



# Characterizing the spatiotemporal variability and interaction in anchovy spawning grounds: A case study in the North Aegean Sea (eastern Mediterranean)

E. Servou,

M. Olmos, M. Huret, P. Petitgas, E. Schismenou, M. Giannoulaki, S. Somarakis

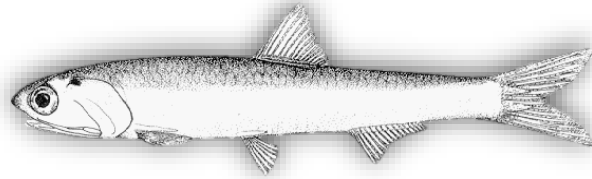
Navigating Changes in Small Pelagic Fish and Forage Communities: Climate, Ecosystems, and Sustainable Fisheries (SPF-2026)

La Paz, Mexico

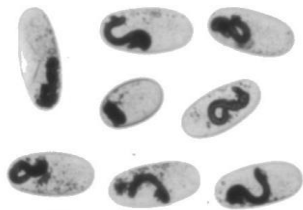
5 May 2026

# Introduction | Target

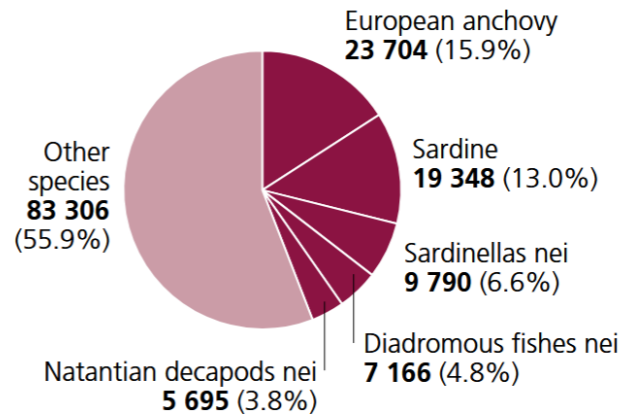
## European anchovy (*Engraulis encrasicolus*)



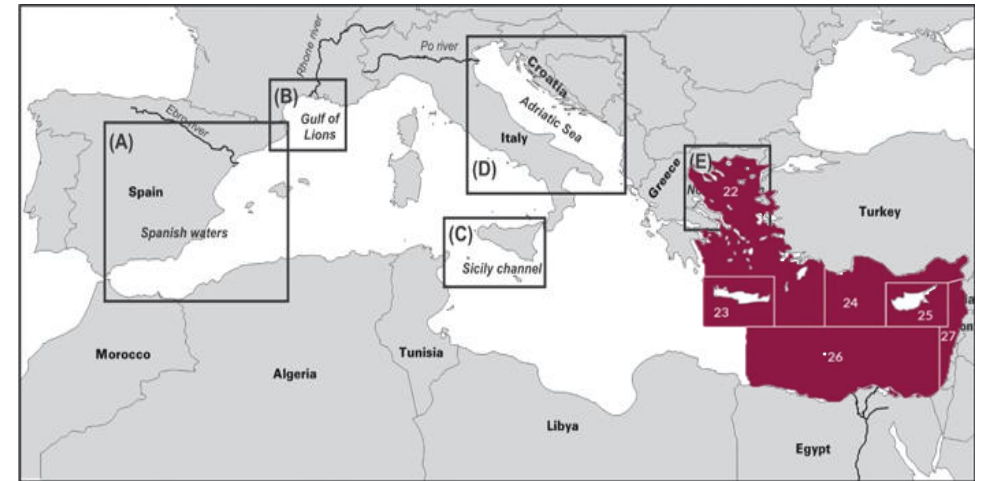
Indeterminate batch spawner that releases pelagic eggs during a protracted reproductive season, peaking in early summer



European anchovy eggs

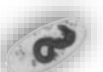


Distributed across the **E. Atlantic**, the **Mediterranean**, and the **Black Seas**

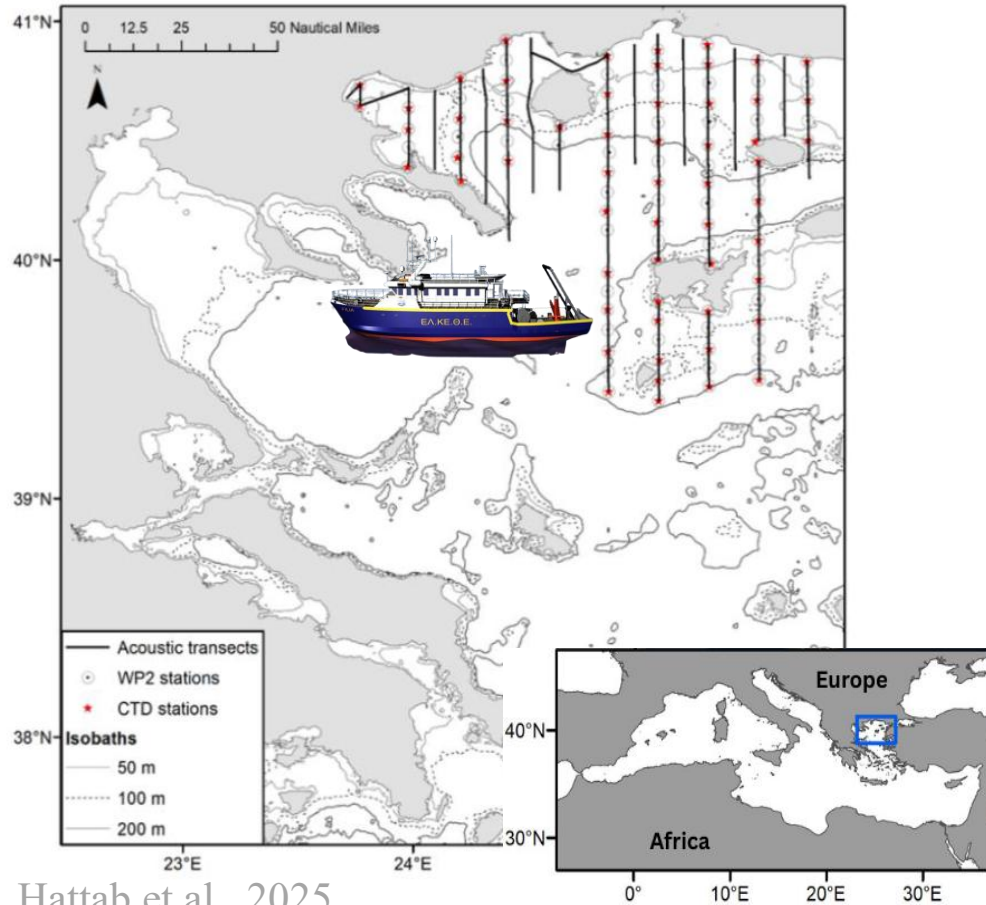


Giannoulaki et al., 2013

It accounts for **16%** of total annual landings in the GFCM **Eastern Mediterranean** subregion (2022–2023)



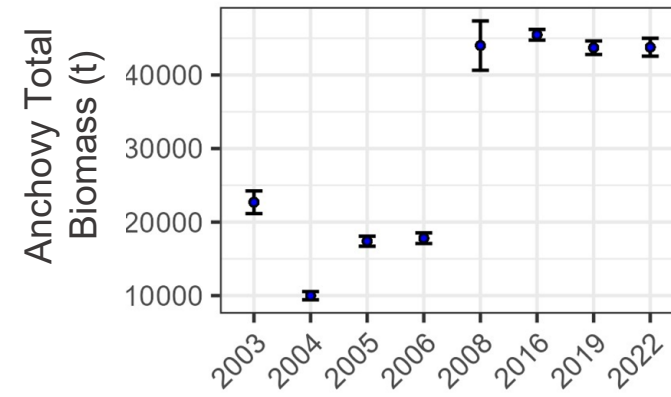
# Introduction | North East Aegean Anchovy



Hattab et al., 2025



## Concurrent Acoustic and Daily Egg Production Method (DEPM) surveys



# Introduction | Modelling spawning habitats

## Previous work

Hydrobiologia (2008) 612:201–214  
DOI 10.1007/s10750-008-9502-1

FISH HABITAT MAPPING

Modeling and predicting **potential** spawning habitat of anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*) based on satellite environmental information

Eudoxia Schismenou · Marianna Giannoulaki ·  
Vasilis D. Valavanis · Stylianos Somarakis

FISHERIES OCEANOGRAPHY

Fish. Oceanogr. 22:2, 69–89, 2013

Characterizing the **potential** habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages

M. GIANNOULAKI ✉, M. IGLESIAS, M. P. TUGORES, A. BONANNO, B. PATTI, A. DE FELICE, I. LEONORI, J. L. BIGOT, V. TIČINA, M. M. PYROUNAKI, K. TSAGARAKIS, A. MACHIAS, S. SOMARAKIS, E. SCHISMENOU, E. QUINCI, G. BASILONE, A. CUTTITTA, F. CAMPANELLA, J. MIQUEL, D. OÑATE, D. ROOS, V. VALAVANIS

Hydrobiologia (2017) 788:17–32  
DOI 10.1007/s10750-016-2983-4



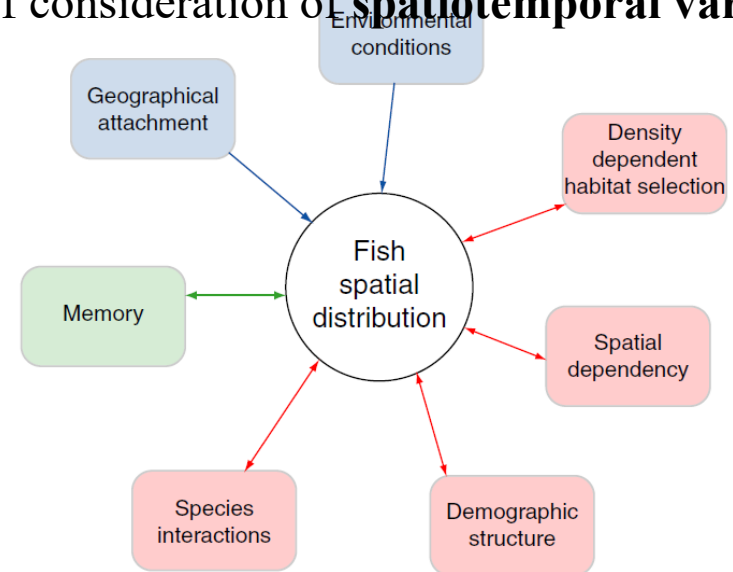
PRIMARY RESEARCH PAPER

Modelling small pelagic fish **potential** spawning habitats: eggs vs spawners and in situ vs satellite data

Eudoxia Schismenou · Stavroula Tsoukali · Marianna Giannoulaki · Stylianos Somarakis

## Gaps

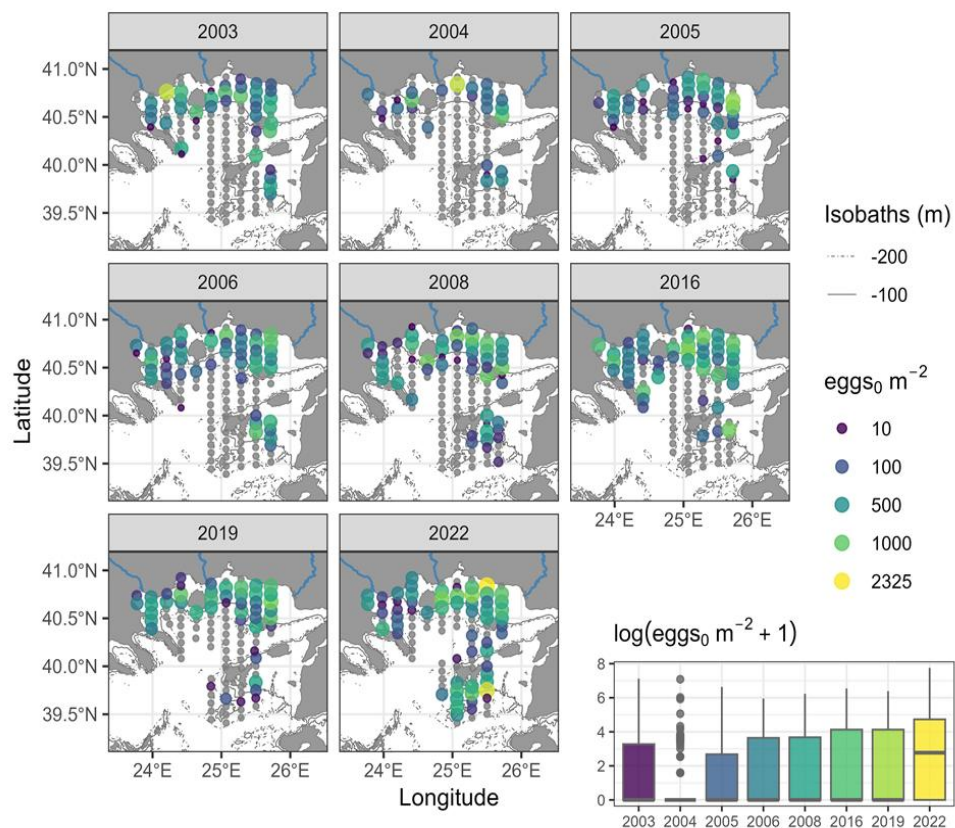
- **Potential spawning habitats:** areas where the environmental conditions are suitable for spawning
- Fish **spatial distributions** are controlled by factors both **extrinsic** and **intrinsic** to the adult population
- Lack of consideration of **spatiotemporal variability**



Planque et al., 2011

# Introduction | Study aims

## Observed egg data



## Questions:

- ✓ Does the **spatial distribution** of egg abundance **vary interannually**?
- ✓ How do **drivers, extrinsic and intrinsic** to the adult population, **contribute** to shaping their **spatiotemporal dynamics**?

Spatiotemporal Generalized Additive Mixed-effect Models (GAMMs)



# Materials & Methods | Covariates selection

## Extrinsic Factors

### Bathymetry

- Depth of the seabed (m) measured at each sampling station.
- Describe variable topography
- Aim to model preference for spawning over the continental shelf

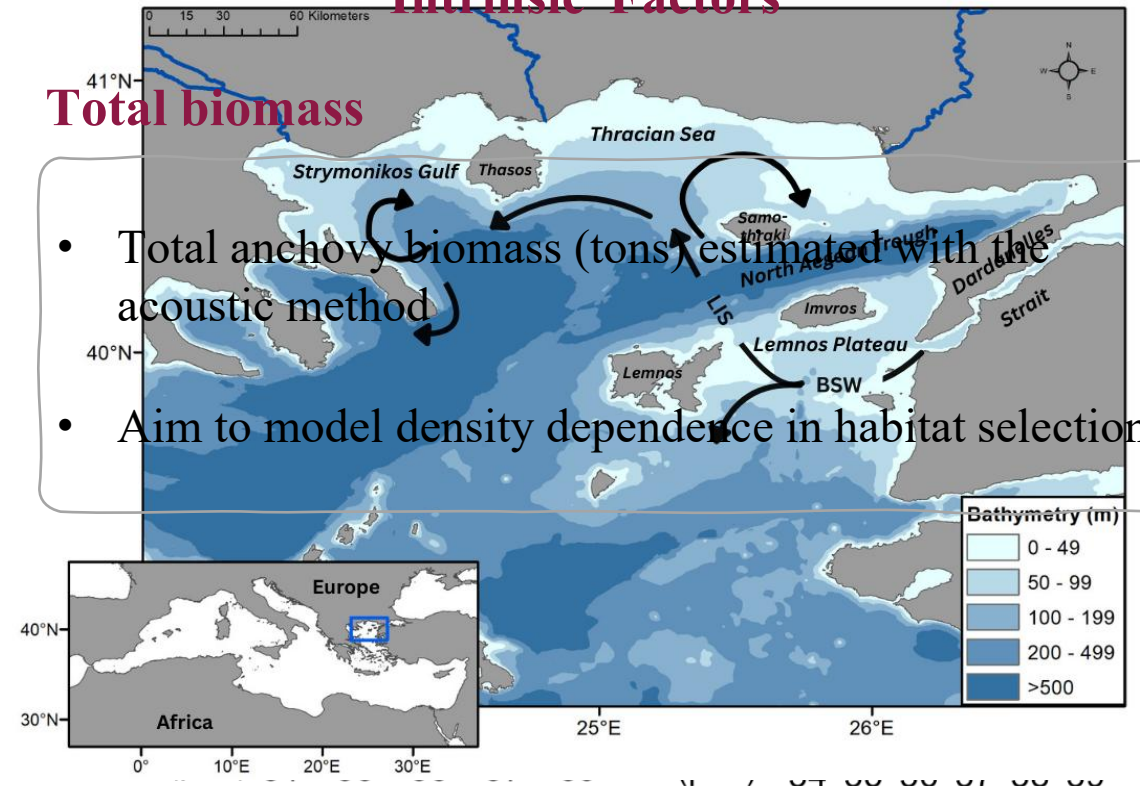
### Sea Surface Salinity

- Average salinity in the upper 2-7 m of the water column measured with CTD
- Describe the main surface circulation pattern
- Aim to model preference for spawning in low-salinity waters

## Intrinsic Factors

### Total biomass

- Total anchovy biomass (tons, estimated with the acoustic method)
- Aim to model density dependence in habitat selection



Step 1

Variance partitioning

$$a_t + \omega_s + \varepsilon_{s,t}$$

Step 2

Sequential covariates inclusion

↓

$$a_t + \omega_s + \varepsilon_{s,t} + s(\text{depth})$$

↓

$$a_t + \omega_s + \varepsilon_{s,t} + s(\text{depth}) + \text{SSS}$$

↓

$$a_t + \omega_s + \varepsilon_{s,t} + s(\text{depth}) + \text{SSS} + \text{TB} + \text{svc}(\text{TB})$$

Step 1

- **Temporal variation**: interannual variation is constant in space
- **Spatial variation**: spatially structured variation constant in time
- **Spatiotemporal variation**: spatially structured variation change in time

$a_t$ : random intercept,  
 $\omega_s$  and  $\varepsilon_{s,t}$ : Gaussian random fields approximated by SPDE



Step 1


Variance partitioning


$$a_t + \omega_s + \varepsilon_{s,t}$$

Step 2

Sequential covariates inclusion


$$a_t + \omega_s + \varepsilon_{s,t} + s(\text{depth})$$


$$a_t + \omega_s + \varepsilon_{s,t} + s(\text{depth}) + \text{SSS}$$


$$a_t + \omega_s + \varepsilon_{s,t} + s(\text{depth}) + \text{SSS} + \text{TB} + \text{svc}(\text{TB})$$

Step 2

- **Covariate-driven variation**
- **Temporal variation** not accounted for by the covariates
- **Spatial variation** not accounted for by the covariates
- **Spatiotemporal variation** not accounted for by the covariates



**Step 1**

## Variance partitioning

$$a_t + \omega_s + \epsilon_{s,t}$$

**Step 2**

## Sequential covariates inclusion



$$a_t + \omega_s + \epsilon_{s,t} + s \text{ (depth)}$$



$$a_t + \omega_s + \epsilon_{s,t} + s \text{ (depth)} + \text{SSS}$$



$$a_t + \omega_s + \epsilon_{s,t} + s \text{ (depth)} + \text{SSS} + \text{TB} + \text{svc(TB)}$$

- Models comparison:
- Standard deviation of  $a_t$ ,  $\omega_s$ , and  $\epsilon_{s,t}$  random effects
  - cAIC
  - Percentages of deviance explained

- Residual checking:
- QQ plots
  - Residual versus predicted values plots
  - Moran's I autocorrelation test

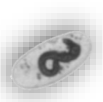


## Results | GAMMs

Model	Covariates	Temporal $\sigma_t$	Spatial $\sigma_\omega$	Spatiotemporal $\sigma_\varepsilon$	Deviance explained (%)	$\Delta\text{cAIC}$
M0	No explanatory covariate	0.67	8.94	7.49	79	92
M1	Bathymetry	0.67	5.72	5.85	81	67
M2	Bathymetry + SSS	0.69	3.94	4.44	83	25
M3	Bathymetry + SSS + TB	-	3.51	4.19	84	0

### M0

- A stable-over-time **spatial variation** pattern dominates egg distributions
- The **spatiotemporal variation** term showed no evidence of directional change with time
- The **temporal variation** contributes the least to the overall variability



# Results | GAMMs

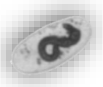
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## M1

- At given depths, the **spatiotemporal variation** term is the dominant source of unexplained variance

## M2

- SSS drives both **spatial** and **spatiotemporal variability**
- None of the included environmental covariates drives the **temporal variability**



## Results | GAMMs

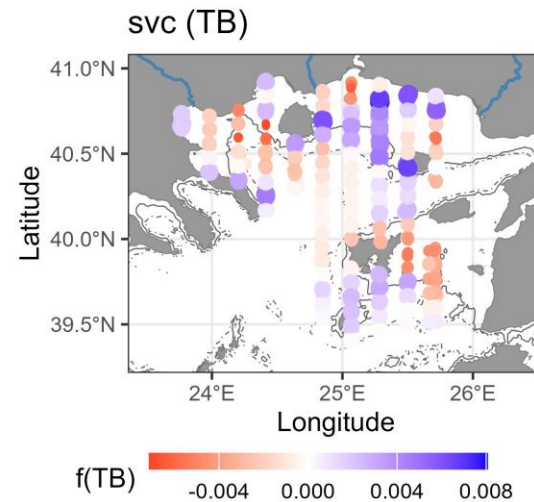
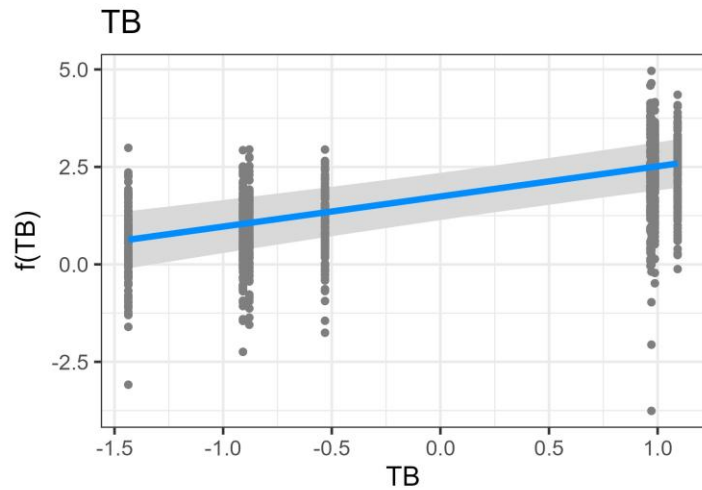
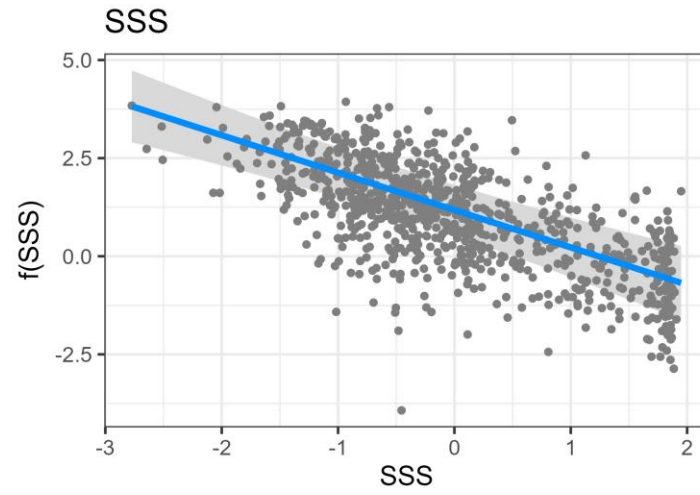
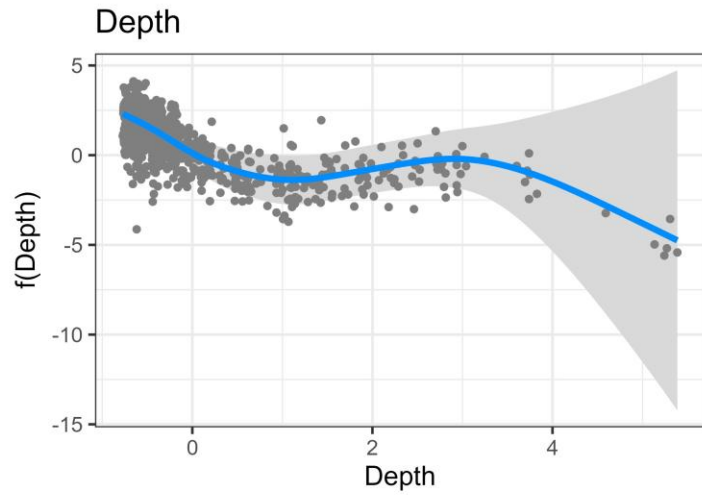
Model	Covariates	Temporal $\sigma_t$	Spatial $\sigma_w$	Spatiotemporal $\sigma_\varepsilon$	Deviance explained (%)	$\Delta cAIC$
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M3	Bathymetry + SSS + TB	-	3.51	4.19	84	0

### M3

- Temporal variation is primarily driven by TB
- TB introduces spatial and spatiotemporal variation in egg abundance distributions



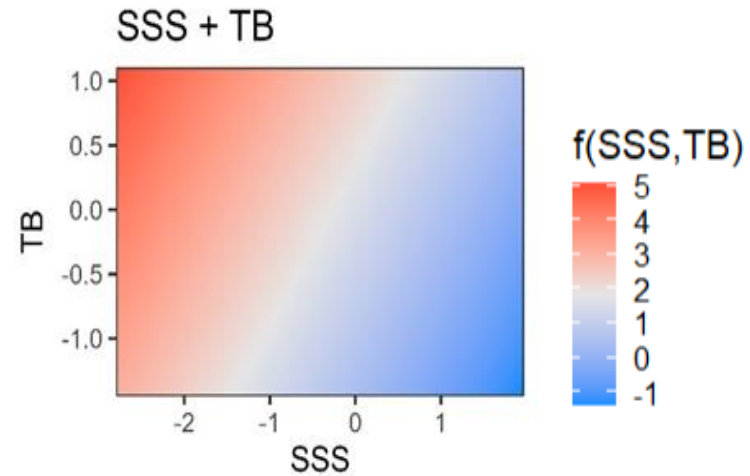
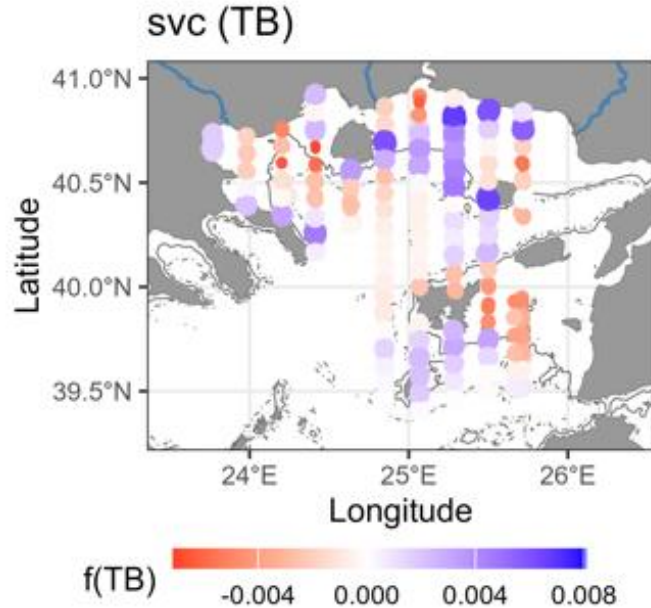
# Results | M3 conditional effects



- Preference for spawning over the continental shelf
- Preference for spawning in low-salinity waters
- Positive relationship with TB that varies locally



# Results | M3 conditional effects

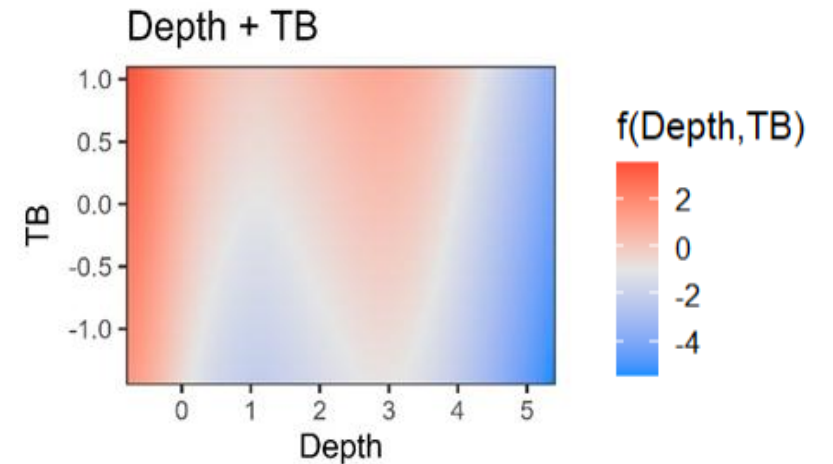


TB increase is followed:

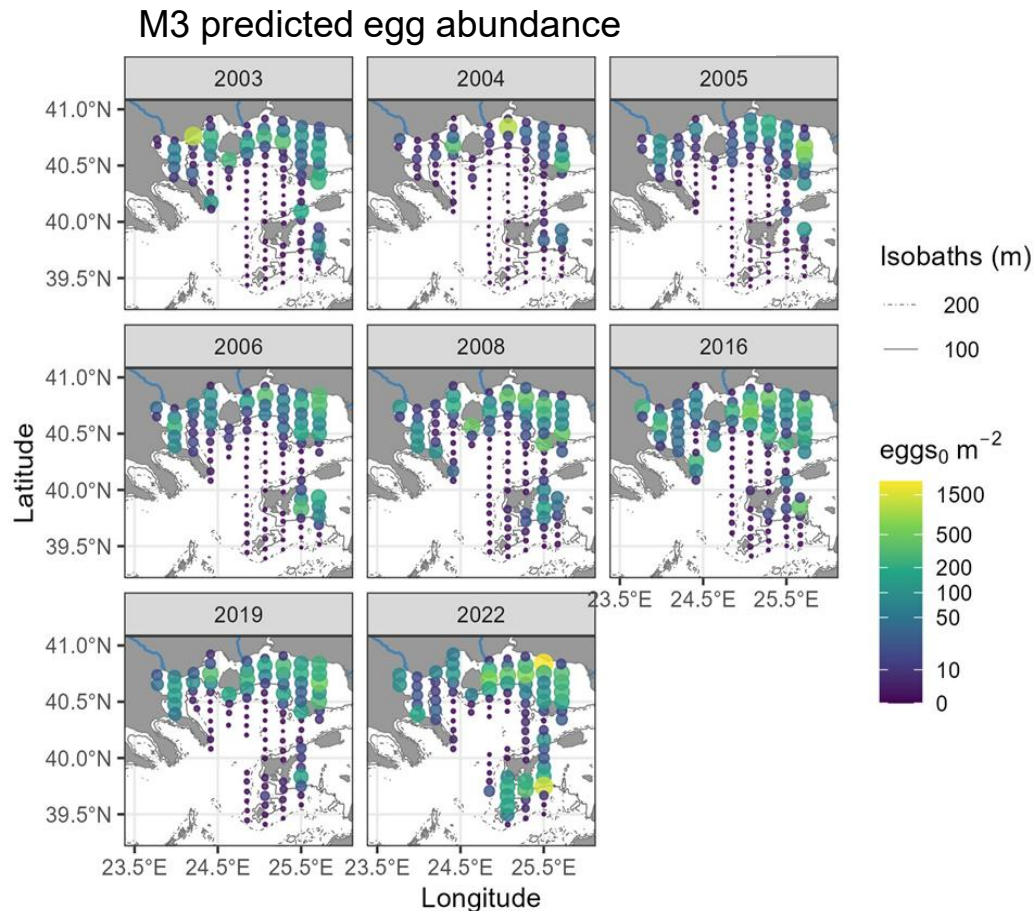
- Positive effect prominent in areas with already favorable conditions
- Positive effect at a broader range of bottom depths and SSS values.



**Basin Model Theory**



# Discussion & Conclusions



- ✓ Anchovy spawning grounds in the North East Aegean Sea are highly spatially persistent across the studied years
- ✓ Bathymetry and Sea Surface Salinity emerged as key drivers of spatial and spatiotemporal variability in egg abundance distributions
- ✓ Population biomass emerged as the primary driver of temporal variability
- ✓ Density-dependent effect on habitat selection was revealed by SVC
- ✓ Additional mechanisms, potentially behavioral, promote spawning in specific locations

# Thank you for your attention!

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