	0.02	0.03	0.02	0.00	0.00	0.00	0.00	0.07
Release Area 7	0.00	0.00	0.00	0.00	0.01	0.32	0.30	0.16	0.20	0.13	0.09	0.02	0.04	0.14	0.09	0.00	0.00	0.00	0.00	0.02
Release Area 6	0.00	0.06	0.15	0.29	0.42	0.41	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Release Area 5	0.00	0.13	0.29	0.40	0.47	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Release Area 4	0.01	0.43	0.51	0.29	0.10	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Release Area 3	0.01	0.13	0.04	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Release Area 2	0.24	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00
Release Area 1	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.07	0.00	0.00	0.00	0.00	0.00

ABSOLUTE VALUES

	Settlement Area 1	Settlement Area 2	Settlement Area 3	Settlement Area 4	Settlement Area 5	Settlement Area 6	Settlement Area 7	Settlement Area 8	Settlement Area 9	Settlement Area 10	Settlement Area 11	Settlement Area 12	Settlement Area 13	Settlement Area 14	Settlement Area 15	Settlement Area 16	Settlement Area 17	Settlement Area 18	Settlement Area 19	Settlement Area 20
Release Area 20	0	0	0	0	1	4733	64885	62926	13235	46009	18309	17214	16431	1774	1315	14716	3368	2733	1431	69467
Release Area 19	0	0	0	0	0	74	4636	6465	1540	7252	2799	3986	2419	157	50	13905	6521	14958	2980	22434
Release Area 18	0	0	0	0	0	4	2164	3846	1192	5052	3657	4189	6536	163	14	21370	10894	56213	24578	26590
Release Area 17	0	0	0	0	0	3	186	313	27	318	70	198	33	2	0	2149	1591	11072	2793	2507
Release Area 16	0	0	0	0	0	1	539	804	720	3377	3328	3465	5217	127	9	20698	11169	26428	2876	4057
Release Area 15	696	287	0	0	2	41	1225	75	2699	2494	6727	3423	33320	24319	184266	5155	232	13	0	283
Release Area 14	0	0	0	0	0	1	682	419	2669	3704	7030	3263	20210	8813	7055	7309	932	383	0	1075
Release Area 13	0	0	0	0	0	63	2486	2629	8696	22013	32394	23423	71754	2683	523	46615	10165	7692	833	10178
Release Area 12	0	0	0	0	0	61	4542	4373	5580	22425	17033	15544	24046	921	216	14883	2183	833	43	9821
Release Area 11	0	0	0	0	0	120	6239	4710	18423	54671	39403	22404	65746	5166	1717	14506	1350	961	7	6691
Release Area 10	0	1	0	0	3	712	48623	35788	57514	179314	67190	28310	73061	13690	6514	9816	974	399	5	15542
Release Area 9	0	1	0	0	1	39	8016	5164	23905	55669	24470	8585	33191	9102	5548	3273	207	310	0	2404
Release Area 8	0	9	0	0	55	11243	87820	39801	16477	38763	10775	2528	7891	2965	5048	390	13	10	19	13539
Release Area 7	0	60	0	8	283	30626	99653	31757	38626	66769	21718	3010	15899	11616	23095	477	10	0	0	4310
Release Area 6	19	5398	2981	16734	19186	39023	2262	440	92	97	16	0	2	18	179	0	0	0	0	12
Release Area 5	12	12403	5878	23199	21502	8383	0	0	0	0	0	0	0	6	12	0	0	0	0	0
Release Area 4	283	41726	10375	16925	4645	1021	0	0	0	0	0	0	0	5	5	0	0	0	0	0
Release Area 3	414	12822	887	1208	1	0	0	0	0	0	0	0	0	27	10	0	0	0	0	0
Release Area 2	7014	23494	33	46	24	74	0	0	0	0	3	0	40	794	1677	0	0	0	0	0
Release Area 1	20823	0	0	0	0	0	8	0	22	1	147	23	1600	3033	18930	21	0	0	0	0

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