

Reviewer #1

*Quantification has long been an important issue in larval dispersal research. The Japanese anchovy (*Engraulis japonicus*) is one of the most ecologically and economically important small pelagic fish in the China Seas. However, a comprehensive and quantitative understanding of its larval dispersal patterns and underlying drivers has been lacking. This manuscript applies both 1D and 2D dispersal kernels to give a high spatiotemporal resolution, multi-factor, quantitative analysis of larval dispersal in Japanese anchovy across the China Seas, providing some new insights into the quantification of larval dispersal patterns. It also reveals the critical connectivity role of the Changjiang Estuary spawning ground, which is quite interesting and beyond expectations. However, I still have some concerns on the manuscript, and addressing them would, in my view, improve its quality.*

Response: We sincerely thank the reviewer for reading and commenting on this manuscript. We have carefully considered all comments and addressed them point by point in the revised manuscript.

Main concerns:

1. What is the meaning of connectivity matrix?

Connectivity matrices have been used primarily for reef fish, where reef areas can function simultaneously as spawning grounds and nursery grounds. In this study, the y-axis of connectivity matrices represents spawning locations, but the x-axis represents settlement locations rather than nursery grounds. What, then, is the meaning of connectivity between a spawning location and a settlement location?

I suggest that the authors provide a more detailed explanation of the connectivity matrices, including their ecological interpretation and limitations.

Response: We agree that retaining the analysis could lead to over-interpretation, and therefore chose to remove it. Connectivity matrices have been widely applied to a variety of marine fish species, not only reef fishes. However, we agree that calculating connectivity among known spawning locations is of limited ecological relevance in our study. A more meaningful approach would be to quantify connectivity between spawning grounds and nursery areas. Because the nursery habitats of Japanese anchovy in the study region remain insufficiently defined, such an analysis cannot be conducted reliably with the available data.

Following the reviewer's suggestion, we have removed the connectivity matrix analysis from

the manuscript, including Section 2.5 (Methods) and Section 3.3 (Results).

2. *Are Chinese stock and Japanese stocks connected through CJ ground?*

I do not think that the connectivity (dispersal rate) of larvae from the CJ spawning ground to the TWC and PS spawning grounds is sufficient to prove that the Chinese stock and the Japanese stock are connected. Although some larvae originating from CJ may reach the TWC region, larvae spawned at TWC may already have been advected further eastward by that time, resulting in limited spatial or temporal overlap between the two groups. Under such circumstances, the mere arrival of CJ larvae at TWC does not necessarily imply effective stock connectivity. Stronger evidence would come from demonstrating that larvae originating from CJ and TWC are transported to the same or nearby nursery habitats and overlap in space and time, thereby increasing the likelihood of mixing and subsequent recruitment into a common population. Such convergence of dispersal trajectories would provide a more convincing mechanism linking the two stocks.

I suggest that the authors discuss this point and greater caution should be exercised in both the wording and the conclusions of the manuscript, particularly when inferring stock connectivity from modeled dispersal pathways alone.

Response: We thank the reviewer for this suggestion. We have revised the discussion about connectivity between China Sea and Japanese Sea Stocks (Section 4.4) as follows:

Whether Japanese anchovy populations from the China Seas and the Japan Sea spawning grounds belong to a single stock or represent distinct stocks remains unresolved. Using genetic analyses, Yu et al. (2002) reported that the Japanese anchovy populations from spawning grounds near northeastern Taiwan, in the Pacific Ocean, and near southwestern Taiwan, in the Taiwan Strait, were indeed separate stocks. In contrast, Yu et al. (2005) and Zheng et al. (2015) found no significant genetic differentiation among populations from the Yellow Sea and East China Sea. Furthermore, marginally significant genetic structure was detected between the Bohai Sea and Japan Sea populations, as well as between the North Yellow Sea and Japan Sea population (Zhang et al., 2020a).

Results from the present larval dispersal study suggest that the CJ spawning ground may provide a potential pathway for larval exchange among regional populations. Larvae originating from CJ were transported not only to the central Yellow Sea, where they potentially overlap with larvae from other China Sea spawning grounds, but also to the northwest of Kyushu (TWC) and south of Kyushu (PS) in the Japan Sea. These results suggest the potential for larval exchange between the China Seas and Japan Sea regions. However, the arrival of CJ-derived larvae in TWC and PS alone is insufficient to

demonstrate effective stock connectivity. Larvae spawned at TWC and PS may already have been transported elsewhere by the time CJ-derived larvae arrive, resulting in limited spatial and temporal overlap between the two groups. Consequently, the observed dispersal pathways indicate only the potential for connectivity, rather than direct evidence of population mixing or recruitment into a common stock. A more convincing demonstration of stock connectivity would require showing that larvae originating from CJ, TWC, and PS converge in the same or adjacent nursery habitats and overlap in space and time, thereby increasing opportunities for mixing and recruitment into a shared population.

Minor suggestions:

3. L21: *pattern, instead of patten.*

Response: We have revised it.

4. L21: *ranges from 44.53 to 150.56, replace “-” with “to”.*

Response: We have revised it.

5. L100: *hydrodynamic model, instead of modal.*

Response: We have revised it.

6. L128: *you said “30 days” in L81, but why you used 30, 40, 50, 60 days here.*

Response: Japanese anchovy larvae typically require approximately 30 days to grow to 20 mm in length, and therefore 30 days was used as the baseline scenario in our particle-tracking simulations. To further evaluate how dispersal patterns may vary with larval duration and to assess the sensitivity of our results to this parameter, we additionally simulated travel durations of 40, 50, and 60 days. These extended-duration scenarios were not intended to represent the typical larval period, but rather to examine the potential effects of prolonged transport on larval dispersal and connectivity.

7. L130: *15 times, instead of 15 days.*

Response: We have revised it.

8. L131: *The position of a particle stopped at the end...*

Response: We have revised it.

9. L255-260: *I think you need a Table S2 to give the values of modal dispersal distance, median-dispersal distance, and long-distance dispersal. It's hard to read these values from the figure.*

Response: We think the reviewer is asking for the values of modal dispersal distance, median dispersal distance, and long-distance dispersal threshold. We have now added a Table S2 to provide the values of these metrics as follows:

Table S2. *Values of modal dispersal distance, median-dispersal distance, and long-distance dispersal threshold.*

	Modal dispersal distance (km)	Median-dispersal distance (km)	Long-distance dispersal (km)
From ZH	89.27	113.18	253.09
From BHB	93.12	110.96	233.69
From LZB	48.07	73.09	186.47
From YT	127.65	145.88	292.92
From SDI	150.56	177.53	369.65
From HZB	44.53	117.46	376.23
From CJ	131.23	196.02	494.69
All	77.31	128.37	344.03
April	76.39	104.92	250.22
May	93.74	128.97	307.97
June	109.29	162.91	410.61
July	86.52	145.22	391.36
August	53.10	108.85	320.57
30 days	63.68	98.97	255.82
40 days	79.45	121.71	311.91
50 days	92.20	141.79	364.23
60 days	101.5	158.77	411.89

10. L372: *dispersal kernels, instead of dispersal kernel.*

Response: We have revised it (the second line in Section 4.3).

11. L365: need a figure S2 to show the correlation between individual dispersal distances and PLD.

Response: We have added a figure S2 as below:

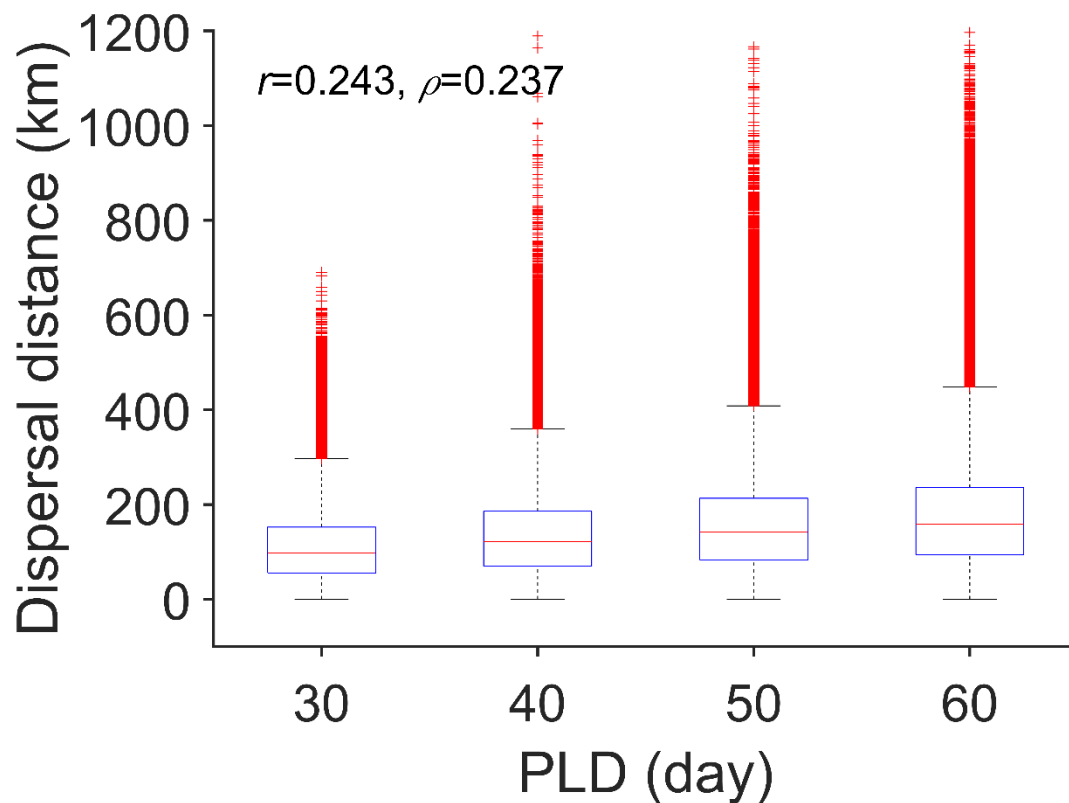


Figure S2. Box plots of dispersal linear distances showing a weak relationship between pelagic larval duration (PLD) and dispersal distance (Pearson's correlation: $r=0.243$; Spearman's correlation: $\rho=0.237$).

12. L366: The suggestion that PLD is not a reliable predictor of dispersal distance at the individual level, yet can capture broad average trends in dispersal potential, is interesting. Alvarez-Noriega et al. (2020), in their study "Global biogeography of marine dispersal potential," used PLD multiplied by average flow velocity to estimate mean dispersal distance and quantified the overall latitudinal gradient in larval dispersal distance. You could discuss this study to further contextualize or support your findings.

Response: We thank the reviewer for this helpful suggestion. We have incorporated a discussion of Alvarez-Noriega et al. (2020) into the manuscript. Specifically, we note that Alvarez-Noriega et al. (2020) assumed that larval dispersal distance is proportional to pelagic larval duration and estimated global latitudinal patterns in dispersal distance by multiplying PLD by local mean

ocean current velocity. Our results provide additional context for this assumption by showing that, although PLD is a weak predictor of dispersal distance at the individual level, it remains useful for capturing broad-scale average trends in dispersal potential. This distinction helps reconcile the widespread use of PLD-based estimates in large-scale biogeographic studies with the substantial variability in dispersal outcomes observed among individual larvae. We have revised the Section 4.2 as below:

Previous studies have reported conflicting results on using PLD as a proxy for dispersal distance. Our results help reconcile these findings by showing that PLD can capture broad-scale average patterns of dispersal potential, but is a poor predictor of realized dispersal distance at the individual level. Shanks et al. (2003) and Shanks (2009) compiled independent, direct estimates of dispersal distance and compared them to propagule duration (a broader term encompassing PLD). Both studies found that, at a coarse scale, propagule duration was moderately correlated ($R^2=0.6$) with dispersal distance. Selkoe and Toonen (2011) further demonstrated a consistent, moderate fit between genetic proxies of dispersal (using either isolation-by-distance slope or global Wright's fixation index F_{ST}) and PLD. Similarly, Alvarez-Noriega et al. (2020) assumed that larval dispersal distance is proportional to PLD and thus computed the global latitudinal gradient in dispersal distance by multiplying PLD by local mean ocean current velocity. In contrast, D'aloia et al. (2015) observed that individual PLDs were not correlated with dispersal distance based on genetic parentage analysis. More recently, Shi et al. (2024) reported a very strong linear correlation ($R^2=0.98$) between PLD and travel distance (distance along transport trajectories), while only a moderate correlation ($R^2=0.85$) between PLD and linear distance.

In this study, mean orthodromic distance from release location center to settlement center (d_m) increased with increasing PLD (Fig. 7), indicating that PLD captures average dispersal trends. However, the correlation between individual dispersal distance and PLD was weak (Pearson correlation = 0.243, Spearman correlation = 0.237; Fig. S2). These suggest that, PLD captures broad, average trends in dispersal potential, but it is not a reliable predictor of dispersal distance at the individual level. Longer PLD does not necessarily lead to a longer dispersal distance for individual larvae because larval trajectories are strongly influenced by topographic constraints on flow, and oscillatory flows, such as tides and seiches.

13. L402: as stated above, you can change the descriptions here, for example, we suggest that they may be connected through Changjiang spawning ground.

Response: We have revised the whole section 4.4.

Reviewer #2

This study employs a Lagrangian particle tracking model to simulate larval dispersal processes and uses a suite of statistical approaches to characterize dispersal patterns. Clarifying larval dispersal pathways in this manuscript is undoubtedly valuable for understanding recruitment dynamics and informing fisheries management. Nevertheless, several methodological limitations should be acknowledged. Moreover, the overall analyses and conclusions could be substantially strengthened through more rigorous treatment and deeper conceptual integration.

Response: We sincerely thank the reviewer for reading and commenting on this manuscript. We have carefully considered all comments and addressed them point by point in the revised manuscript.

1. The hydrodynamic model used here has been validated against observed current velocity at selected stations in the previous publication. Given that this study relies heavily on particle transport pathways, it would be highly desirable to compare modeled trajectories with surface drifter observations. Such a validation would greatly enhance the credibility and robustness of the particle tracking simulations.

Response: We thank the reviewer for this valuable comment. The hydrodynamic model and particle-tracking framework used in this study were adopted from our previous publications (Xing et al., 2020; Xing et al., 2021), in which the hydrodynamic model was extensively validated against observed current velocities at multiple stations.

We agree that direct comparison between simulated particle trajectories and surface drifter observations would provide a valuable evaluation of the particle-tracking simulations. Although satellite-tracked drifters have documented broad transport pathways in parts of the region (Moon et al., 2010), these observations were not released from the same spawning grounds, months, or years as the larval simulations and therefore do not provide a direct trajectory-by-trajectory validation dataset for the present particle-tracking experiments. As a result, validation of the particle-tracking results against drifter trajectories is currently not feasible.

We acknowledge this limitation and note that many larval dispersal studies similarly rely on validation of the underlying hydrodynamic model (Siegel et al., 2008; Hinrichsen et al., 2016; Hinrichsen et al., 2012; Huret et al., 2010; Johns et al., 2020; Lett et al., 2010), owing to the scarcity of suitable drifter observations. Because particle trajectories are directly driven by the

modeled flow field, the demonstrated skill of the hydrodynamic model provides confidence in the reliability of the simulated transport pathways for passive particles. Nevertheless, future comparisons with drifter observations, when available, would further strengthen the evaluation of particle-tracking performance.

2. A point of ambiguity concerns the origin of the particle tracking data: were the larval trajectories directly adopted from Xing et al. (2020; 2021), or did the authors perform their own tracking using the hydrodynamic fields from those studies? This should be clarified in the Methods. Additionally, the hydrodynamic model in Xing et al. (2020) covers 1992–2018, whereas the manuscript states 1987–2018; this discrepancy needs to be addressed. The rationale for splitting the study period into 1987–2004 and 2016 also requires explanation.

Response: We thank the reviewer for this suggestion. We clarify that the larval trajectories used in this study were directly adopted from the particle-tracking simulations reported in Xing et al. (2020, 2021); we did not perform new particle-tracking simulations using the hydrodynamic fields. In those studies, passive particles representing larvae were released throughout the Yellow Sea in 2016 (Xing et al., 2020) and during 1987–2004 (Xing et al., 2021). In the present study, we extracted and analyzed only the trajectories of particles released from the larval release locations defined here. We have corrected the description of the model periods to avoid implying that a single hydrodynamic simulation covered all years from 1987–2018. The trajectories analyzed here come from Xing et al. (2021) for 1987–2004 and Xing et al. (2020) for 2016. We have revised Section 2.2 accordingly. We have clarified this in the Section 2.2 as below:

Lagrangian particle tracking simulation outputs from Xing et al. (2020) and Xing et al. (2021), which investigated larval retention of Japanese anchovy in 2016 and during 1987–2004, respectively, were applied in this study. In those simulations, passive particles representing larvae were released in surface waters throughout the Yellow Sea (YS). From these datasets, we extracted and analyzed the trajectories of particles released from the larval release locations defined in the present study. The hydrodynamic model and Lagrangian particle tracking model were described as follows.

The particle trajectories analyzed here were taken from Xing et al. (2021) for 1987–2004 and Xing et al. (2020) for 2016. Details of the corresponding hydrodynamic-model configurations and validation are provided in those studies. Briefly, the Finite Volume Coastal Ocean Model (FVCOM) was used to simulate the hydrodynamic fields for larval dispersal. This model has been successfully applied to study larval retention of Japanese anchovy in the Yellow Sea (Xing et al., 2020; Xing et al., 2021). The model configuration features a horizontal resolution of 6.5 km (41 sigma layers vertically), with a mesh of 44,682

nodes and 86,107 grids. The time step was 40 s and hourly current data from the published simulations were used to drive the particle tracking model. Over 4 months in 2012 and 2013 the model reproduced subtidal current velocities with root-mean-square errors of 0.70 to 3.24 cm/s.

3. The spawning grounds, named the initial positions in the model, partially determine dispersal pathways and settlement distributions. However, the spawning grounds are approximated as simple rectangles without considering bathymetric constraints, and their spatial extents are not fully consistent with those in Xing et al. (2020; 2021) or the cited references. A more thorough justification for the chosen spawning grounds geometries is required.

Response: We thank the reviewer for this comment. As noted above, we directly adopted the particle trajectories from Xing et al. (2020, 2021). In those studies, passive particles representing larvae were released throughout the Yellow Sea, whereas in the present study we extracted and analyzed only the trajectories of particles originating from the larval release locations defined here.

The release locations were represented by standardized rectangular areas to ensure comparable release areas and particle numbers among spawning grounds. Had spawning grounds with different spatial extents or irregular geometries been used, differences in release area and particle abundance could have introduced biases into estimates of dispersal rates and connectivity. We acknowledge that larval production likely varies among spawning grounds in nature; however, quantitative information on larval production is not available for the study region. Therefore, to facilitate unbiased comparisons among spawning grounds, we used standardized rectangular release areas rather than actual sampling locations or spawning-ground boundaries. We now emphasize that these standardized release areas should be interpreted as experimental source regions for comparing dispersal potential, not as exact reconstructions of realized egg-production fields.

4. In field surveys, eggs are distributed heterogeneously, yet particles are released uniformly across the spawning areas. The results uncertainty introduced by this simplification should be assessed or at least discussed.

Response: We thank the reviewer for this valuable suggestion. We agree that egg production and distribution are heterogeneous in nature and that releasing particles uniformly across spawning areas and spawning season introduces uncertainty into the simulations. Quantifying this uncertainty is challenging because spatially explicit information on egg abundance and spawning intensity is unavailable for the study region. Therefore, we have acknowledged this limitation in Section 4.6 and note that the simulations represent a simplified approximation of natural conditions rather than a complete replication of field processes.

Second, although egg production and distribution are spatially and temporally heterogeneous in nature, particles were released uniformly in space and time in the present study. This simplification may affect estimates of dispersal rates and connectivity strength among spawning grounds.

5. The manuscript states that larvae are released in the near-surface layer, but the exact release depth is not specified—whether at the uppermost sigma level of FVCOM model or at a fixed depth (e.g., 1 m). Given that horizontal velocity varies vertically, the tracking depth selection can substantially influence transport pathways. Therefore, a clear specification is required.

Response: Particles were released from the uppermost sigma layer of the FVCOM model. We have revised it in the Section 2.2 as below:

All particles were released from the center of the grid; and they were released in the surface layer (the uppermost sigma layer of FVCOM model) as living eggs and larvae for Japanese Anchovy have typically been found near the surface.

6. The key conclusions are largely predictable: spawning grounds dominating the dispersal pattern is unsurprising given the wide spatial separation of grounds and complex coastal circulation; larvae from the Changjiang Estuary can spread into the Japan Sea through the Tsushima Strait, which has been demonstrated by float drifters and tracking models (e.g., Moon et al., 2010, particle tracking for jellyfish). The finding that interannual variability contributes least should be interpreted carefully, as the model's ability to reproduce realistic interannual circulation variability has not been independently validated. Further, interannual variations of spawning grounds and egg numbers are ignored in this study. Analysis of seasonal and interannual variations of dispersal patterns should be accompanied by more specific discussions of the circulation dynamics (also plotting some current figures). Moreover, simulated settlement patterns should be discussed against observational data, to examine whether they are reasonable.

Response: We thank the reviewer for this thoughtful comment. This comment contains four separate concerns; we thus address them point by point as below.

(1) We agree that some aspects of larval dispersal patterns identified in this study are consistent with previous knowledge. For example, the potential transport of larvae from the Changjiang Estuary to the Sea of Japan through the Tsushima Strait have been suggested by previous observational and modeling studies. We have added a statement about this in Section 4.5 as: “This is consistent with trajectories of satellite-tracked surface drifters deployed between the Changjiang River mouth and Jeju Island in summer from 1993-2003, some of which were

transported to Jeju and Korea/Tsushima Strait (Matsuno et al., 2006; Moon et al., 2010).” However, the primary objective of this study was not to demonstrate these transport pathways, but to provide the first quantitative comparison of the relative contributions of spawning ground, release date, and release year to dispersal patterns and connectivity across the major Japanese anchovy spawning grounds in the China Seas.

(2) We have deleted the statement from the Abstract that “The relatively minor contribution of interannual variability compared to spatial factors suggests that management should focus more on persistent spatial structures rather than short-term fluctuations” to avoid overstating the influence of spawning year. We have also removed the Conclusion section, as it largely duplicated information already presented in the Abstract and Discussion. We have added a new Section 3.2.5 to present the interannual variability in the latitude of the settlement center.

3.2.5 Interannual Variability of Dispersal

Spawning year explained the smallest proportion of variance in geographic position, relative position, ellipse metrics, aggregation, and the LR and SR indices (Table 1). Interannual variability in larval dispersal patterns is illustrated in Fig. S2 and further quantified using the latitude of the settlement center (Fig. 8). For most spawning grounds, the settlement center exhibited a slight southward shift over time, as indicated by the negative slopes of the fitted regression lines. However, these trends were weak, as reflected by the low R^2 values. In contrast, a slight northward shift was observed for the CJ spawning ground from the positive slopes of the fitted line.

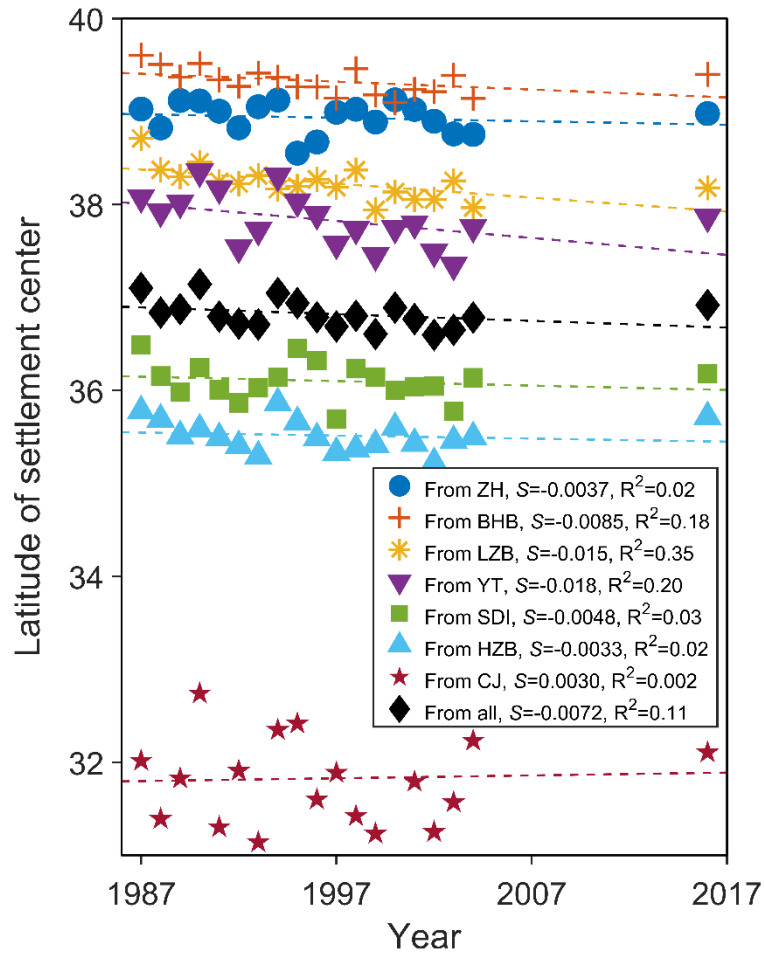


Figure 8. Interannual variability in the latitude of the settlement center of Japanese anchovy (*Engraulis japonicus*) larvae. S represents the slope of the fitted line.

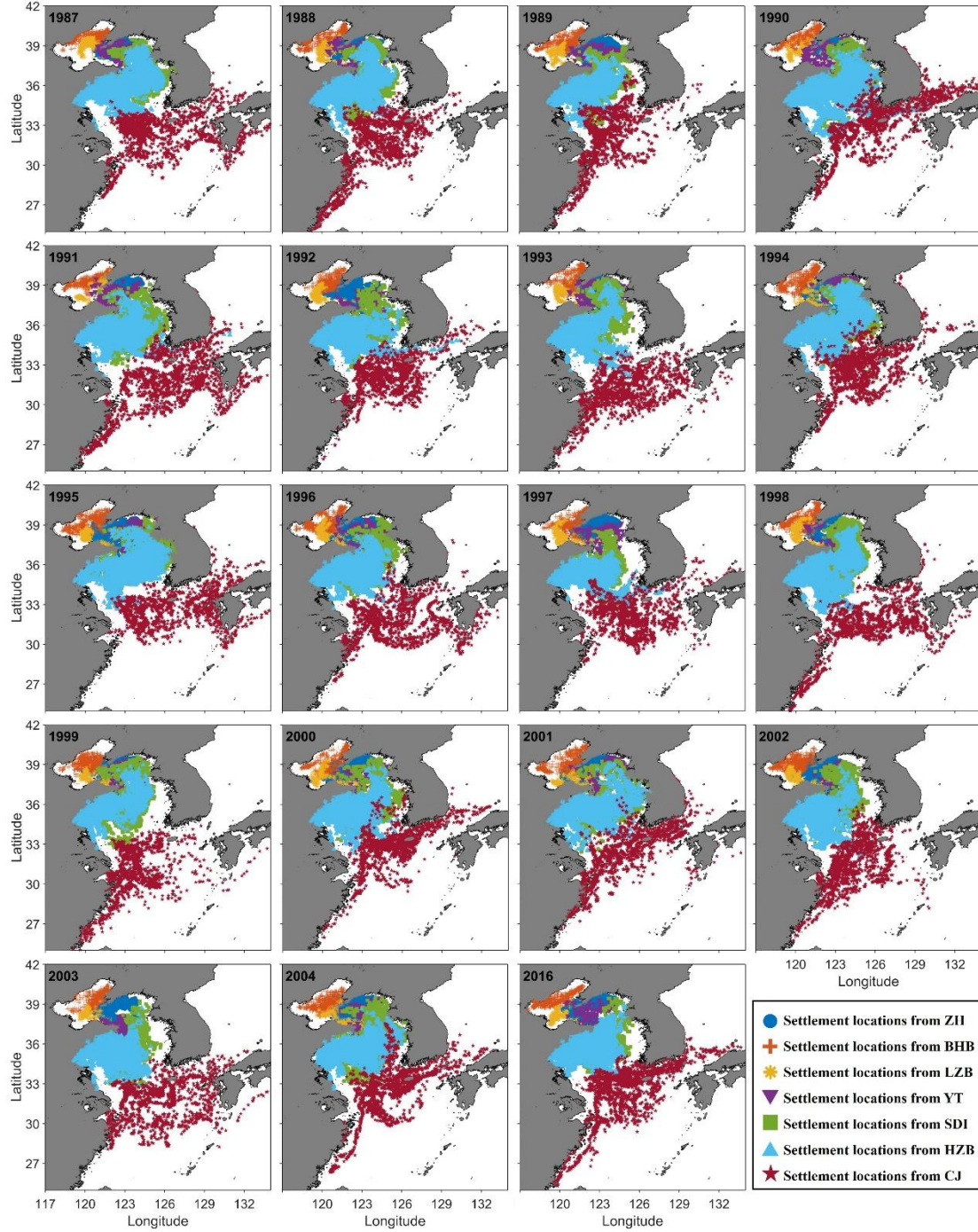


Figure S2. Interannual variability in larval dispersal pattern of Japanese anchovy (*Engraulis japonicus*).

(3) We have expanded the Discussion (Section 4.2) to address the effects of spawning month and spawning year on larval dispersal as below. Because the present study re-analyzes previously published particle-tracking outputs rather than conducting new hydrodynamic simulations, we did not add new current-field diagnostics. Instead, we expanded the Discussion to link the observed seasonal shift in settlement centers to the published monthly surface velocity fields from Xing et al. (2020), as follows:

The settlement center shifted eastward and northward from April to June, but westward and southward after July (Fig. 5, bottom right panel), a pattern that can be explained by seasonal changes in circulation. For example, the monthly mean surface velocity fields from FVCOM around the SDI spawning ground in 2016 showed predominantly eastward and northward transport from May to June, followed by westward and southward transport after July (Fig. B6 in Xing et al., 2020). The apparent southward shift in the settlement center over the period 1987–2004 warrants further investigation, given the weak relationship indicated by the low R^2 values.

(4) We have added a new Section 4.1 to discuss larval settlement patterns against previous observation data:

4.1 Larval Dispersal Patterns of Japanese Anchovy

The modeled larval dispersal patterns in the present study are generally consistent with the observations reported by Wan et al. (2002), partly consistent with those of Wan et al. (2008), and partly inconsistent with the patterns described by Zhang et al. (2025). In Wan et al. (2002), larval abundance decreased along a survey transect extending from approximately 120.6°E, 35.9°N to 125.8°E, 33.0°N, consistent with the density gradient shown in Fig. 2b. Furthermore, along the transect from 123.0°E, 31.0°N to 125.8°E, 33.0°N, larval abundance peaked near the midpoint of the transect (approximately 125.0°E, 32.5°N), corresponding closely to the high-density region simulated in the northern East China Sea (Fig. 2b). Wan et al. (2008) reported the presence of larvae in the vicinity of Haizhou Bay during 2000–2003, which is consistent with the simulated settlement patterns. In contrast, Zhang et al. (2025) found relatively few larvae around Haizhou Bay during 2016–2018, with most individuals occurring in nearshore waters around 34°N, south of Haizhou Bay. This discrepancy may reflect the existence of additional spawning grounds that were not considered in the present study to provide those larvae around 34°N, or the simplifying assumption of passive larval transport. Incorporating active larval behaviors, such as directional swimming or rheotaxis, may alter settlement distributions and help reconcile model predictions with observed patterns. These possibilities are quite interesting and warrant further investigation.

Some specific comments:

7. In Section 3.1 and Figure 2, it should be stated whether the settlement pattern is from a single model case or integration of all experiments.

Response: We have revised the Figure 2 title as:

Figure 2. (a) Larval settlement patterns of Japanese anchovy (*Engraulis japonicus*) for different spawning grounds, integrated across all spawning months, spawning years, and

tracking durations. White areas represent the ocean, grey areas represent land, and each color corresponds to settlement locations originating from a specific spawning ground. (b) Density distribution of all settled larvae, calculated as the number of larvae settled in each cell divided by the total number of larvae.

8. *In Section 2.6, the sentence "The factors included spawning ground, travel duration, spawning year and spawning month" is redundant and should be deleted.*

Response: We have deleted the sentence.

9. *Citations of Xing et al. (2020) and Xing et al. (2021) should be formatted as Xing et al. (2020; 2021).*

Response: We have corrected it.

In the reference list, Chinese author names such as Hao, W., Jian, S., Ruijing, W., Lei, W., and Yi'an, L. appear to have given and family names reversed.

Response: We have corrected it.

Reference

Hinrichsen, H.-H., Kühn, W., Peck, M. A., and Voss, R.: The impact of physical and biological factors on the drift and spatial distribution of larval sprat: A comparison of the Baltic and North Seas, *Progress in Oceanography*, 107, 47-60, 10.1016/j.pocean.2012.05.004, 2012.

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Xing, Q., Yu, H., Ito, S.-i., Ma, S., Yu, H., Wang, H., Tian, Y., Sun, P., Liu, Y., Li, J., and Ye, Z.: Using a larval growth index to detect the environment-recruitment relationships and its linkage with basin-scale climate variability: A case study for Japanese anchovy (*Engraulis japonicus*) in the Yellow Sea, *Ecological Indicators*, 122, 10.1016/j.ecolind.2020.107301, 2021.