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## **Numerical simulations of barnacle larval dispersion coupled with field observations on larval abundance, settlement and recruitment in a tropical monsoon influenced coastal marine environment**

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### A B S T R A C T

Larval abundance in an area depends on various factors which operate over different spatial and temporal scales. Identifying the factors responsible for variations in larval supply and abundance is important to understand the settlement and recruitment variability of their population in a particular area. In view of this, observations were carried out to monitor the larval abundance, settlement and recruitment of barnacles on a regular basis for a period of two years. The results were then compared with the numerical modelling studies carried out along the west coast of India. Field observations of larval abundance showed temporal variations. The least abundance of larvae was mostly observed during the monsoon season and the peak in abundance was mostly observed during the pre-monsoon season. The peak in larval abundance during the pre-monsoon season coincided with the consistency in settlement and recruitment of barnacles. Numerical simulations also showed a seasonal change in larval dispersion and retention patterns. During pre-monsoon season the larval movement was mostly found towards south and the larvae released from the northern release sites contributed to larval abundance within the estuaries, whereas during the monsoon season the larval movement was mostly found towards north and the larvae released from southern release sites contributed to larval abundance within the estuary. During post-monsoon season, the larval movement was found towards the north in the beginning of the season and is shifted towards the south at the end of the season, but the movement was mostly restricted near to the release sites. Larval supply from the adjacent rocky sites to the estuaries was higher during the pre-monsoon season and the retention of larvae released from different sites within the estuaries was found to be highest during the late post-monsoon and early pre-monsoon season. Maximum larval supply and retention during the pre-monsoon season coincided with maximum larval abundance, settlement and recruitment of barnacles observed in the field studies. These observations showed that the pattern of larval dispersion and retention in the region are predominantly driven by local hydrodynamics operating in the vicinity. Linking larval dispersion and retention with settlement and recruitment of barnacles indicated that the processes are mainly influenced by wind and resultant current patterns. These findings facilitate unravelling the processes operating in the region and to understand the distribution pattern of the intertidal organisms in general in this tropical environment influenced by monsoons.

*Keywords:* Barnacle larvae; Larval settlement; Recruitment; Numerical simulations; Tropical environment; Monsoons.

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### **1. Introduction**

Monitoring the larval abundance and their distribution on spatial and temporal scales provides an idea of the processes which interact with observed patterns and helps to understand their settlement and recruitment variability in a particular locality (Sponaugle et al., 2002; Tapia et al., 2010). Larval supply and abundance in an area is affected by multiple factors operating at different spatial and temporal scales (Shanks et al., 2003). Which processes are the primary drivers in the variation of larval abundance and dispersal needs to be studied in detail in order to understand the variability in settlement and recruitment of barnacles in a particular locality. Barnacle *Balanus amphitrite* is a dominant species found along the coast of India. The development of this species is through six planktotrophic naupliar stages followed by a pre-settling non-feeding cyprid stage. Cyprids explore for a suitable substratum to settle and metamorphose to an adults. Since the life cycle of barnacles includes both pelagic as well as benthic stages, success of their population generally depends on the dispersal or transport of larval stages to suitable habitats. Larvae can disperse to different localities and settle far away from the parental habitat from where they were released (Gaines and Bertness, 1992; Gaines et al., 2007). As the larval life cycle of barnacles also includes both feeding as well as non-feeding stages, success of larval populations depends on its dispersal/retention to habitats with sufficient food. The non-feeding larval stage (cyprids) can last for several days depending on the stored energy content (Anil and Kurian, 1996; Anil et al., 2001; Desai and Anil, 2004). If the nauplii or cyprids are dispersed far away from the adult habitats or away from the coast where there is less availability of food or lack of suitable substratum to settle, then the survival chances are reduced. Again the survival capability depends on the time taken by the cyprids to explore a suitable substratum; earlier they settle, better the chances of survival. Larval metamorphosis can be delayed if they do not find a suitable substratum to settle (Gaines and Bertness, 1992). Excessive prolongation of the larval period can also result in lower survival and growth rates (Pechenik et al., 1998; Anil et al., 2001). Consequently, local hydrodynamics plays a decisive role in the final destination of larval populations and, in turn, their metamorphic success. Moreover, hydrodynamics has a significant role in the cross-shore distribution of larvae, their dispersal ranges and connectivity (Pineda, 1994; 2009).

In this study, observations were carried out to monitor the abundance and distribution of barnacle larvae along with their settlement and recruitment. These observations have been compared with the results of numerical simulations. It is envisaged that numerical simulations provide some physical/dynamical insights into the processes operating in the region; numerical models are employed nowadays to study the distribution of various larval forms. Several studies have been carried out using numerical models. For e.g. George et al. (2011) studied fish larval transport in the macro-tidal regime of

Gulf of Kachchh along the west coast of India. Vethamony et al. (2007) generated oil spill trajectories off the Goa coast to illustrate the importance of having pre-validated trajectories for selecting eco-sensitive regions for preparedness and planning suitable response strategies whenever spill episode occurs. Miyake et al. (2009) simulated larval dispersal processes for abalone using a coupled particle-tracking and hydrodynamic model. Stephens et al. (2006) modeled the dispersal and transport of larval New Zealand abalone (*Haliotis iris*) using coupled two-dimensional hydrodynamic and Lagrangian particle-trajectory models. However no such studies are conducted along the west coast of India to monitor simultaneously larval abundance along with settlement and recruitment of barnacles on different spatial and temporal scales and evaluated the results with numerical simulation studies. The aim of the present study is to elucidate the larval abundance, dispersal and retention processes to assess the settlement and recruitment of barnacles in this unique tropical environment which is influenced by monsoons so that the underlying processes governing the distribution of intertidal organisms inhabiting the region can be understood in general.

## 2. Materials and methods

This study was carried out along the coast of Goa (west coast of India) including the estuarine region (Fig. 1A, B and C), is a tropical monsoon influenced environment. Goa is influenced primarily by three seasons; south-west monsoon (June-September), post-monsoon (October-January) and pre-monsoon (February-May) with a break in monsoon during the month of August. Winds during the south-west monsoon are very stronger compared to other seasons. Tides along the west coast of India are semi-diurnal mixed and a large variation in the tidal range is noticed between the southern and northern end. The Mandovi and Zuari estuaries are the two major estuaries in Goa, characterized by mixed tides with semi-diurnal dominance and heavy fresh water influx during the south-west monsoon. Field observations of larval abundance, settlement and recruitment of barnacles were carried out for a period of 2 years (2005-2007) from different locations (Fig. 1 A and B) and the results were compared with the simulation results (Please see Fig. 1C for the model domain).

Location for Fig. 1

### 2.1. Larval abundance

Larval samples were collected from 7 different stations (Fig. 1A) in and around the Mandovi and Zuari estuaries of Goa on a bimonthly basis for a period of two years (2005-2007). Horizontal plankton tows were made using a Haron-Trantor net of mesh size 100 $\mu$ m fitted with a flow meter. The volume of

water filtered was calculated using the number of revolutions obtained from a flow meter. The samples were preserved in 5% formaldehyde onboard and later sorted out and counted in the laboratory using stereo-zoom microscope to determine the larval abundance. Larval abundance is expressed in terms of No./100m<sup>3</sup>.

## 2.2. Settlement and recruitment of barnacles

Settlement and recruitment of the barnacle *Balanus amphitrite* was monitored at 4 different stations (Dona Paula, MPT, INS-Mandovi and Arambol) (Fig. 1B), for a period of 2 years (June 2005-May 2007) at stations Dona Paula and MPT and for a period of 1 year (June 2006-May 2007) at stations INS-Mandovi and Arambol. Panels of aluminium material were used as a substratum. Aluminium as the substratum for evaluating settlement and recruitment of barnacles in the study area has been used earlier (Anil, 1986; Desai, 2002) and provides a good picture of the events. Every month, new set of panels were immersed in triplicate and observations were taken from six marked quadrats of size 25cm<sup>2</sup> each. Settled and recruited barnacles on the panels were counted at the end of respective months with the help of a hand-held magnifying lens. 0-2mm size classes were considered as settlers and above 2mm size classes were considered as recruits. Settlement and recruitment of the barnacles is expressed in terms of numbers per decimetre square (No./dm<sup>2</sup>).

## 2.3. Hydrodynamic modeling

Mandovi and Zuari are partially-mixed estuaries with tidally averaged circulation, consisting of a downstream-directed surface flow of fresh water and an upstream-directed flow of more saline water at the bottom. This circulation, however, is much weaker than the circulation observed during a tidal cycle, particularly when the tidal range is large. For practical applications such as determination of the fate of pollutants and other passive and active tracers, it is often important to simulate this more energetic circulation within a tidal cycle. The simplest types of these models are one-dimensional models, often used for a narrow estuary with very shallow depths. If wider sections are present in such an estuary and if it is a stratified estuary, then two-dimensional models have to be used (Unnikrishnan et al., 2007). A feature of Mandovi and Zuari estuaries is such that the width of these estuaries are large up to a distance of about 10 km near the mouth, after which the channel narrows down considerably. Manoj and Unnikrishnan (2009) studied the tidal circulation and salinity distribution using a hybrid model that uses a two-dimensional model for the wide portion near the mouth of these estuaries and a one-dimensional network model for the rest of the estuarine system.

Hydrodynamics of a particular area primarily determines the larval movement and retention. The hydrodynamic conditions off Goa coast and in the Mandovi-Zuari estuarine system were simulated using a depth averaged two-dimensional hydrodynamic model, MIKE 21 HD, developed by DHI Water & Environment, Denmark (<http://www.dhigroup.com>) (DHI, 2001). It simulates unsteady two-dimensional flows in one layer (vertically homogeneous) fluids. Surface elevation and current velocities (u and v components) are calculated by solving dynamic and vertically integrated equations of continuity and conservation of momentum in X and Y directions. This model has been used earlier to study the flow characteristics at various coastal and estuarine regions (Chubarenko and Tchepikova, 2001; Babu et al., 2005; George et al., 2011).

Study area and model domains are shown in Fig. 1C. Larger and smaller domains were set up with coarse and fine resolution rectangular Cartesian grids of 500m x 500m and 50m x 50m spacing, respectively. The bathymetry file was created by digitising the depth values obtained from the Naval Hydrographic chart (Naval Hydrographic office, Dehra Dun, India) and MIKE-CMAP by linearly interpolating to each grid in the model domain. The larger domain extends to 206 km and 144 km in X and Y directions, covering the area bounded by longitudes  $73^{\circ} 08'$  to  $74^{\circ} 09'$  E and latitudes  $14^{\circ} 44'$  to  $16^{\circ} 00'$  N. This domain is considered specifically to simulate the hydrodynamics and larval dispersion at the open coast off Goa. However, the finer details of the hydrodynamics in the estuaries could not be resolved accurately in this larger domain. Hence, we used a small domain also for the simulation of hydrodynamics and larval dispersion in the Mandovi-Zuari estuarine system. The smaller domain extends to 16 km and 11 km in X and Y directions covering an area bounded by  $73^{\circ} 43'$  to  $73^{\circ} 52'$  E and  $15^{\circ} 24'$  to  $15^{\circ} 31'$  N. The time step interval for the simulation has been selected in such a way to satisfy the stability criterion. Time steps of 20s and 15s were considered in the coarse model and fine model respectively. The corresponding Courant numbers are 1.7 and 3.6 respectively. The calibration parameters applied in the simulations are eddy viscosity, resistance and wind friction factor. A velocity-based Smagorinsky scheme with a constant value of  $C_s=0.5 \text{ m}^2 \text{ s}^{-1}$  has been applied to calculate the eddy viscosity. A Manning number of  $32 \text{ m}^{1/3} \text{ s}^{-1}$  has been considered as the calibration parameter for the bed resistance. The wind friction factor is taken as 0.0026.

Bathymetry, tides and winds are the basic input parameters required for the hydrodynamic simulations. Accuracy of the model results primarily depends on the accuracy of these input parameters, and especially resolution of the bathymetry. The south and north boundaries of the domain are placed at two major tidal stations, Karwar and Vengurla, respectively. The tidal elevations at these boundaries

were predicted using the Global Tide Model (Andersen, 1994; Anderson, 1995). The tide elevations along the west boundary were prescribed based on the interpolation between the tidal elevations predicted at south and north boundaries. Winds measured at Dona Paula coast (Fig. 1) using Autonomous Weather Station (AWS) were applied as the input winds. Winds are assumed to be uniform over the whole domain. As winds such as NCEP are in coarse grid ( $2.5^\circ \times 2.5^\circ$ ), AWS winds were applied over the entire model domain. Rose diagrams showing the changes in seasonal wind speed and direction are given in Fig. 2. The transfer boundary data (levels and fluxes) for the smaller domain were extracted from the larger domain output and applied as the boundary condition to simulate the currents in the estuaries.

#### Location for Fig. 2

The simulated water levels and current velocities have been validated with predicted water levels and measured currents at Captain of Ports (COP), Panaji. Currents were measured for every 10 minutes interval using Recording Current Meter (model: RCM7; make: Aanderaa, Norway) during 14 November – 10 December, 2007. The depth of current meter mooring was approximately 8.0 m. The current speeds and directions were resolved into u-velocity and v-velocity components representing east-west direction (east is considered as positive and west is negative) and north-south direction (north is considered as positive and south is negative), respectively. The validated model has been used to simulate the flow patterns at the study area. Further, the simulated hydrodynamic data for larger and smaller domains was given as inputs to particle analysis model to simulate the larval transport along the open coast off Goa and in the estuarine system.

#### 2.4. Larval transport modeling

Barnacle larvae are defined as neutrally buoyant, passive particles and they follow the prevailing flow without being settled. The particle analysis module did not include larval swimming behavior and mortality rates. Pelagic larval duration (PLD) phase of the barnacle *Balanus amphitrite* is approximated as 10 days for the study (10 days is considered as an approximate period to complete the larval life cycle of barnacles in this region under normal conditions) after which they can be considered to have gained the potential to settle (Anil and Kurian, 1996; Anil et al., 2001). It is possible to assume that on completion of its PLD, the larvae will settle if they encounter a suitable substratum or else they perish if they fail to settle on a suitable substratum. Larval transport simulation was achieved with Particle-

tracking module of MIKE model, which uses a Lagrangian ‘random walk’ technique. This module is effectively utilized for tracking retention or dispersion of hypothetical larvae released in the domain (Stephens et al., 2006). The hydrodynamic simulation produces the advection term for tracking the particles that coincides with seasonality of larval production. This model includes the minimal requirements for assessing connectivity between accurate flow field, locations and time of larval release and potential site of settlement (Siegel et al., 2003; North et al., 2009). Particle (larval) mass and horizontal dispersion coefficients were tested for sensitivity using simulations in which individual parameter values were varied. The dispersion coefficient varied from 0 to 1 in horizontal direction, depending on current speeds. Sensitivity simulations were based on larval release from eleven source locations in which six were along the coast (Fig 1C-i) and five were inside the two estuaries (Fig 1C-ii).

In the numerical simulations, it is defined that one particle is equivalent to 1000 larvae as it is difficult to model larval transport with huge number of particles. At each time step 4000 number of larvae were released making it into 11.92 million hypothetical larvae over 2980 time steps (with a time step interval of 30s). The release is so continued for 24 hours and 50 minutes covering 2 tidal cycles as the source flux. Assuming a mass of 5 $\mu$ g for each larva, 0.2mg of larvae per second was released in each time step. Dispersion of the larvae according to the prevailing flow were analysed in each of the season and station. The dispersal pattern at the end of the simulations were plotted to visualize the larval dispersion and retention at different stations and seasons. The concentration, viz., number of hypothetical larvae for each unique hydrodynamic situation is also extracted at various sampling stations and seasons to assess the intensity of retention or dispersal of larvae under the influence of fluid transport and the associated dispersion processes to compare them with the field observations of larval abundance, settlement and recruitment of barnacles.

### *2.5. Data analysis*

Larval abundance, settlement and recruitment data of barnacles which were collected during different months were log-transformed to ensure normality of means and homogeneity of variances before subjecting to statistical analysis. The log-transformed data was then subjected to two-way analysis of variance (ANOVA) (Sokal and Rohlf, 1981) to evaluate the variance between different sampling months at each station (temporal variation) and also between different sampling stations (spatial variation).

## **3. Results**

### 3.1. Larval abundance

Cirripede nauplii and cyprid abundances during different sampling months from different stations are presented in Figs. 3 and 4. Abundance of nauplii varied significantly on spatial and temporal scales (ANOVA:  $p < 0.05$ ). Abundance of cyprids also varied significantly on the temporal scale (ANOVA:  $p < 0.05$ ), whereas it did not vary significantly at the spatial scales (ANOVA:  $p > 0.05$ ). Though the larval release from different stations varied significantly, cyprid abundance did not vary significantly. Cyprids are the available larvae for settlement in a particular area. The same trend is reflected in the settlement and recruitment observations of barnacles. Settlement and recruitment of barnacles did not vary significantly on the spatial scales. In general, cirripede nauplii and cyprids were consistently found during the pre-monsoon season (Figs. 3 and 4 a, b, f, g, k, l) at most of the stations, whereas their abundance was lower during the monsoon and early post-monsoon season (Figs. 3 and 4 c, d, h, i).

Location for Figs. 3 and 4

### 3.2. Settlement and recruitment of barnacles

Settlement and recruitment of barnacles varied significantly on a temporal scale ( $p < 0.05$ ), whereas it did not vary at the spatial scale ( $p > 0.05$ ). In general, settlement and recruitment were lower during the monsoon season, except during monsoon breaks. Consistency in settlement and recruitment was mostly observed during the pre-monsoon season at most of the stations sampled (Fig. 5a-d).

Location for Fig. 5

### 3.3. Hydrodynamics of the region

The modelled and predicted water levels show a very good match with no phase difference. The modelled current velocities (u and v components) were compared with the measurements during the period 14 November – 10 December 2007 (Fig. 6). The match is reasonably good. Correlation coefficients between the measured and modeled u and v velocities were 0.71 and 0.68, respectively. The r.m.s. error observed for u and v- velocities are 0.37 m/s and 0.14 m/s respectively.

Location for Fig. 6



The currents along the open coast of Goa flow northerly during the flooding and southerly during the ebbing. Seasonally, a prominent southward drift was observed during pre-monsoon season due to the prevailing NW winds. During monsoon season, the prominent drift is towards north due to the prevailing southwest monsoon winds. During post-monsoon season the prominent drift is towards north, however, at several occasions a southward drift is observed due to the local wind effects. Inside the Mandovi-Zuari estuarine system, the current flows towards east while flooding and towards west while ebbing. The tidal currents play a major role in the cross-shore movement of particles in the estuarine system. However, small-scale tidal eddies also influences the dispersion characteristics inside the estuaries.

#### *3.4. Numerical simulations of larval dispersion and retention*

The results of larval simulations carried out along the coast were analysed to assess the larval dispersion and retention from different release sites during different seasons. During pre-monsoon season the larval movement was found towards south, covering a wide-stretch along the coast (Fig. 7a and b). During monsoon season, the larvae moved predominantly towards north (Fig. 8a and b) whereas during the post-monsoon season the larval movement was towards the north in the beginning of the season (Fig. 9a) and is shifted southwards at the end of the season (Fig. 9b) but the movement was mostly restricted near to the release sites.

Location for Figs.7, 8 and 9

Larval dispersion and retention patterns within the estuaries also differed on a seasonal basis (Figs. 10-15). The larval retention was found to be higher during the late post-monsoon (Fig. 15) and pre-monsoon months (Figs. 10 and 11) at most of the release sites and least numbers were retained during the monsoon season (Figs. 12 and 13). Larval retention was found to be higher at stations MPT and INS-Mandovi during most of the pre and post-monsoon months (Figs. 10, 11, 14 and 15).

Location for Figs.10, 11, 12, 13, 14 and 15

#### *3.5. Modelled and observed larval abundance, settlement and recruitment*

The consistency observed in larval abundance, settlement and recruitment during the pre-monsoon season coincided with the maximum retention of larvae observed in the numerical simulations. The supply of larvae in to the estuary from different release sites along the coast was also found to be

higher during the pre-monsoon season due to the intense southward movement of larvae released from northern rocky sites (Fig. 7a and b).

#### 4. Discussion

Monitoring the larval abundance during different seasons on the basis of regional hydrodynamics is important for understanding seasonal variations in settlement and recruitment of barnacles. Since barnacles dominate the intertidal communities along the coast, they serve as model organisms to understand the overall dynamics of intertidal habitat in general in this tropical region. Their biphasic life cycle (pelagic and intertidal) again gives an advantage to understand the processes operating in both the habitats. Success of such a population in a particular area is strongly influenced by the interactions with their physical environment. They have to depend on the movement of water to deliver their food and to disperse and transport their larvae (Pineda, 2009). If the larvae are carried far away from the coast from where it is impossible to return to their adult habitat then the success rate of such larvae are very less. Again if the larvae are dispersed to habitats where there is less availability of food then the survival chances of such larvae are also very less. Monsoon plays an important role in the overall distribution of organisms in this tropical region. The results of larval simulations indicated that the larval dispersal processes and settlement of barnacles in the region were influenced by local hydrodynamics and varying wind systems during different seasons. The prevailing SW winds during monsoon, NE winds and sea breeze during post-monsoon and sea breeze during pre-monsoon season are highly influential in the larval dispersion along the coast and in the estuary. The increased abundance of larvae is favored by flood currents and high tides, pushing the larvae into the inshore area and vice-versa during the low tide and ebb currents. The dispersal patterns indicated that the larval population in the area is well-mixed with seasonally changing patterns. Model results and field observations indicated that higher larval abundance in the estuaries occurs during late post-monsoon and pre-monsoon seasons. These results suggest that the transport success of larvae and settlement are influenced by currents induced by winds and tides. The wind along the west coast of India during pre-monsoon season is characterized by sea breeze from NW, which has an extension up to 180km off Goa (Aparna et al., 2005). It has a magnitude of the order of 5–8m/s. This results in a frequent and intense movement of larvae in southward direction and hence the spread of larvae is wide-stretched southwards along the coast during the pre-monsoon season. As a result, larval supply to the estuaries also increases during this season. Since the rocky sites to the north are situated closer to the estuaries than the southern rocky sites, southward movement will facilitate the supply of larvae to the estuaries which are released from

the northern rocky sites. During monsoon season, the predominant winds near the coast are from southwest, which results in the movement of larvae towards north. However, the general circulation during monsoon is towards south along the west coast of India (Shetye et al., 1990). The large scale open ocean monsoonal currents are not considered in the present study because the study region is shallow and very close to the coast, where the local hydrodynamics are least affected by these currents. During post-monsoon, the general trend of larval movement is towards north. However, the local sea breeze (NW winds) enables larval transport to some extent towards south, but the movement is mostly restricted near to the release sites. The NW winds formed in the Arabian Peninsula during winter shamal events (called shamal winds) extend up to the west coast of India (Aboobacker et al., 2011). This occurs during post-monsoon and early pre-monsoon season and has significant impact along the west coast of India. The periodicity of these events is between 2 and 5 days, and it occurs more frequently during the months of January and February. These winds could have significant impact on the wind-induced circulation along the west coast of India, which in turn influence the advection-dispersion processes. Since the present study aims primarily at understanding the larval transport during various seasons, we have not treated well the role of shamal winds in larval transport, even though they are significant. This is mainly due to two reasons; (i) The model domain selected for the present study is small and the entire circulation in the Arabian Sea due to shamal winds could not be well incorporated and (ii) shamal events are not continuous and their duration is limited in terms of PLD phase of the larvae. Overall it shows that the current patterns determine the differential distribution of larvae among different seasons. Food supply to the existing settled population is also relied upon these current patterns. This indicates that the different distribution patterns of barnacles observed among different seasons are the consequences of variability in the environmental factors (either physical or biological) and illustrates that the environment or the habitat where they inhabit drives their overall distribution patterns.

Larval movement and retention also showed some specific spatial patterns within the estuarine area during different seasons. Larvae released at stations MPT and INS-Mandovi were mostly retained during post and pre-monsoon months. These two locations are positioned inside small bays, hence conducive for retention compared to other locations and also the post and pre-monsoon periods are fairly calm seasons, hence favorable for high retention of larvae. Coastal topography can have an effect on the larval dispersal and supply through its interaction with near-shore oceanographic conditions (Gaylord and Gaines, 2000; Roughan et al., 2005; Webster et al., 2007). Inshore and open coast sites can differ in settlement rates because of the interaction of topography with winds and tides (Gaines and Bertness,

1992). The importance of larval retention zones with reference to currents, where larval exchange with the adjacent waters is documented in most part of the world (Largier, 2004 and references therein).

Dispersal of larval forms is also known to be controlled by factors such as the length of time larvae spent as a pelagic phase, larval behaviour, larval feeding mode and larval size (Pechenik, 1999). Larval response to hydrodynamic forces will be mediated by biochemical (settlement inducers, presence of conspecifics and biofilms), physical (light), biological interactions (predation and competition) and larval physiology (age, competency and energy reserves) (Olivier et al., 2000; Qian et al., 2000; Marshall and Keough, 2003; Koehl et al., 2007; Tremblay et al., 2007). Number of larvae released by the individuals in a population can vary because some individuals can produce fewer larvae than the others due to lack of acquired energy. At the same time, some individuals can also produce weaker larvae which can lead to early mortality and the larvae which released are not transported to a suitable habitat then the success rate of such larvae will be very less. In this context, population connectivity of organisms is important in understanding whether reproductive output is correlated with their settlement or recruitment success. The orientation of coastline relative to the prevailing wind can also change larval settlement in an area (Kendall et al., 1985). For example, a change in the structural complexity of a habitat can affect the hydrodynamics at settlement site and this may change the settlement of organisms. Studies along the coast of Goa also showed a decreasing abundance of barnacles over the years in the recent past (Gaonkar and Anil, under review) and it is rather indistinct to point out the factors which are responsible for such changes in the abundance of barnacles in this tropical region. Long-term studies are required to understand the variations in the hydrodynamic processes operating in a particular region and to point out the basis for observed change in abundance of barnacles.

Moreover, the simulation results and field observations did not match all the time in our studies. For example, the retention of larvae observed at station MPT during most of the months did not correlate with the field observations of larval abundance, settlement and recruitment of barnacles. Such mismatch could be due to various reasons. The numerical simulations of larval dispersal have some limitations due to the simplicity of the model in terms of biological and ecological aspects. Larval behavior can change under different circumstances. Environmental variability is the main cause for such differences. Larvae are likely to disperse or retain more without settling behavior or mortality factors. Factors such as food availability and predation can also influence larval survival. Reproductive output of adult barnacles can also vary during different seasons leading to different number of larval release and supply of larvae to adult habitats. Other than these biological factors, environmental factors such as

temperature, salinity, rainfall and turbidity can all influence dispersal. Higher temperatures can lead to early metamorphosis of larval stages leading to early settlement than lower temperatures. Heavy rainfall can lead to lower salinity and increased land runoff leading to turbidity in the surrounding environment which can ultimately lead to larval mortality. Different substrata and the cues offered are also important for the larvae to settle in a particular region. Some larvae can postpone settlement if conditions are not ideal (Seed and Suchanek, 1992), but this carries direct (predation) and indirect costs (depletion of energetic resources) for the larvae. All these factors influence larval dispersion, retention and settlement in one or the other way. Future studies should try to incorporate some of these factors in the numerical simulations. Consequently, the results of the simulations can be interpreted as maximum dispersal and survivorship. Nonetheless, this study has provided some basis for the observed variations in larval abundance, settlement and recruitment of barnacles in this tropical region influenced by monsoons.

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### Legends to figures:

**Fig. 1.** Study locations for the monitoring of (A) larval abundance (1. Old Goa 2. Panjim bridge 3. Miramar 4. Offshore 5. MPT 6. Dona Paula 7. Zuari bridge) (B) Settlement and recruitment of barnacles (1. Dona Paula; 2. MPT; 3. INS-Mandovi; 4. Arambol) and (C) (i) Large and (ii) small domains for numerical simulations. Particle release sites in large domain (1. Arambol 2. Anjuna 3. Sinquerim 4. Bogmalo 5. Cabo-de-Rama 6. Palolem) and small domain (1. Mandovi edge 2. INS-Mandovi 3. Dona Paula 4. MPT 5. Zuari edge). ‘W’ represents the location of weather station and ‘C’ represents the location of current measurement station.

**Fig. 2.** Wind rose of Goa during (a) pre-monsoon (b) monsoon and (c) post-monsoon seasons derived from AWS data (colour version of this figure is available online).

**Fig. 3.** Larval abundance (cirripede nauplii) (No./100m<sup>3</sup>) in the field during different months at different stations for the period 2005-2007 [Months: (a) Mar-05 (b) May-05 (c) Sept-05 (d) Nov-05 (e) Jan-06 (f) Mar-06 (g) May-06 (h) Sept-06 (i) Nov-06 (j) Jan-07 (k) Mar-07 (l) May-07].

**Fig. 4.** Larval abundance (cirripede cyprids) (No./100m<sup>3</sup>) in the field during different months at different stations for the period 2005-2007 [Months: (a) Mar-05 (b) May-05 (c) Sept-05 (d) Nov-05 (e) Jan-06 (f) Mar-06 (g) May-06 (i) Nov-06 (j) Jan-07 (k) Mar-07 (l) May-07].

**Fig. 5.** Settlement and recruitment of barnacles at stations (a) Dona Paula (b) MPT (c) INS-Mandovi and (d) Arambol.

**Fig. 6.** Comparison between predicted and modelled water levels, measured and modelled u-velocity, and measured and modelled v-velocity at COP Panaji.

**Fig. 7.** Larval simulations along the coast at different stations during pre-monsoon season (a) Feb-2007 and (b) Apr-2007 [Release sites: (1) Arambol (2) Anjuna (3) Sinquerim (4) Bogmalo (5) Cabo-de-Rama and (6) Palolem] (colour version of this figure is available online).

**Fig. 8.** Larval simulations along the coast at different stations during monsoon season (a) Jun-2006 and (b) Aug-2006 [Release sites: (1) Arambol (2) Anjuna (3) Sinquerim (4) Bogmalo (5) Cabo-de-Rama and (6) Palolem] (colour version of this figure is available online).

**Fig. 9.** Larval simulations along the coast at different stations during post-monsoon season (a) Oct-2006 and (b) Dec-2006 [Release sites: (1) Arambol (2) Anjuna (3) Sinquerim (4) Bogmalo (5) Cabo-de-Rama and (6) Palolem] (colour version of this figure is available online).

**Fig. 10.** Larval simulations within the estuaries (Mandovi and Zuari) at different stations during pre-monsoon season (Feb-2007) [Release sites: (1) Mandovi edge (2) INS-Mandovi (3) Dona Paula (4) MPT and (5) Zuari edge] (colour version of this figure is available online).

**Fig. 11.** Larval simulations within the estuaries (Mandovi and Zuari) at different stations during pre-monsoon season (Apr-2007) [Release sites: (1) Mandovi edge (2) INS-Mandovi (3) Dona Paula (4) MPT and (5) Zuari edge] (colour version of this figure is available online).

**Fig. 12.** Larval simulations within the estuaries (Mandovi and Zuari) at different stations during monsoon season (Jun-2006) [Release sites: (1) Mandovi edge (2) INS-Mandovi (3) Dona Paula (4) MPT and (5) Zuari edge] (colour version of this figure is available online).

**Fig. 13.** Larval simulations within the estuaries (Mandovi and Zuari) at different stations during monsoon season (Aug-2006) [Release sites: (1) Mandovi edge (2) INS-Mandovi (3) Dona Paula (4) MPT and (5) Zuari edge] (colour version of this figure is available online).

**Fig. 14.** Larval simulations within the estuaries (Mandovi and Zuari) at different stations during post-monsoon season (Oct-2006) [Release sites: (1) Mandovi edge (2) INS-Mandovi (3) Dona Paula (4) MPT and (5) Zuari edge] (colour version of this figure is available online).

**Fig. 15.** Larval simulations within the estuaries (Mandovi and Zuari) at different stations during post-monsoon season (Dec-2006) [Release sites: (1) Mandovi edge (2) INS-Mandovi (3) Dona Paula (4) MPT and (5) Zuari edge] (colour version of this figure is available online).

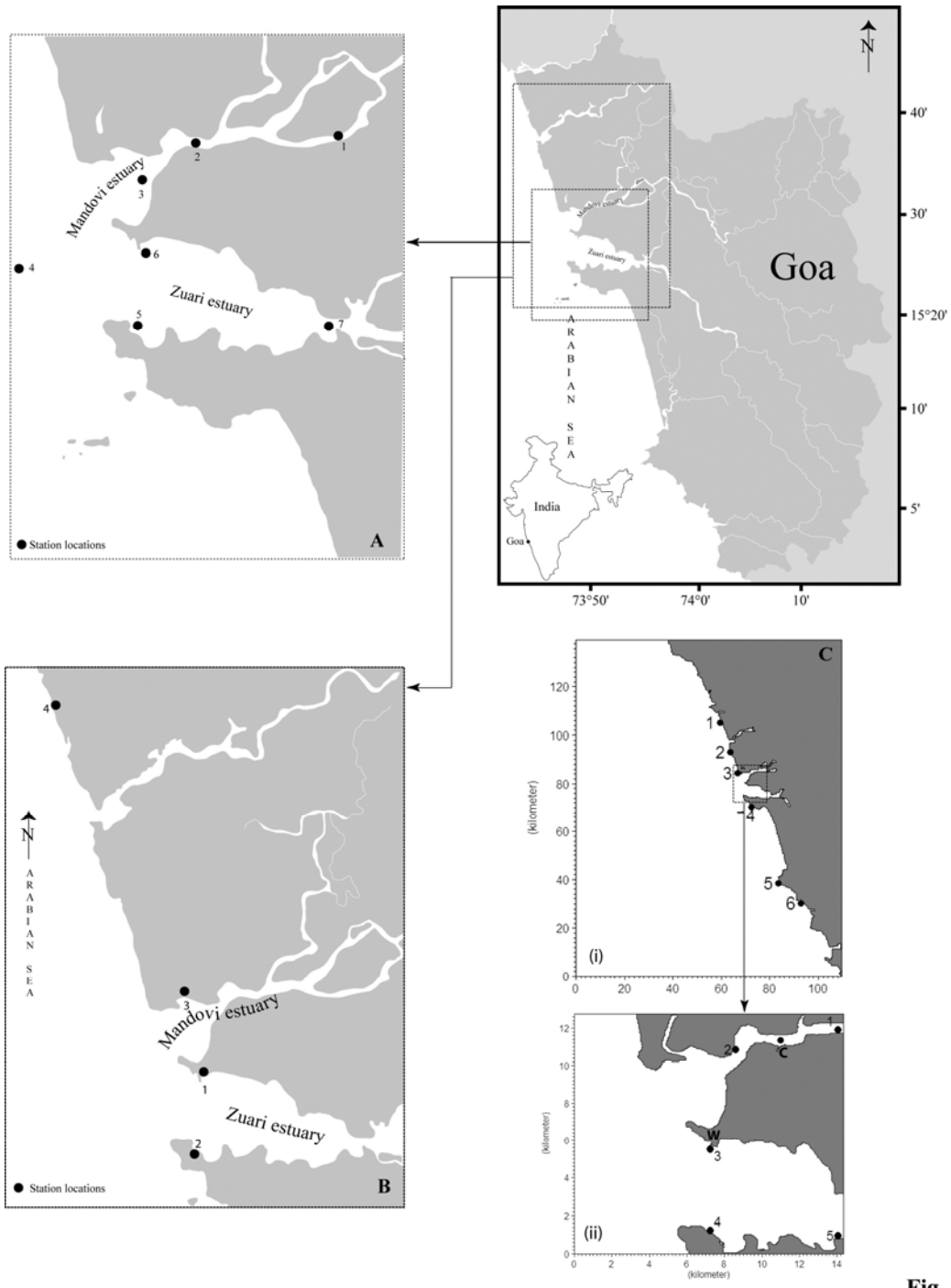


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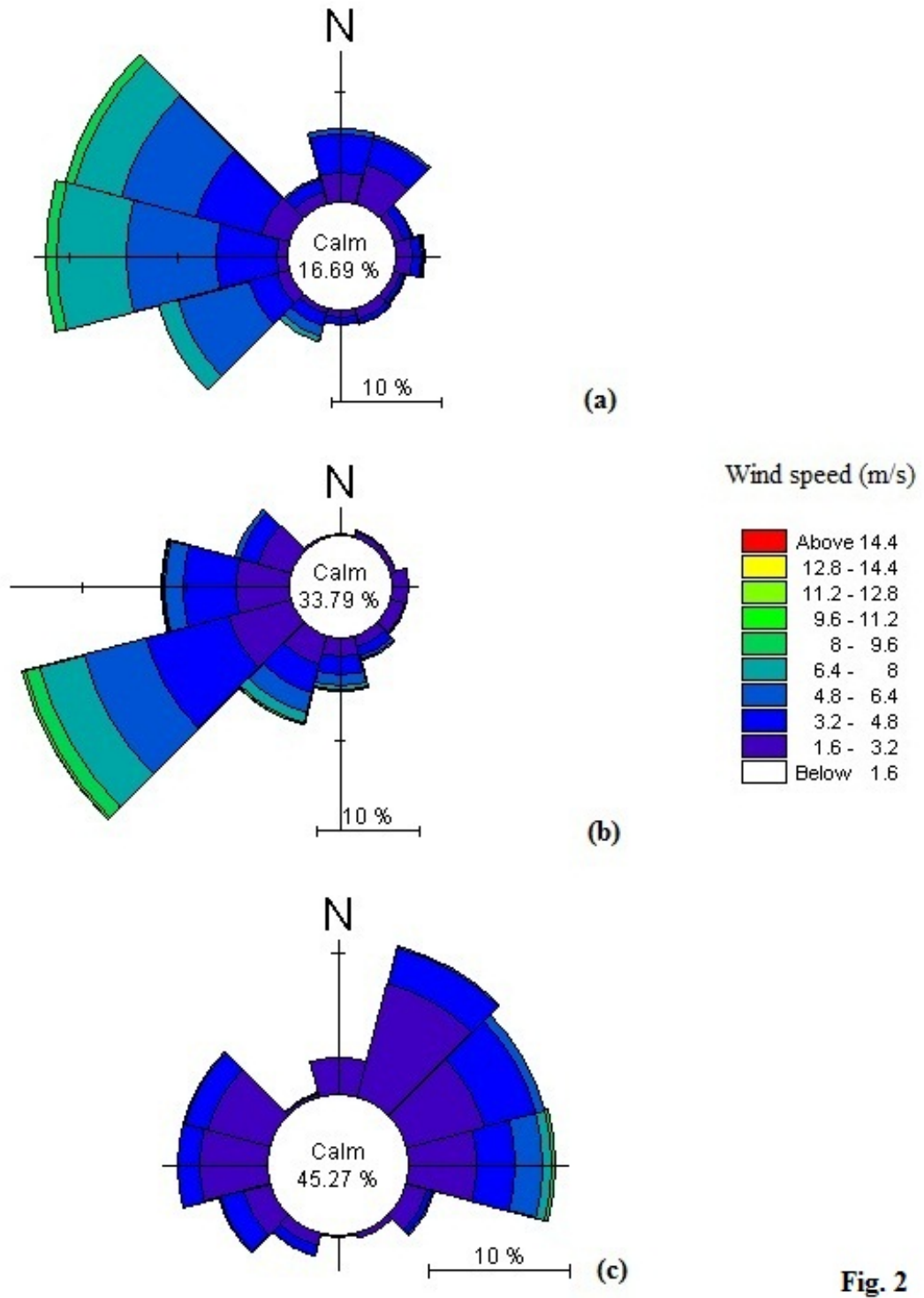


Fig. 2

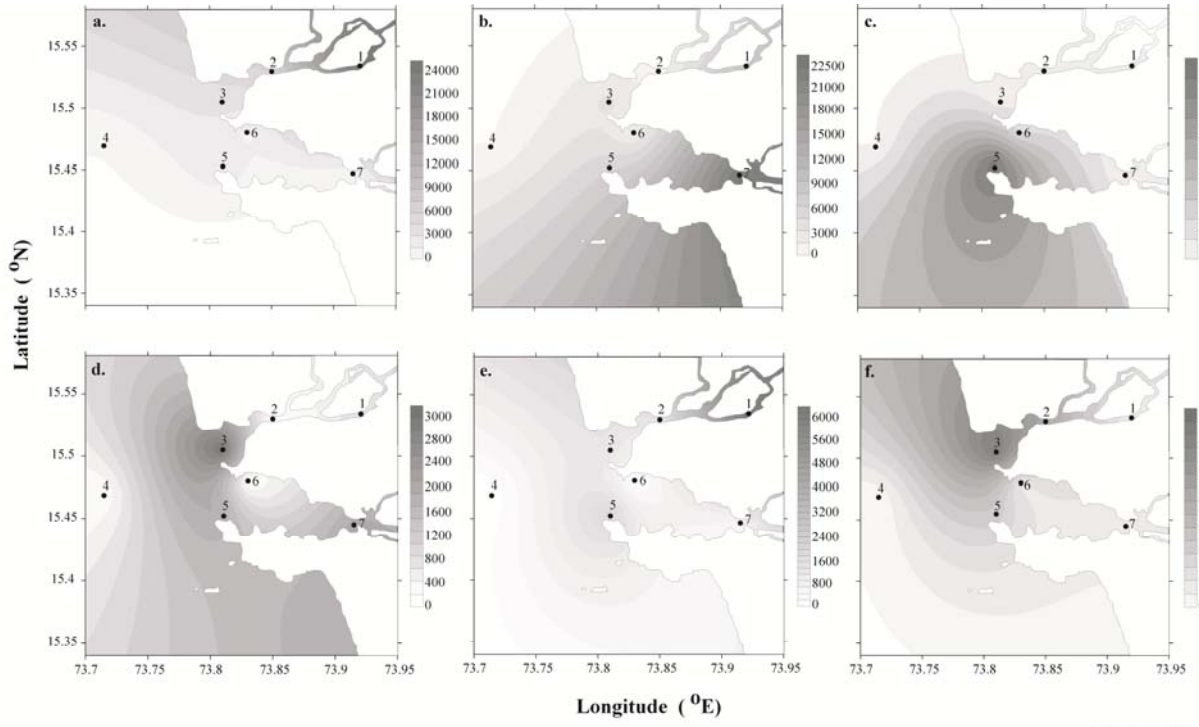


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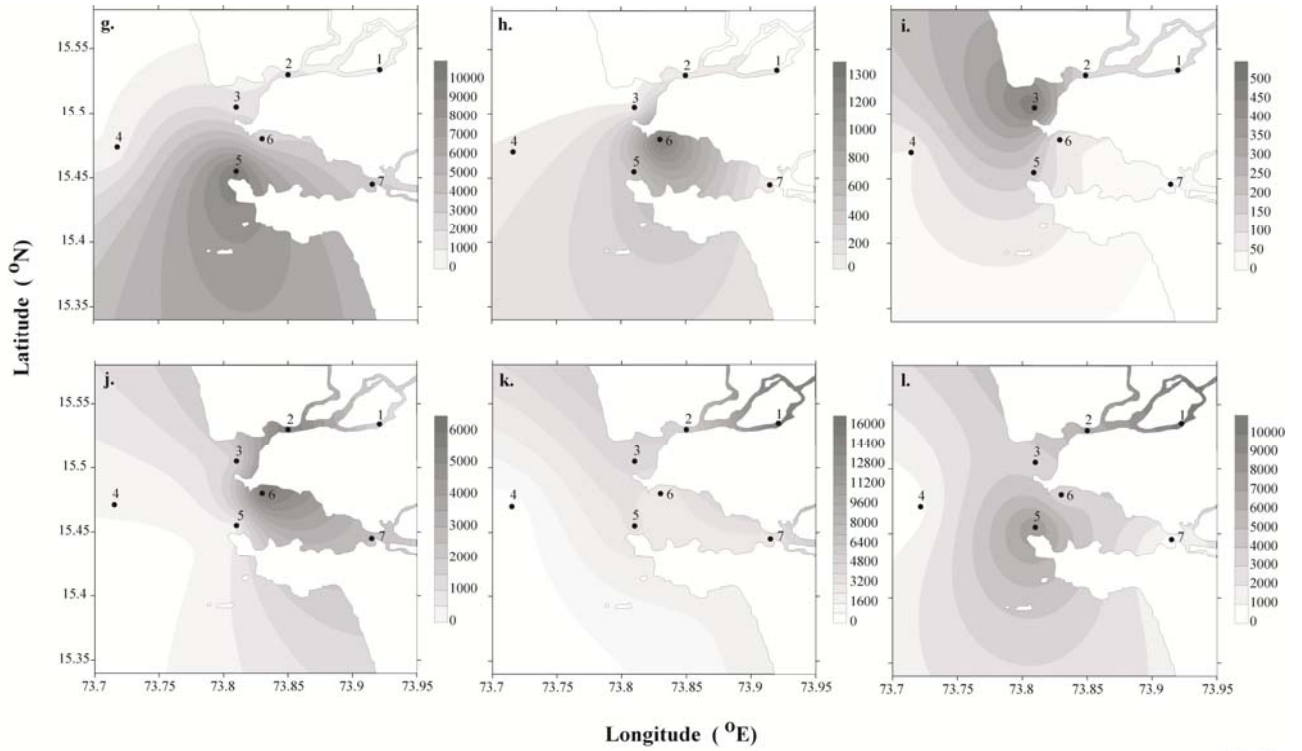


Fig. 3

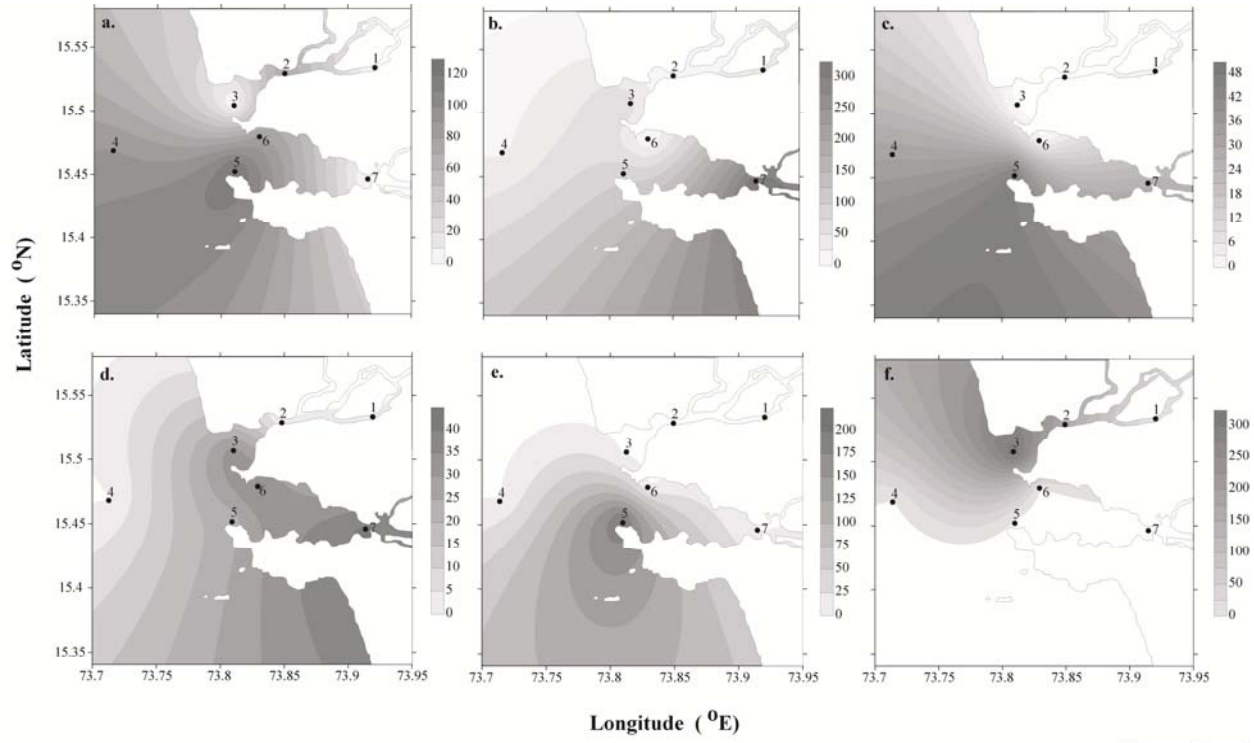


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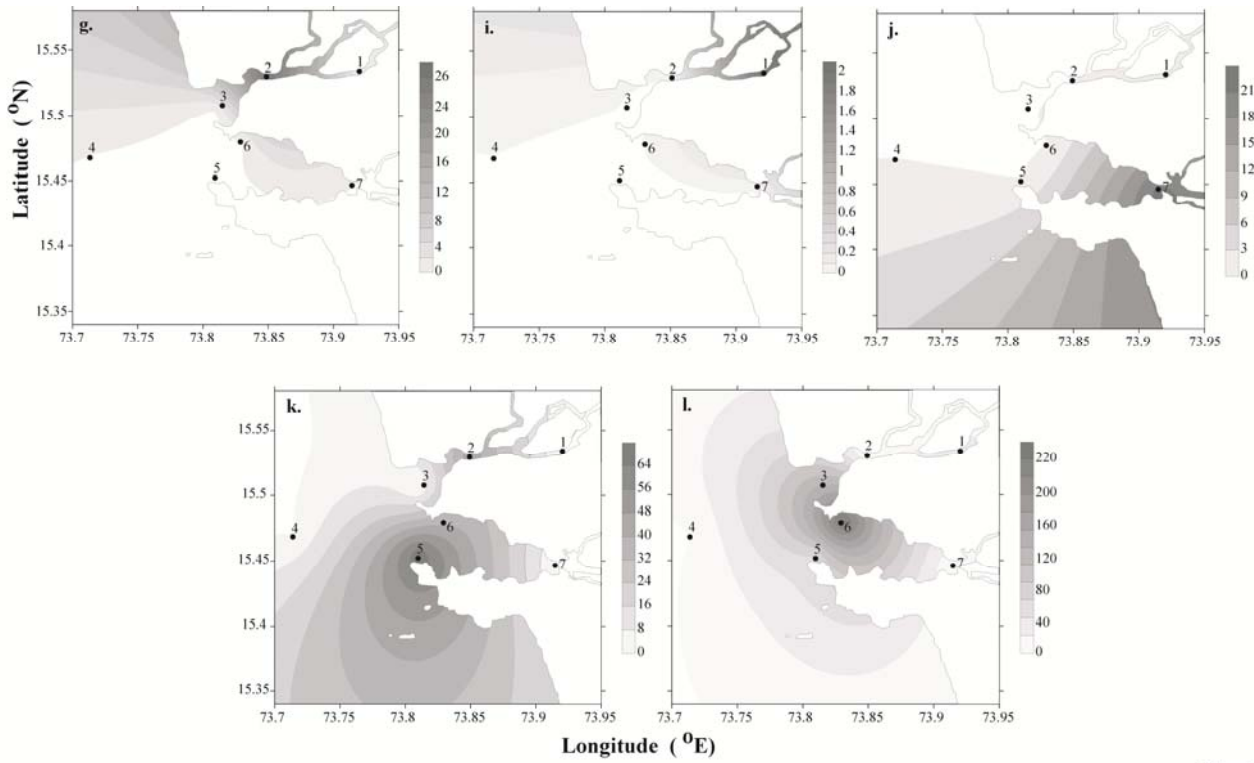


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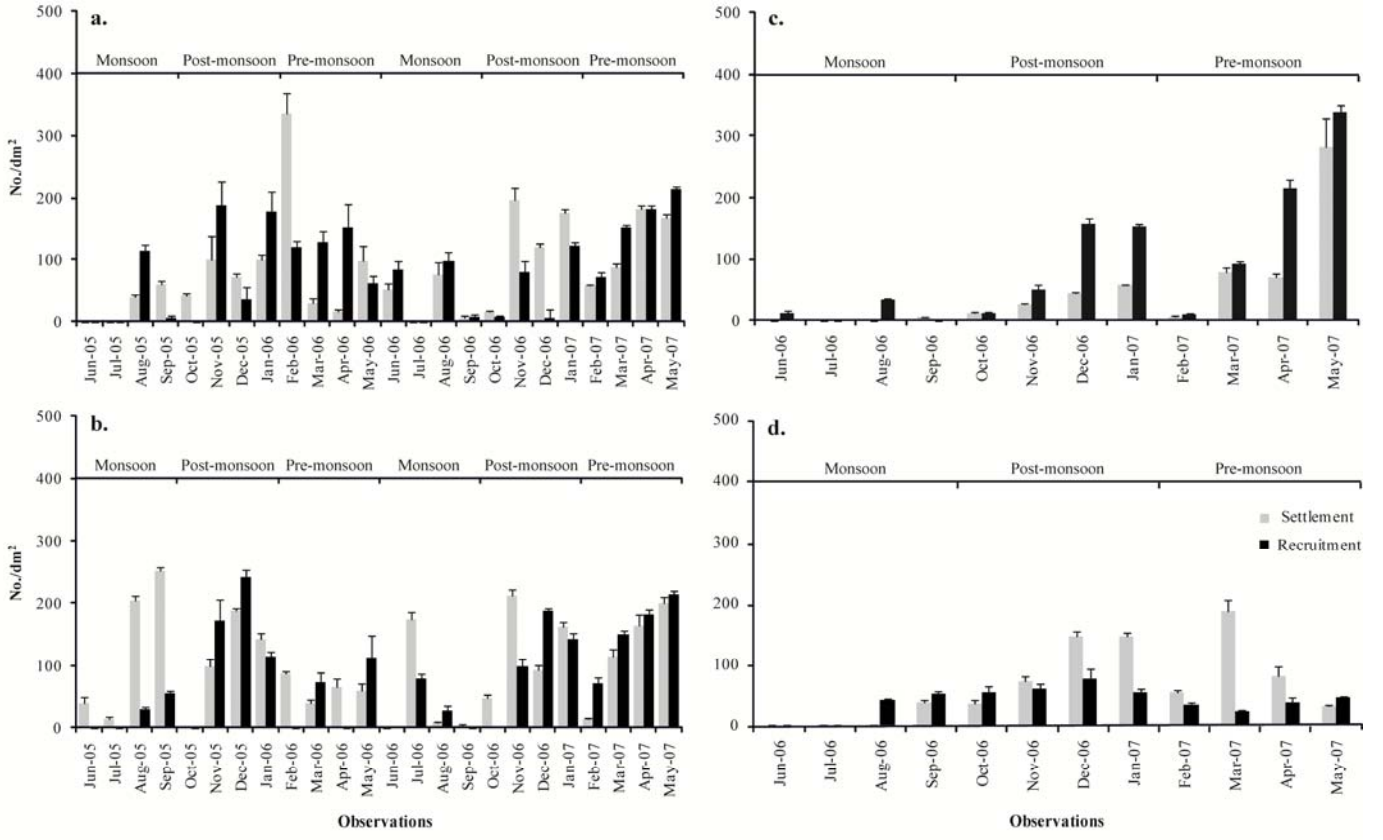


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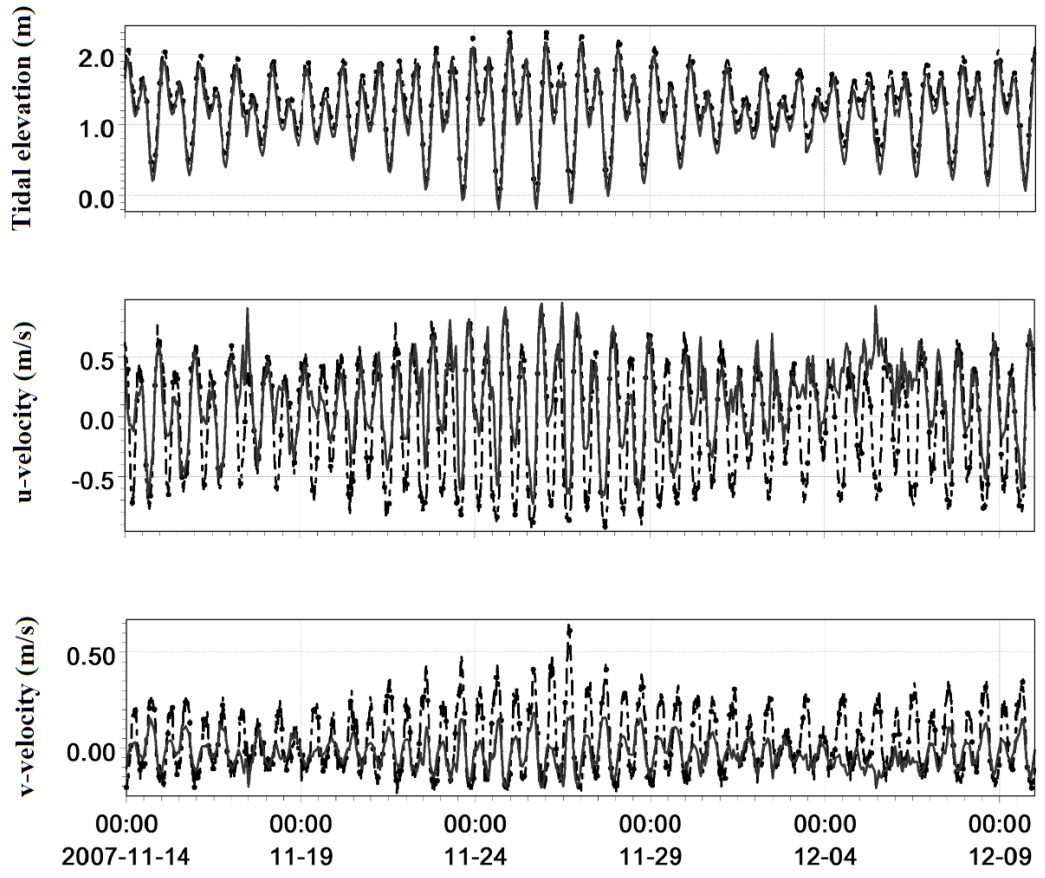


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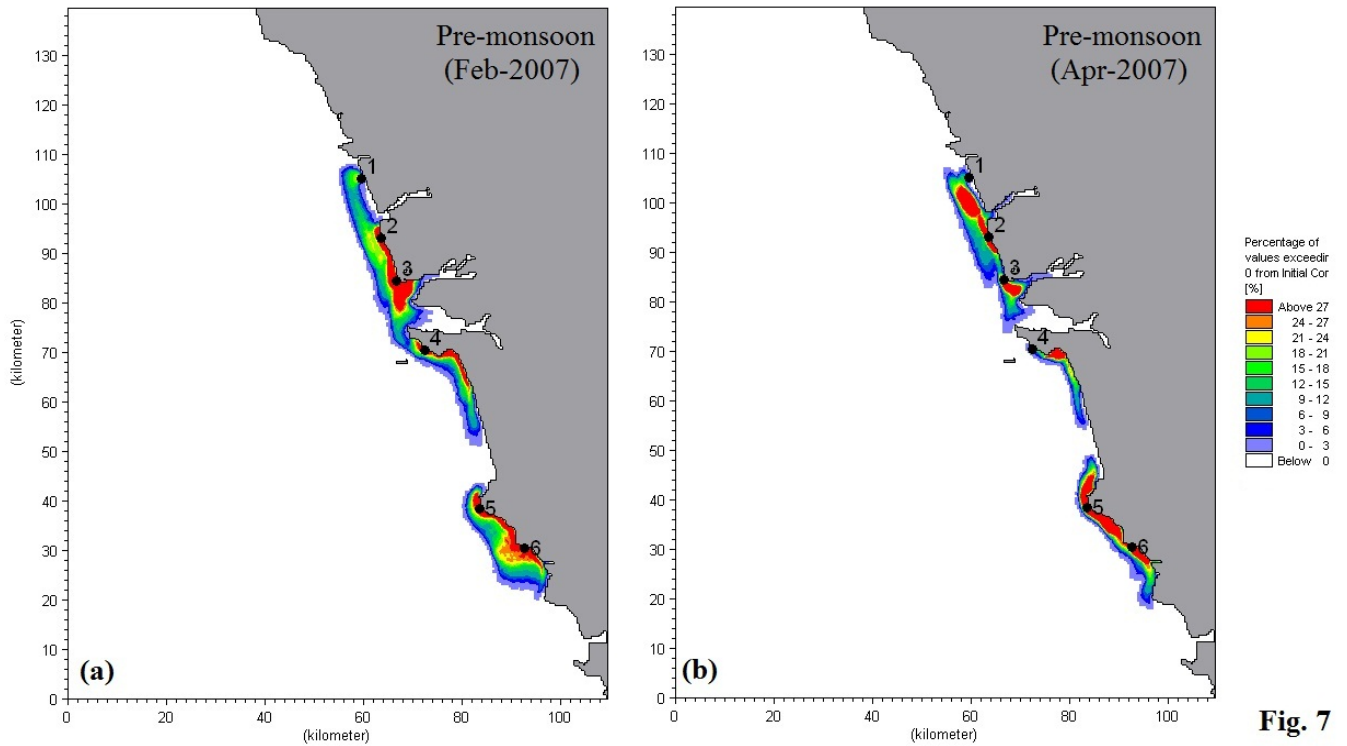


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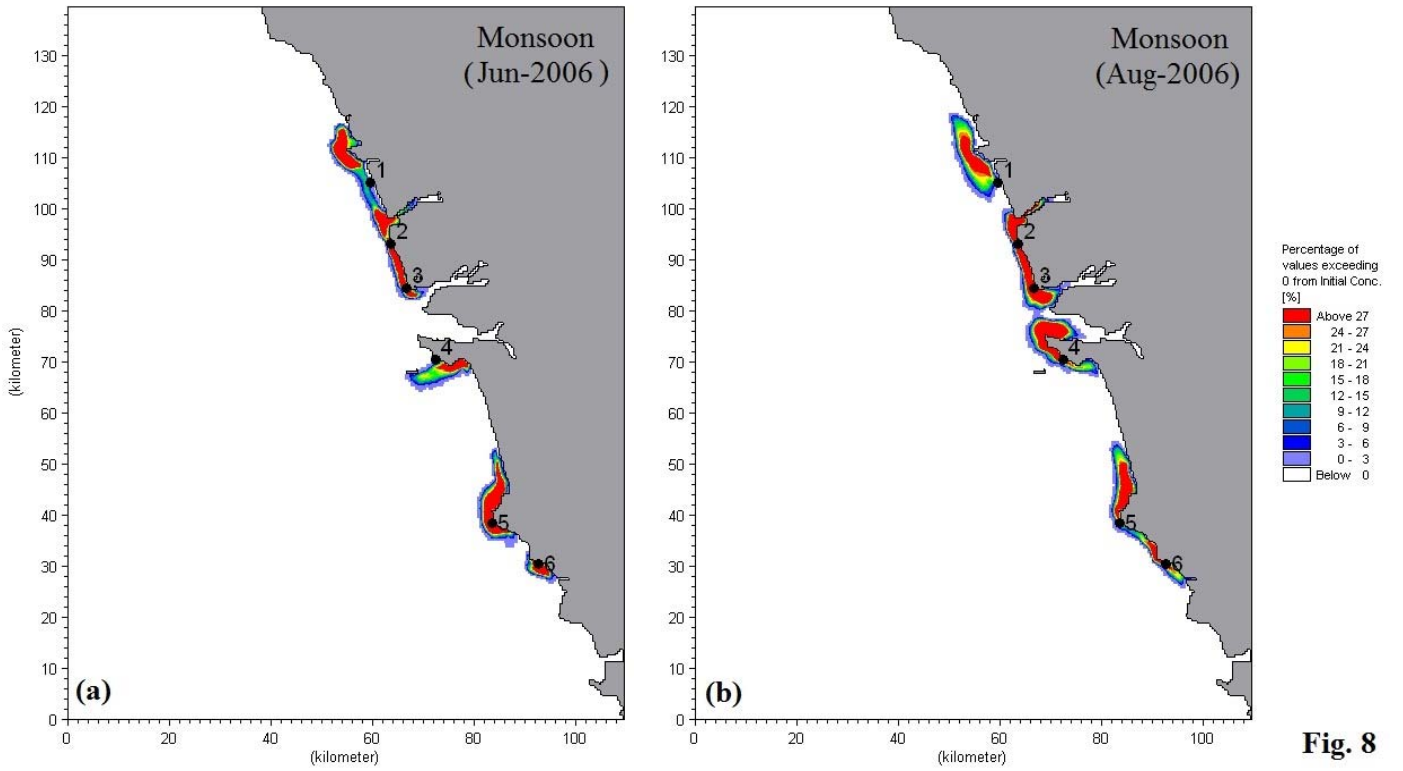


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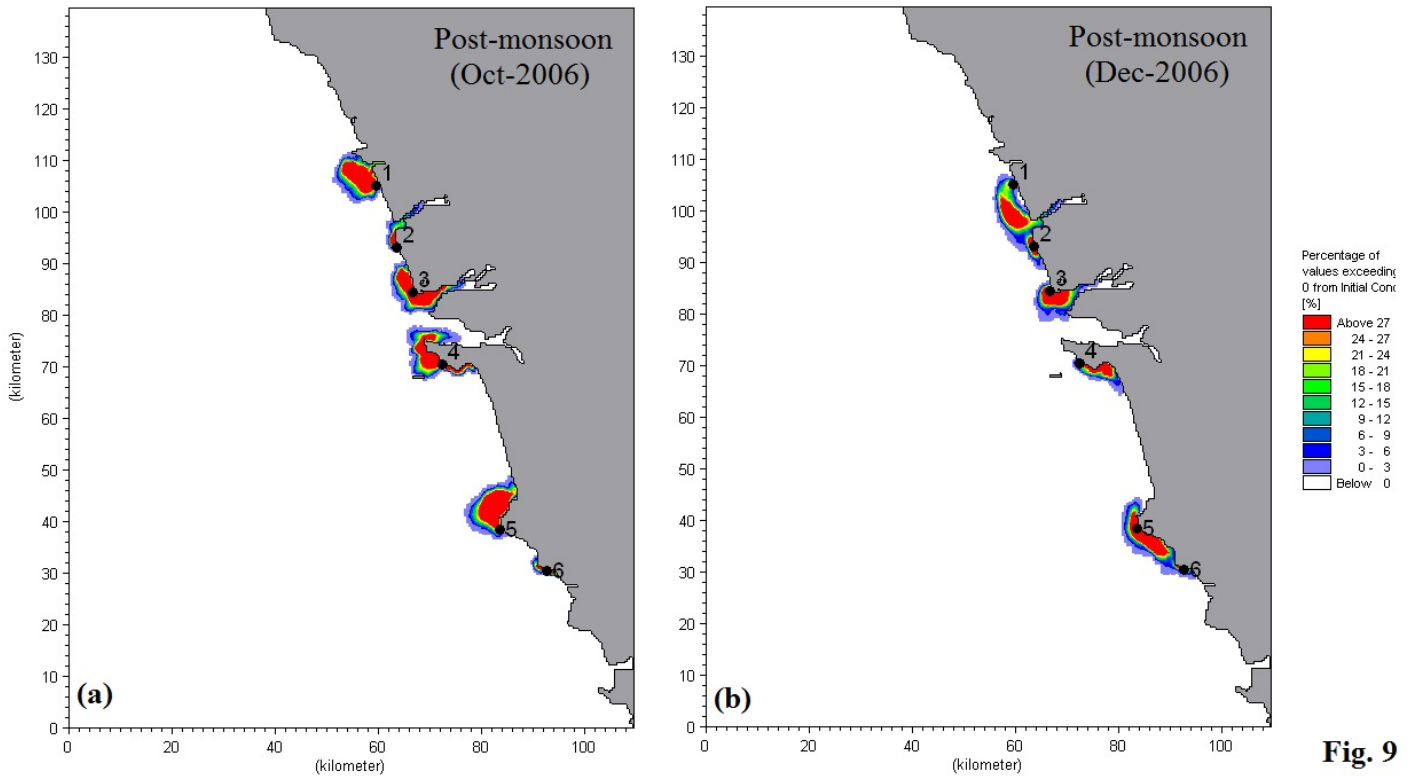


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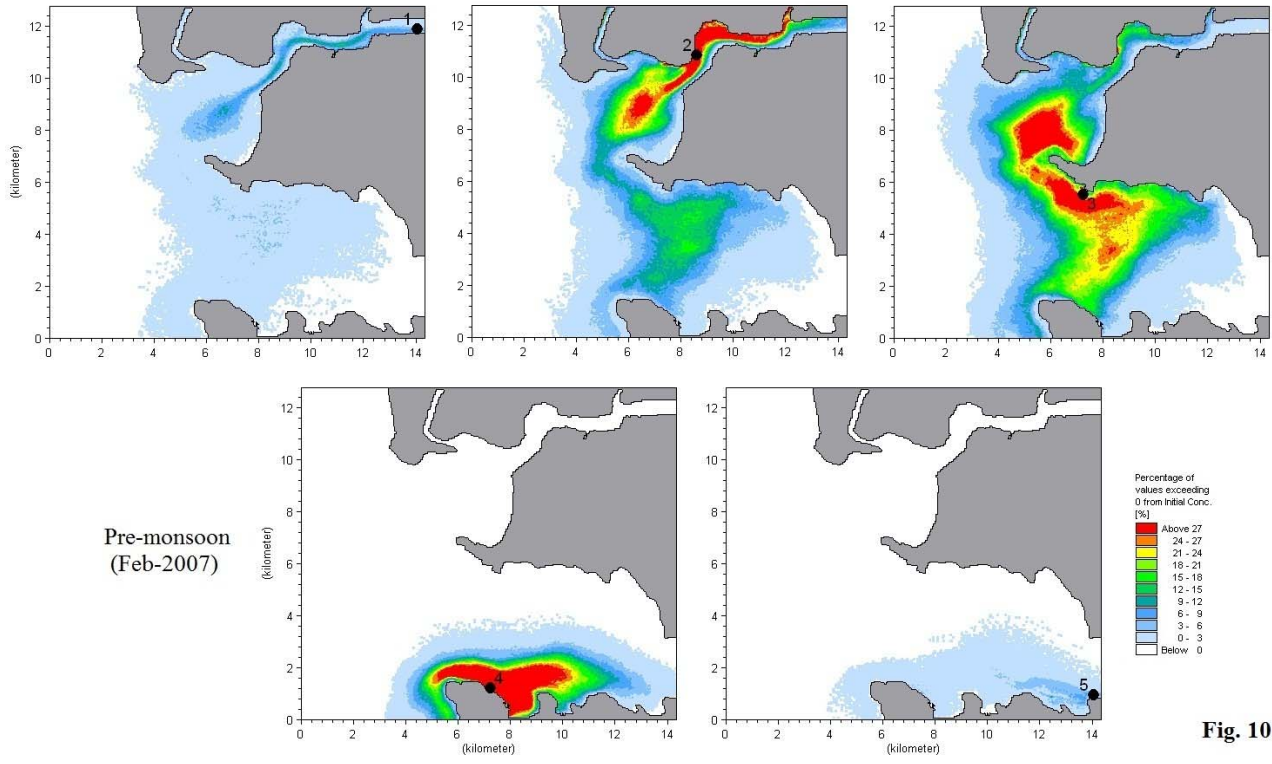


Fig. 10

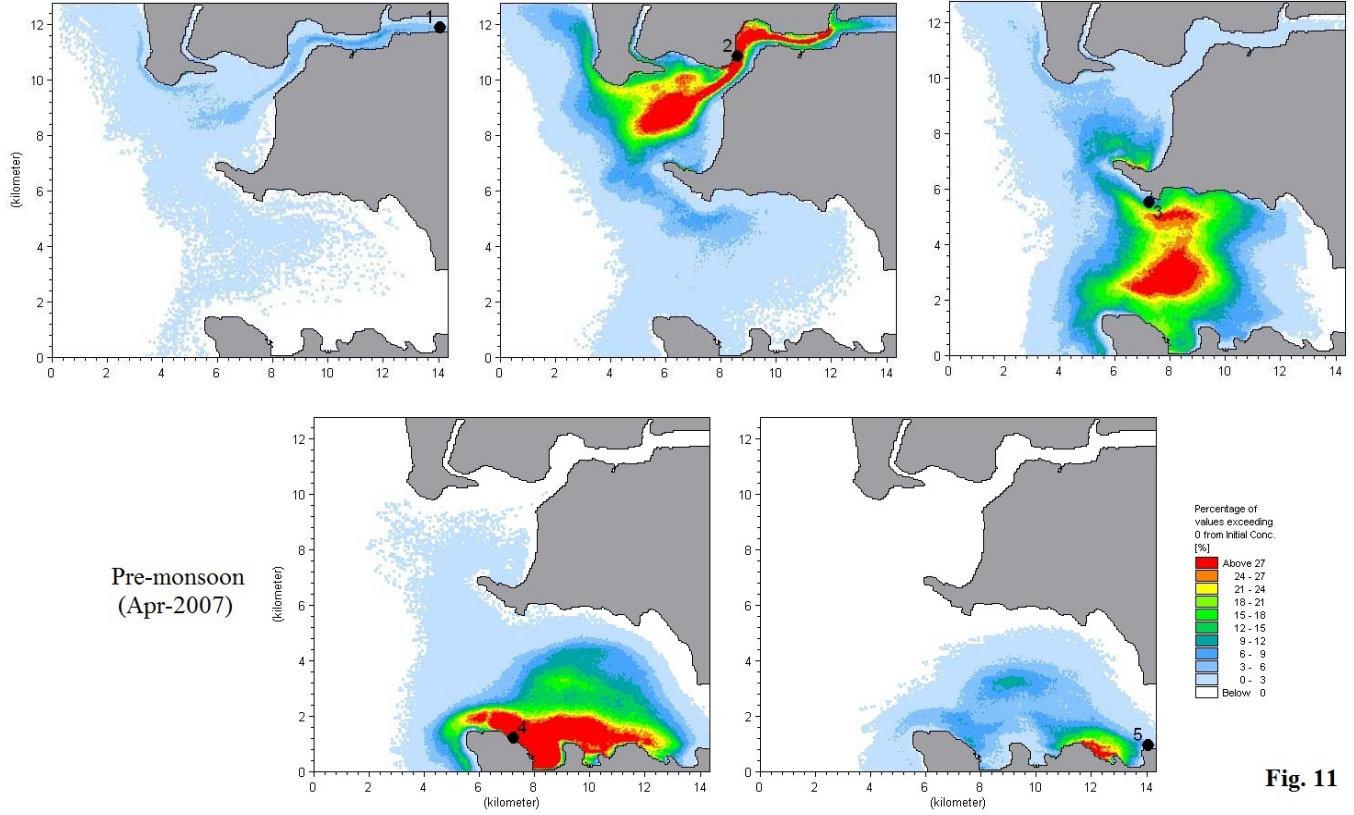


Fig. 11

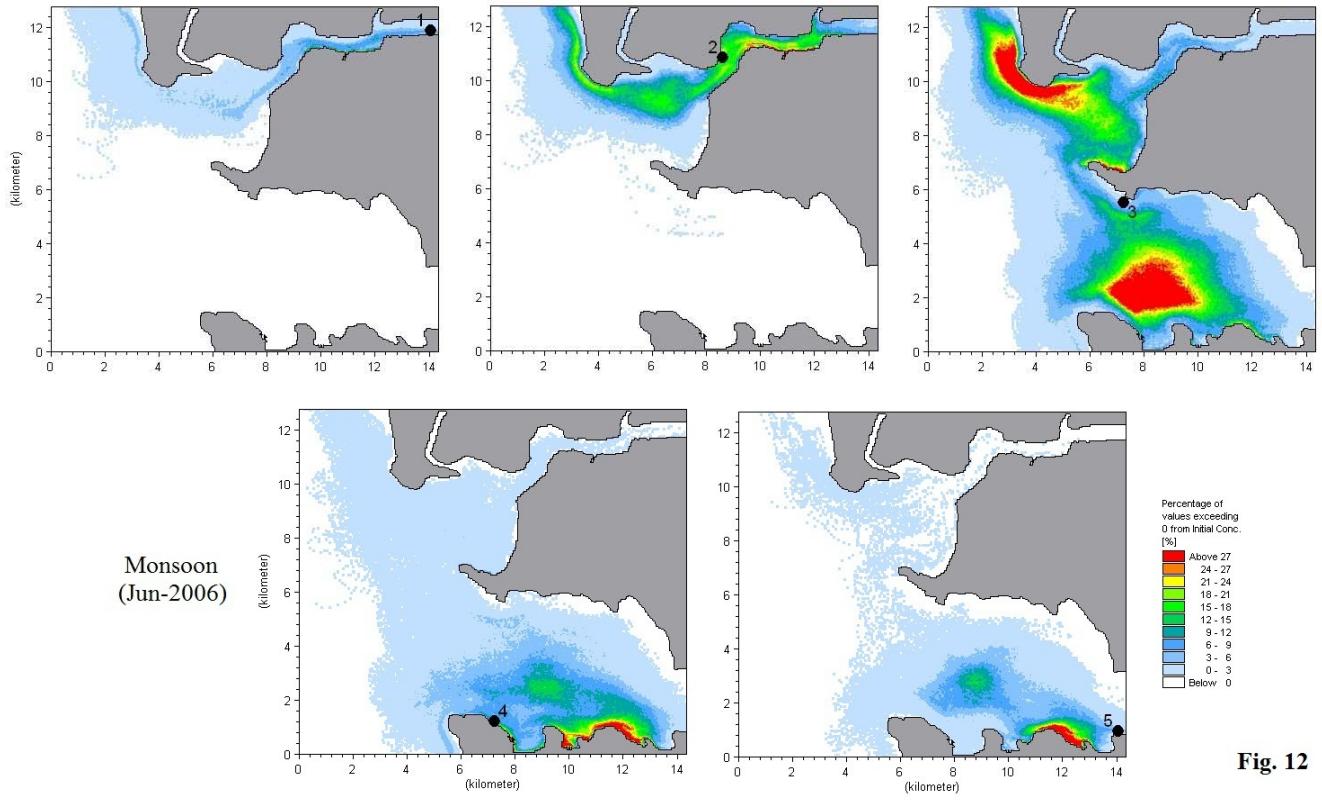


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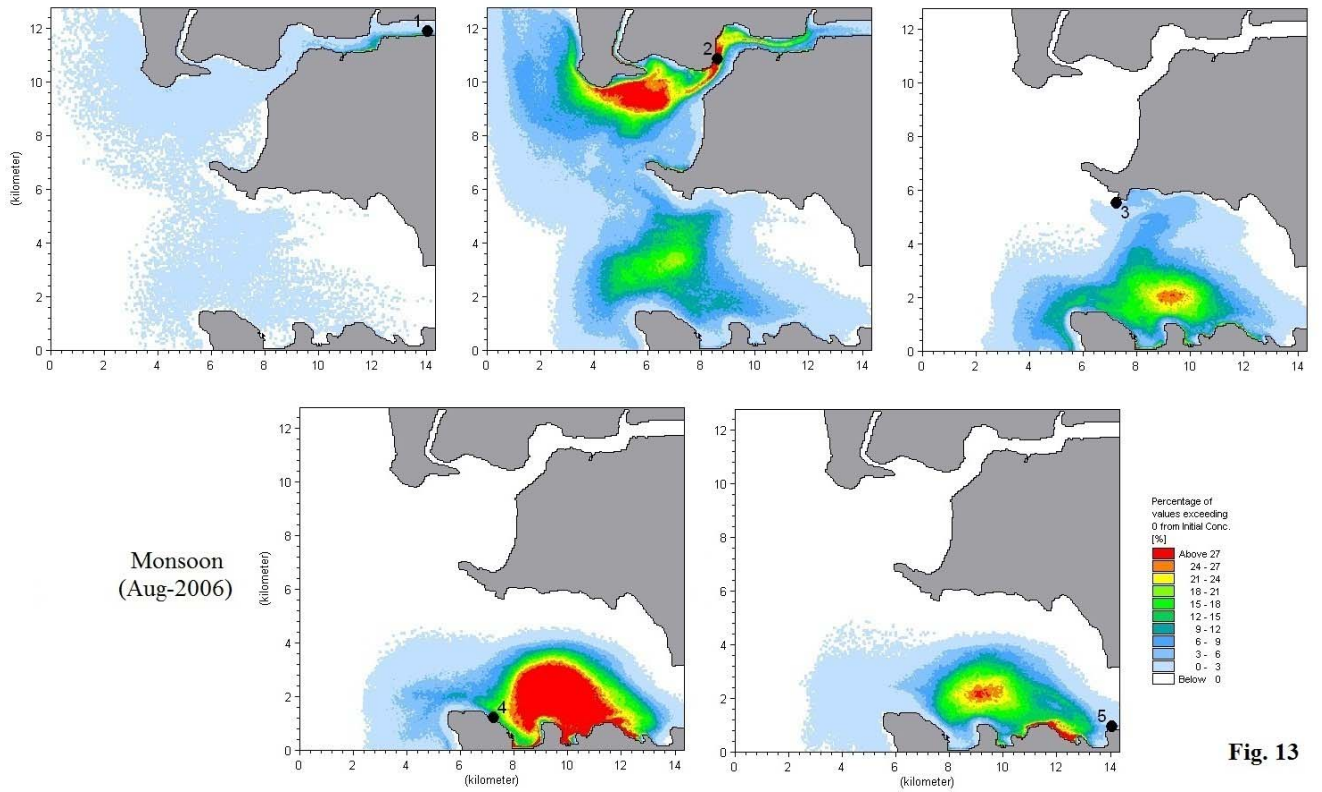


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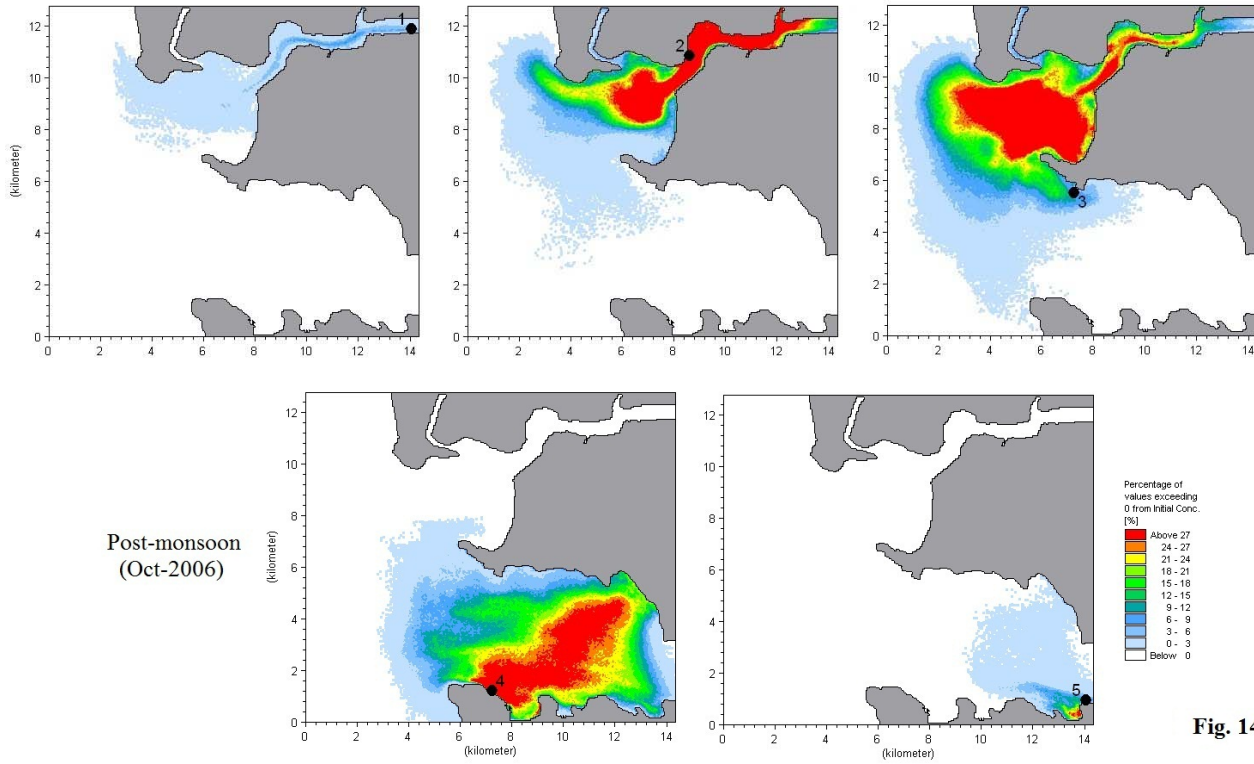


Fig. 14

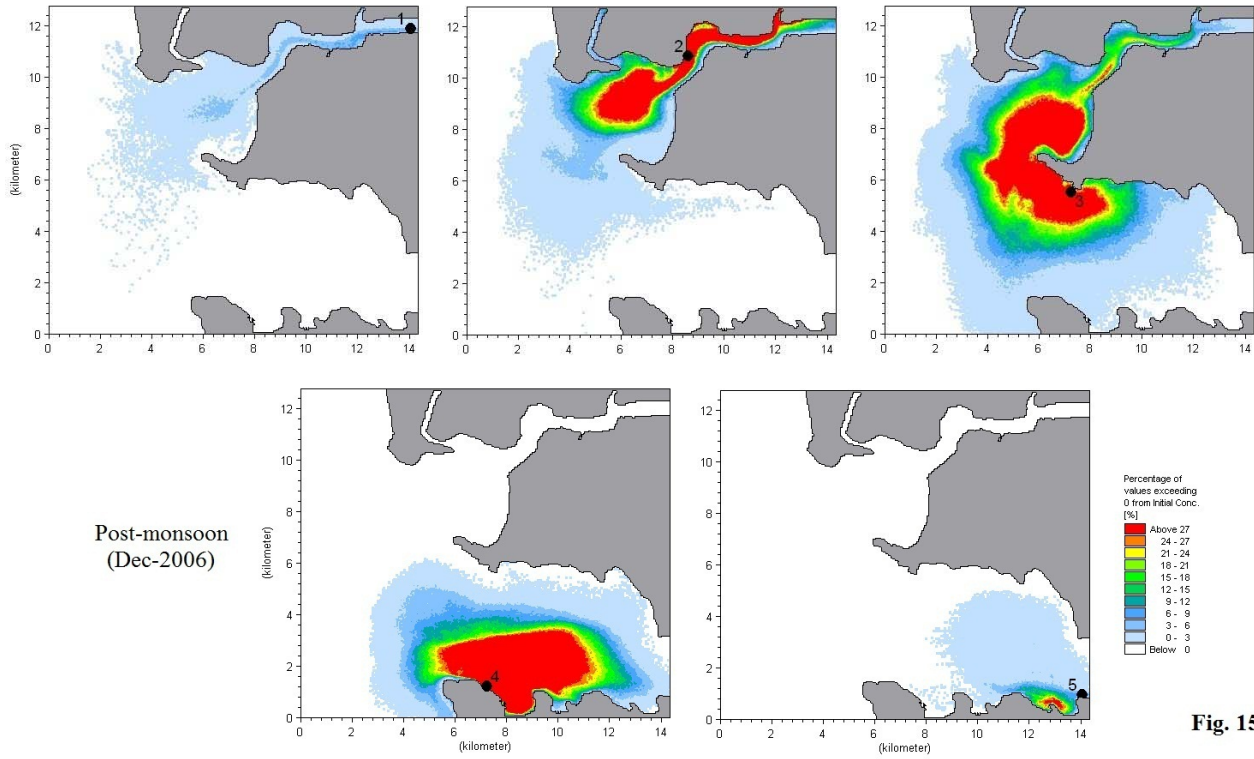


Fig. 15