

Responses of anchovy and sardine spawning to physical and biological factors in the Kuroshio and California Current systems: Interspecific and intersystem comparison

**Akinori Takasuka¹, Sam McClatchie², Ed Weber²,
Yoshioki Oozeki¹, Takahiko Kameda¹,
Yuichi Hirota¹, Hiroshi Okamura³**

¹National Research Institute of Fisheries Science, Fisheries Research Agency

²Southwest Fisheries Science Center, NMFS, NOAA

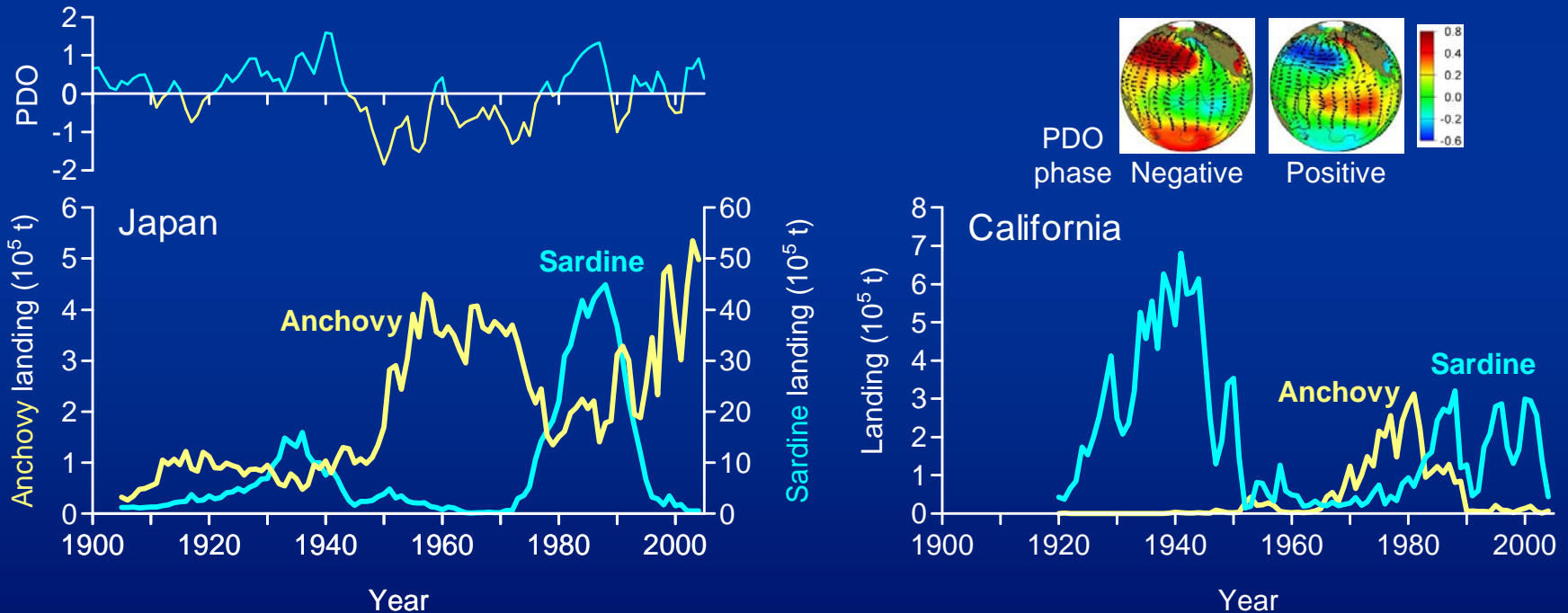
³National Research Institute of Far Seas Fisheries, Fisheries Research Agency

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Species alternations

Climate changes and species alternations

- Anchovy and sardine have exhibited out-of-phase population oscillations in various regions.
- The patterns have been associated with climate changes.
- Yet, the biological processes have been under debate.



Anchovy and sardine alternations off Japan and California in response to Pacific Decadal Oscillation (PDO; Mantua *et al.* 1997).

Various hypotheses

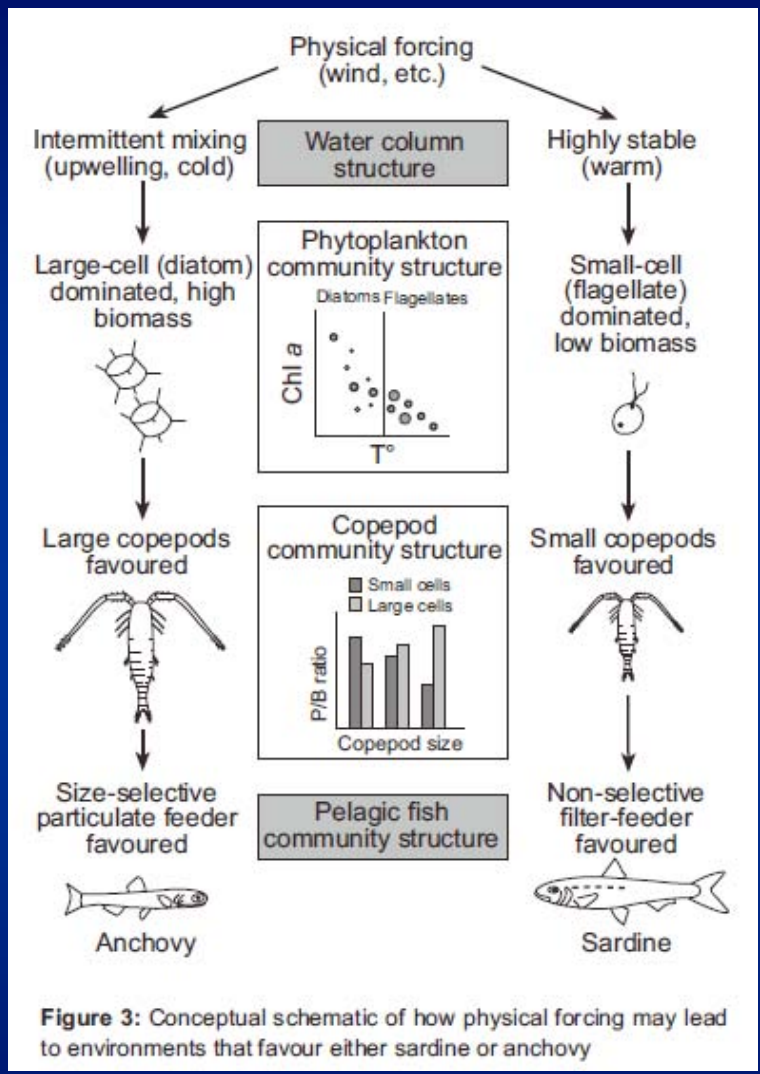
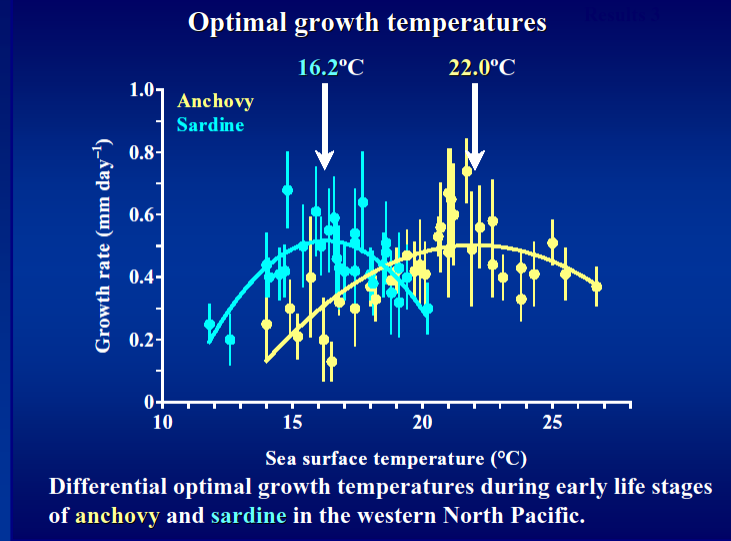
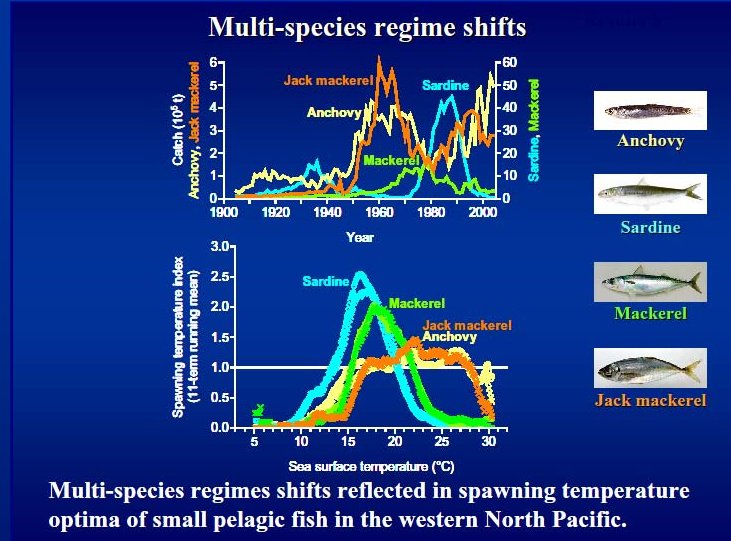


Figure 3: Conceptual schematic of how physical forcing may lead to environments that favour either sardine or anchovy

“Trophic dissimilarity” hypothesis (van der Lingen *et al.* 2006 in *AJMS*, Rykaczewski & Checkley 2008 in *PNAS*)



Differential optimal growth temperatures during early life stages of anchovy and sardine in the western North Pacific.



Multi-species regimes shifts reflected in spawning temperature optima of small pelagic fish in the western North Pacific.

“Optimal growth temperature” hypothesis (Takasuka *et al.* 2007 in *CJFAS*, 2008 in *MEPS*, 2008 in *PO*)

Backgrounds

What is required to test relevant hypotheses

- Different hypotheses based on different factors should be tested in the same framework in the future.
- Responses of vital parameters (e.g. reproduction and early growth) to multiple environmental factors should be examined for the respective species.

Basic question

- How do vital parameters respond to environmental factors?

Previous studies

- Many studies tended to target single species.
- Spatial and temporal scales vary depending on studies, leading to variations in surface relationships of fish biology to environments.
- Methods were often different.

Objectives

Key points

1. Extracting species-specific patterns
2. Interspecific and intersystem comparison
3. A uniform approach within the same study framework

In the present study, ...

- Responses of **anchovy** and **sardine** spawning to physical and biological factors in the Kuroshio and California Current systems
 - I. Extracting the most representative patterns from long-term data sets of egg surveys.
 - II. Interspecific comparison between **anchovy** and **sardine** within the system.
 - III. Intersystem comparison between the Kuroshio and California Current systems.

Kuroshio
Current system
(western boundary)

Japanese anchovy
E. japonicus

Japanese sardine
S. melanostictus

Japan data set
(vertical tows)

California
Current system
(eastern boundary)

Northern anchovy
E. mordax

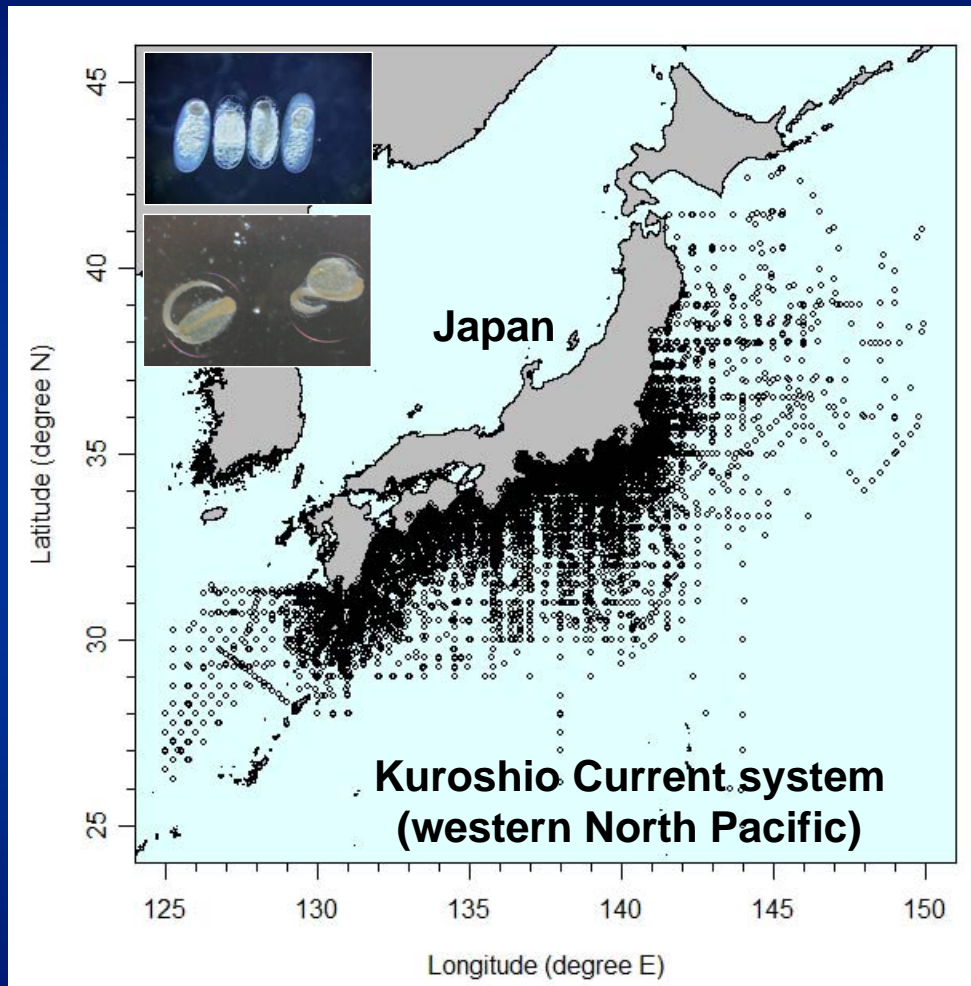
California sardine
S. sagax

CalCOFI data set
(oblique tows)

Focusing on the relationships between
anchovy and **sardine** in comparison

Data set

Long-term data set of monthly egg surveys (Japan data)



- Off the Pacific coast of Japan
- Last 30 years (1978–2007)
- Vertical tows of NORPAC net
- 114,130 samples



Sampling stations in the monthly egg surveys off the Pacific coast of Japan from 1978 to 2007.

Data set

Long-term data set of monthly egg surveys (Japan data)

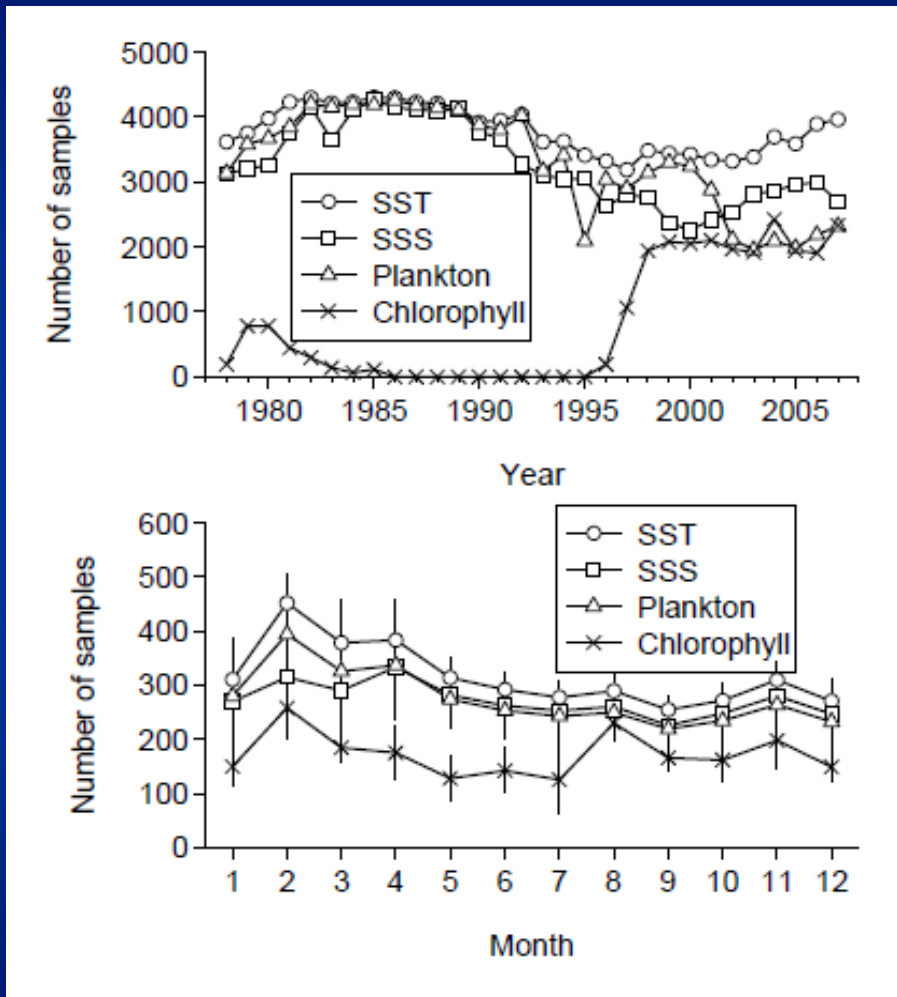
Physical factors

- Sea surface temperature ($^{\circ}\text{C}$; SST)
- Sea surface salinity (SSS)

Biological factors

- Zooplankton deposition volume per unit area (ml m^{-2})
- Chlorophyll-*a* concentration (mg m^{-3}) from SeaWiFS

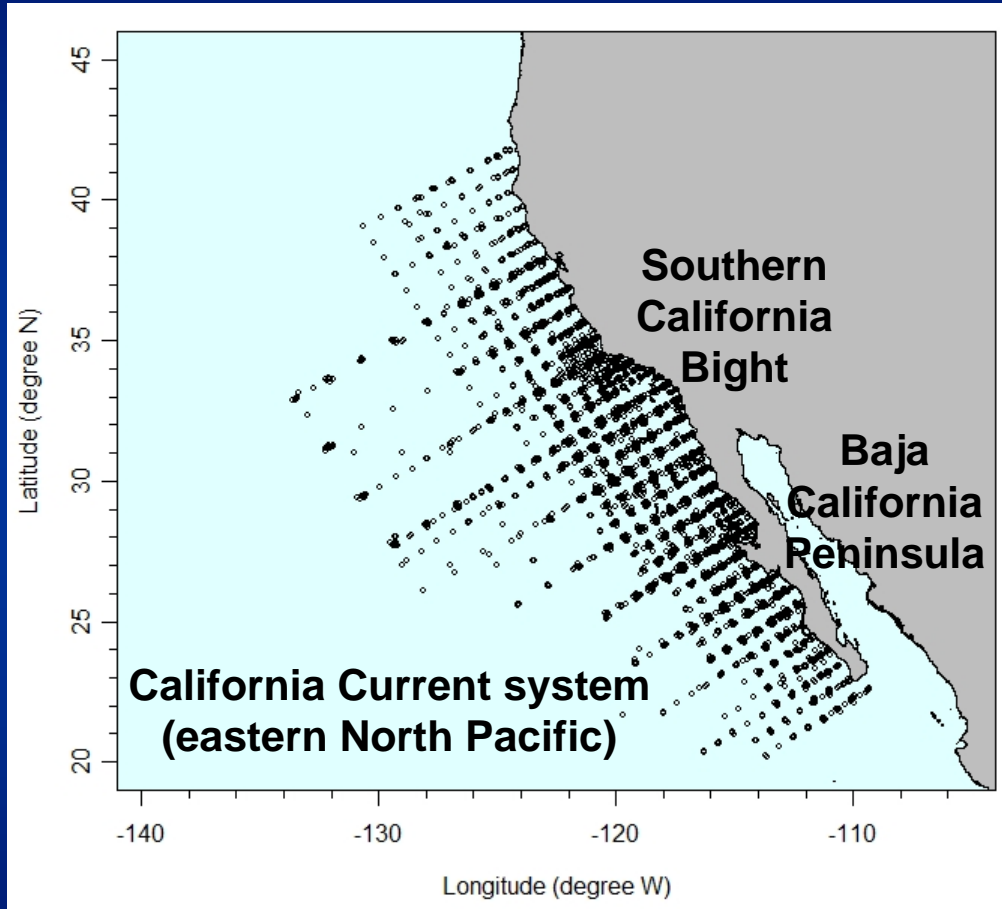
archive



Annual total and monthly mean sample sizes of the monthly egg surveys off the Pacific coast of Japan from 1978 to 2007.

Data set

Long-term data set of CalCOFI surveys (CalCOFI data)

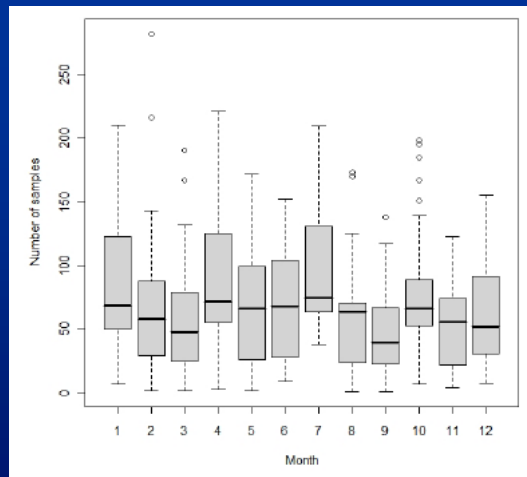
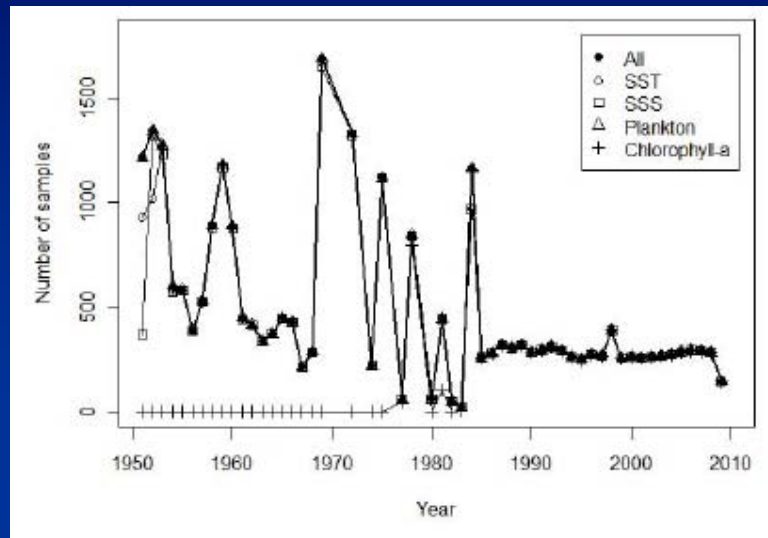


- Off California and Baja California
- Last 51 years (1951–2008)
- Oblique tows of ring or bongo nets
- 25,434 samples

Sampling stations in the CalCOFI surveys off California and Baja California from 1951 to 2008.

Data set

Long-term data set of CalCOFI surveys (CalCOFI data)



Physical factors

- Sea surface temperature ($^{\circ}\text{C}$; SST)
- Sea surface salinity (SSS)

Biological factors

- Zooplankton displacement volume per cubic volume ($\mu\text{g m}^{-3}$)
- Chlorophyll-a concentration (mg m^{-3}) measured at the surface

Annual total and monthly mean sample sizes of the CalCOFI surveys off California and Baja California from 1951 to 2008.

Methods

Spawning responses

- Responses of spawning **occurrence** to environmental factors, assuming that **egg presence** indicates spawning occurrence.

Tool for smoothing

- The effects of environmental factors on probabilities of spawning occurrence were examined by GAMs.

Generalized Additive Models (GAMs)

Flexible nonparametric and additive regression models providing practically smoothed curves (Hastie & Tibshirani 1990, Wood 2006)

- GAMs were fitted to egg presence/absence (1/0) data with multiple environmental variables, using the binomial distribution with a logit link function (software “R” -“mgcv” library) (Maravelias 1999, Fox *et al.* 2000).

Methods

Physical factors

- Sea surface temperature (°C): *SST*
- Sea surface salinity: *SSS*

Biological factors

- Zooplankton volume (ml m⁻² or μg m⁻³): *PL*
- Chlorophyll-a concentration (mg m⁻³): *CH*

GAMs with multiple explanatory variables:

For *SST*, *SSS*, *PL*

$$y = \alpha + s(SST) + s(SSS) + s(\ln(PL))$$

For *CH*

$$y = \alpha + s(SST) + s(SSS) + s(\ln(CH))$$

y: the estimated probability of egg occurrence from 0 to 1

α : an intercept term

“s”: an unique smooth term of thin plate regression spline base

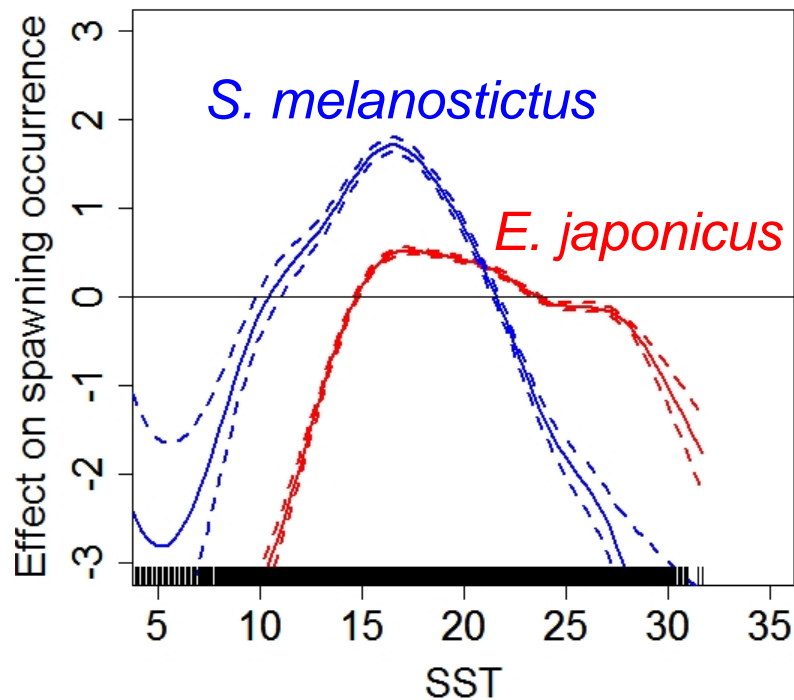
- GAMs were applied to the data subset with all the variables available. Note that *CH* data are very limited.

Spawning responses

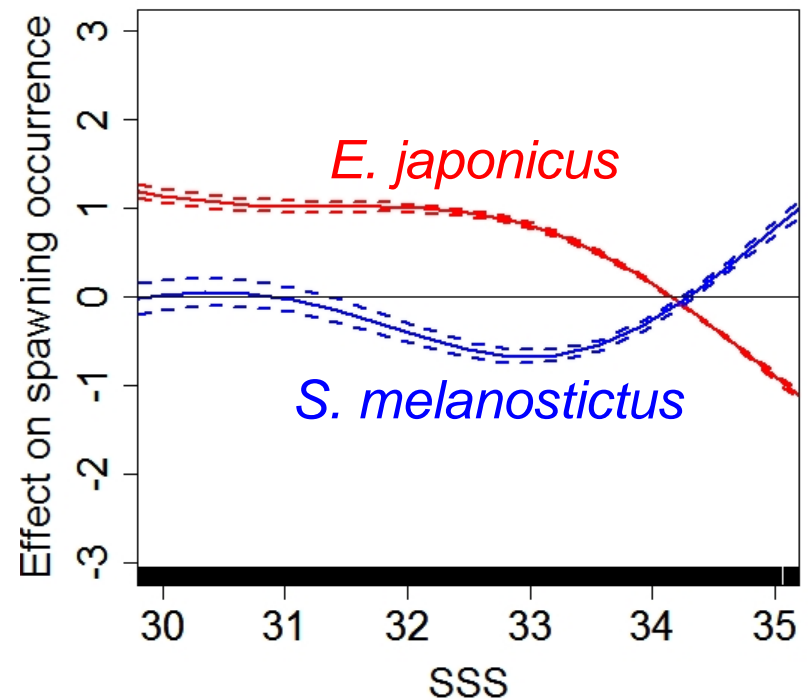
Kuroshio Current system

All areas and seasons included

Sea surface temperature



Sea surface salinity

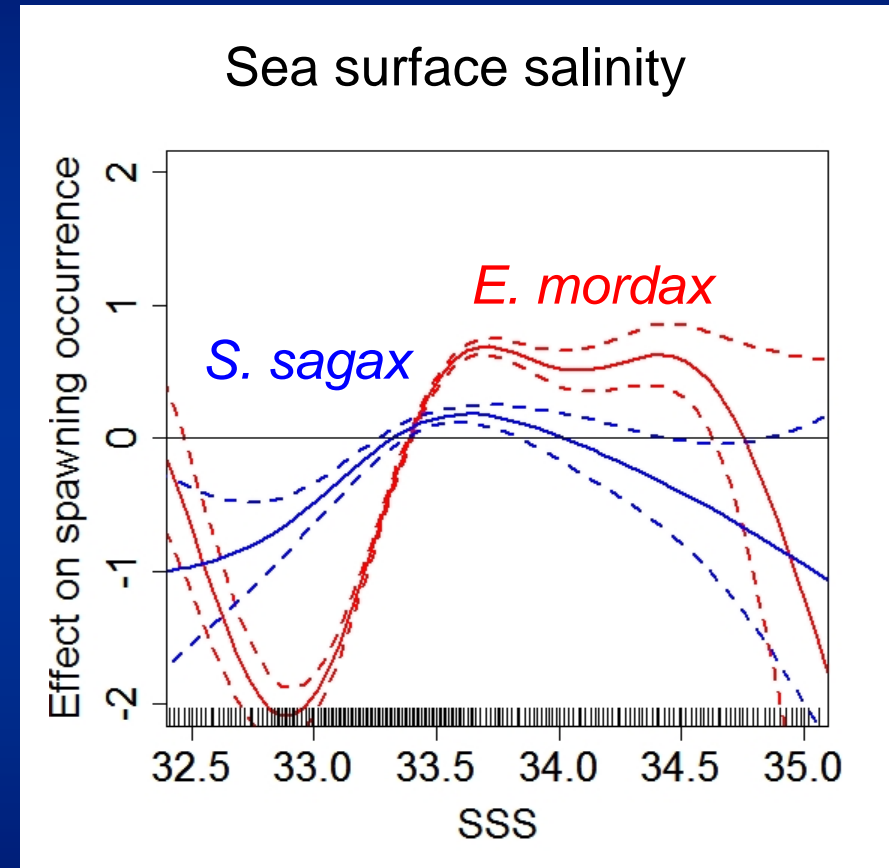
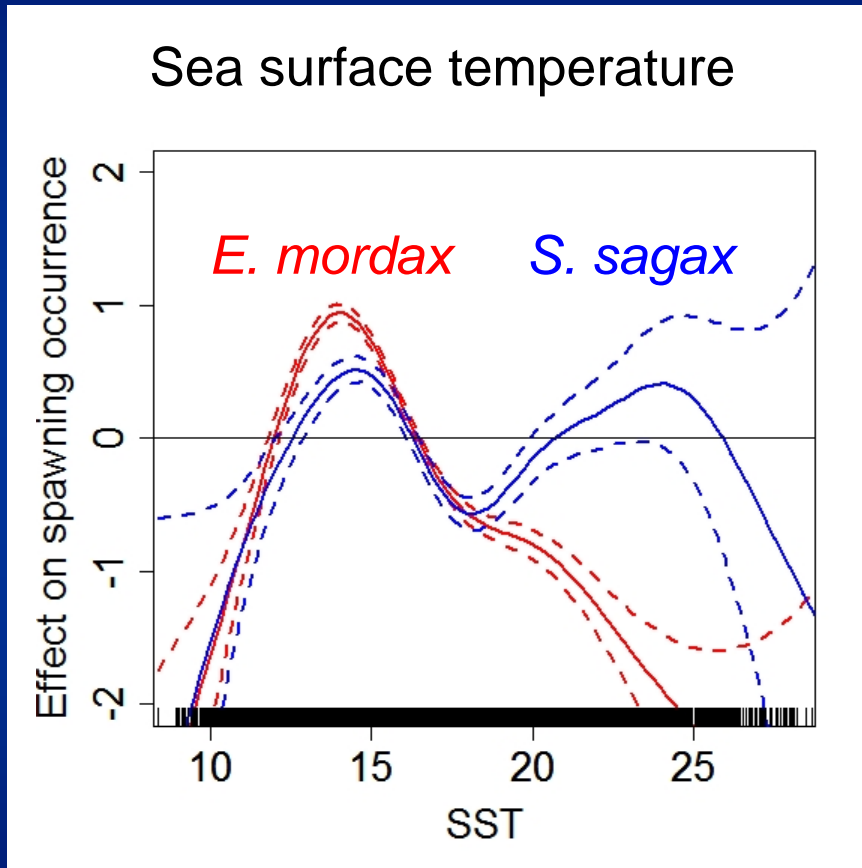


Smoothed effects of environmental factors on spawning probability by the GAMs in the **Kuroshio Current system** (all areas and seasons).

Spawning responses

California Current system

All areas and seasons included

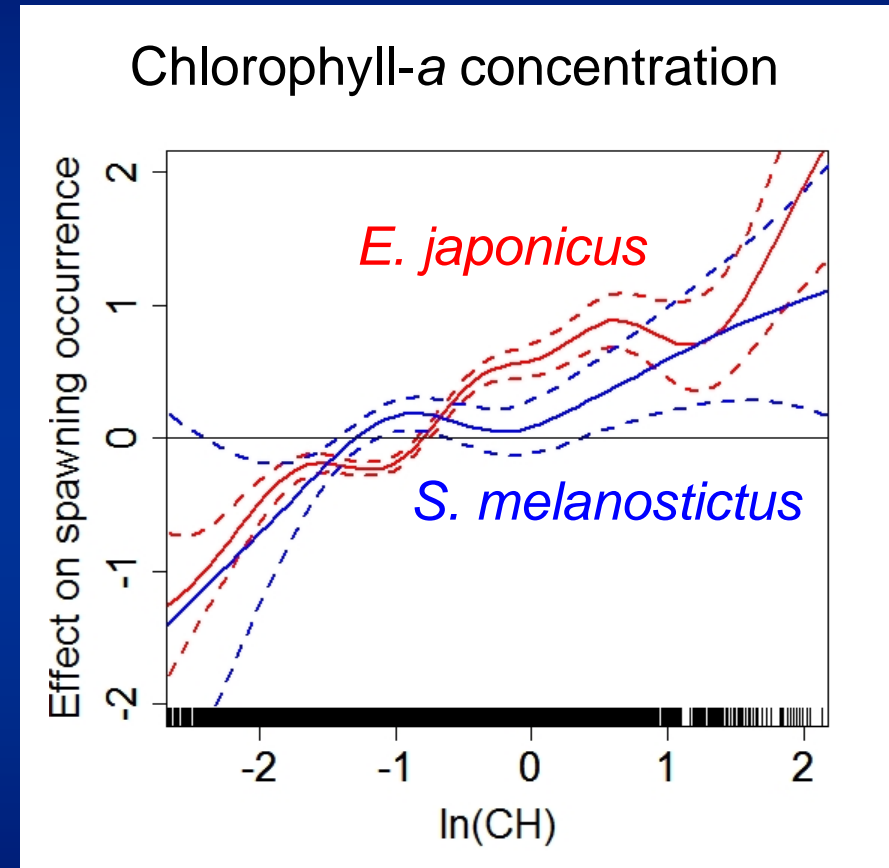
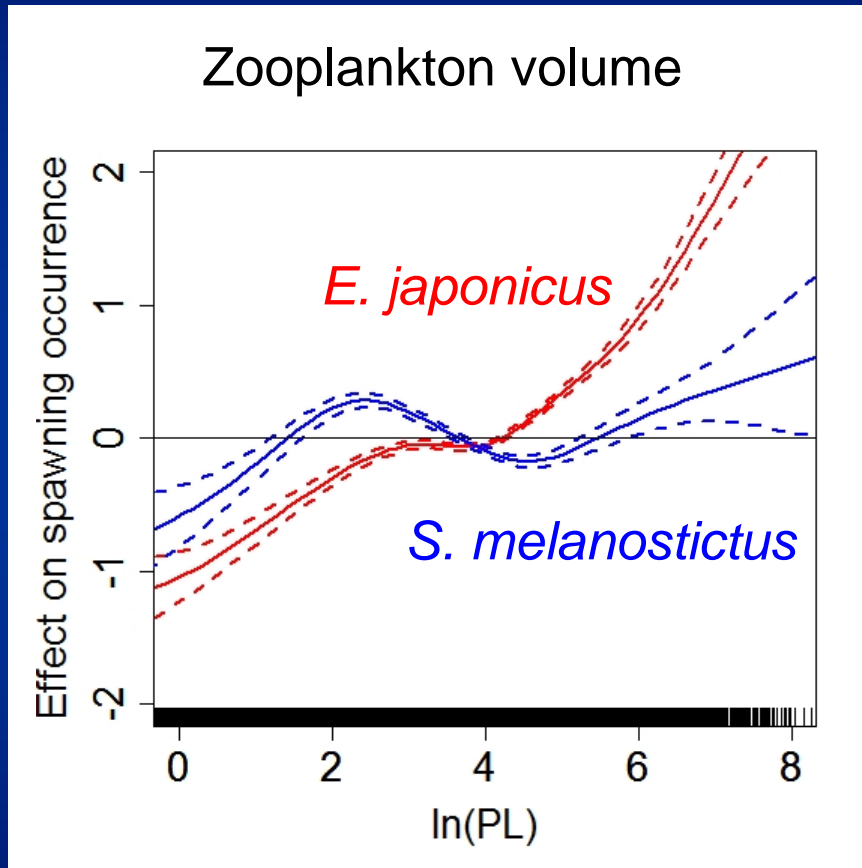


Smoothed effects of environmental factors on spawning probability by the GAMs in the California Current system (all areas and seasons).

Spawning responses

Kuroshio Current system

All areas and seasons included



Smoothed effects of environmental factors on spawning probability by the GAMs in the **Kuroshio Current system** (all areas and seasons).

Income vs capital

Energy allocation strategies for reproduction are viewed as a continuum between reliance on “income” (recently acquired energy) and “capital” (stored energy) for fuelling reproduction.

“Income breeders”

- Expend energy for reproduction soon after that energy is acquired

Typically, ...

- Spawn more with food at the time of spawning
- Keep feeding during spawning periods
- Conditions do not dramatically change before/after spawning

“Capital breeders”

- Gather energy over long periods prior to using the stored reserves for reproduction

Typically, ...

- Spawn irrespective of food at the time of spawning
- Stop feeding during spawning periods
- Conditions dramatically decline before/after spawning

Income vs capital

Anchovy (*E. japonicus*)

Present study

➤ Probability of spawning occurrence monotonically increased with plankton and chlorophyll-*a*.

Experimental studies

- Anchovy fed during spawning periods.
- Conditions recovered when fed during spawning (Tsurura 1987, Tsuruta & Hirose 1989)

Sardine (*S. melanostictus*)

Present study

➤ Probability of spawning occurrence increased with plankton and chlorophyll-*a* up to some extent but not at higher values.

Experimental studies

- Sardine fed during spawning periods.
- Conditions dramatically declined through spawning (Matsubara 1996, Morimoto 1996, Shiraishi *et al.* 1996)

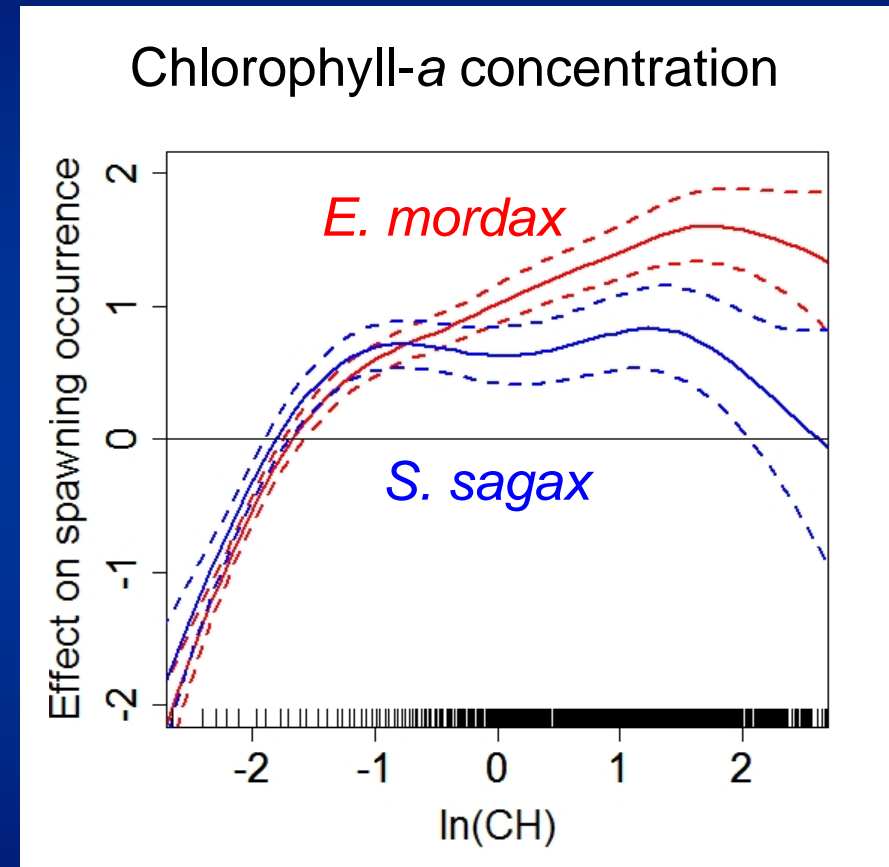
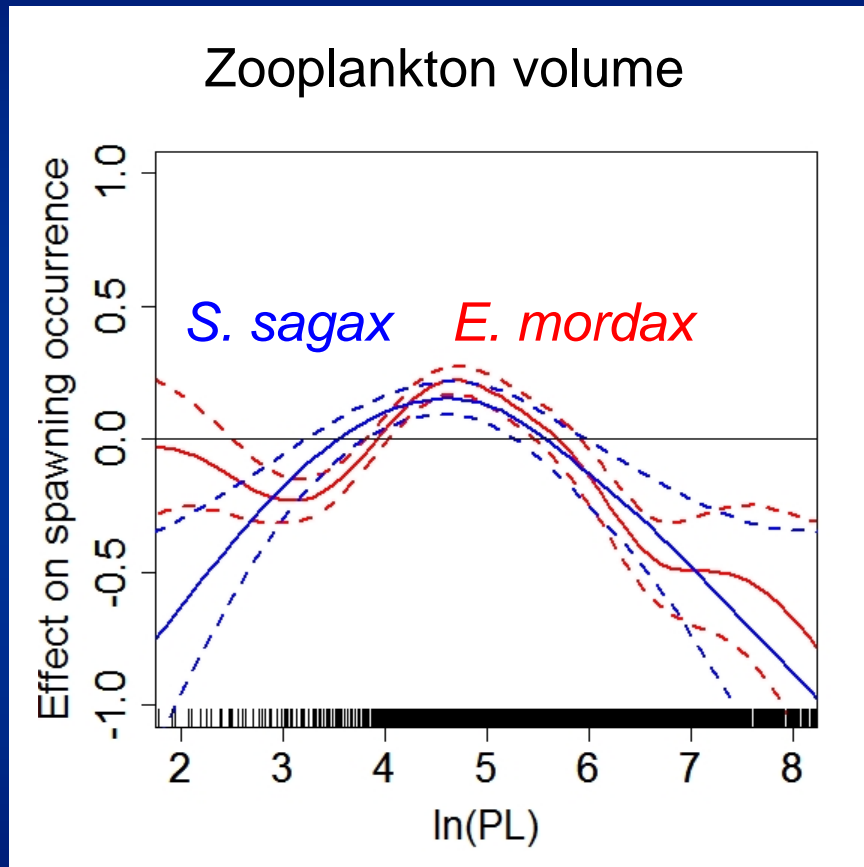
On a continuum between “income” and “capital” breeders



Spawning responses

California Current system

All areas and seasons included



Smoothed effects of environmental factors on spawning probability by the GAMs in the California Current system (all areas and seasons).

Income vs capital

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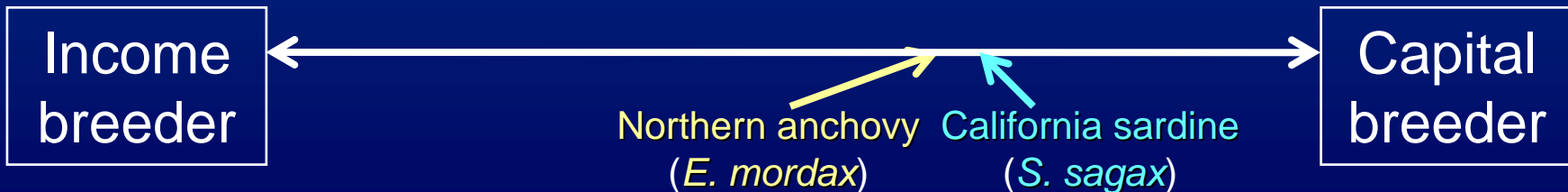
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On a continuum between “income” and “capital” breeders



Summary

Concept: Comparison of species-specific patterns for multiple environmental factors in a uniform approach

I. Interspecific comparison: Kuroshio

- The present study is the first one to link spawning to biological factors at large scales in the Kuroshio system.
- Spawning responses were contrasting between **anchovy** and **sardine** for both physical and biological factors.
- Differential energy allocation strategies for reproduction.

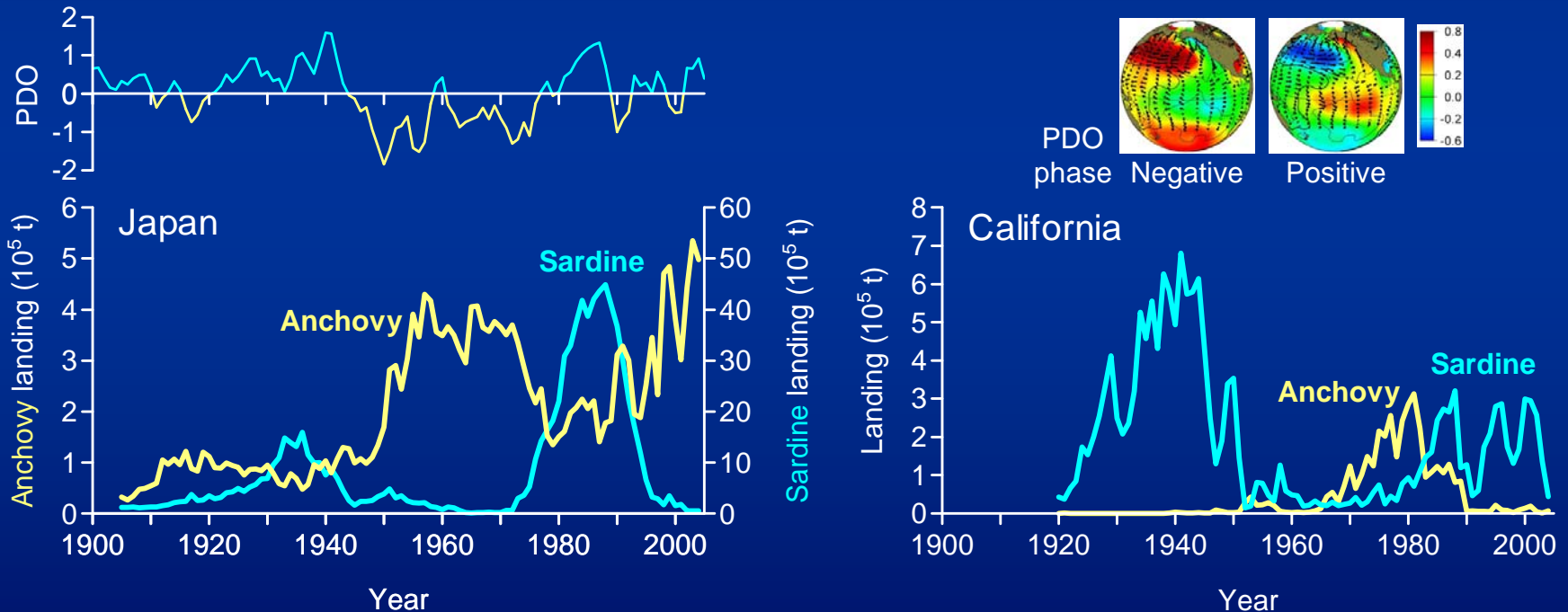
II. Intersystem comparison: Kuroshio vs California

- The patterns were species-specific (not genus-specific).
- The **anchovy**–**sardine** differences were greater in the Kuroshio than in the California Current system.
- The **anchovy**–**sardine** relationships appeared reversed in the responses to physical factors and not reversed, but quite different, in the responses to biological factors.

Species alternations

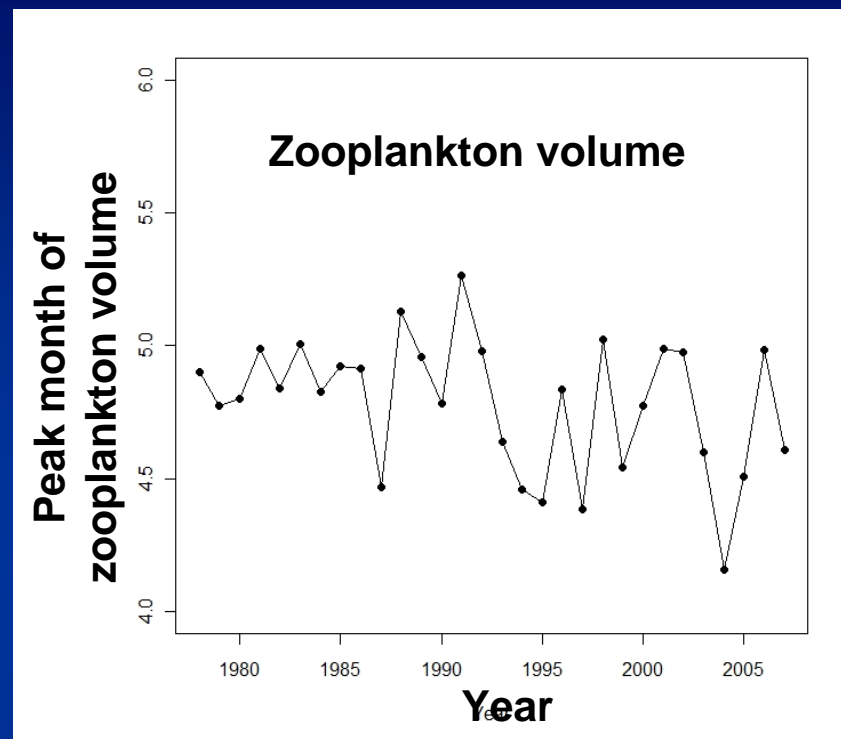
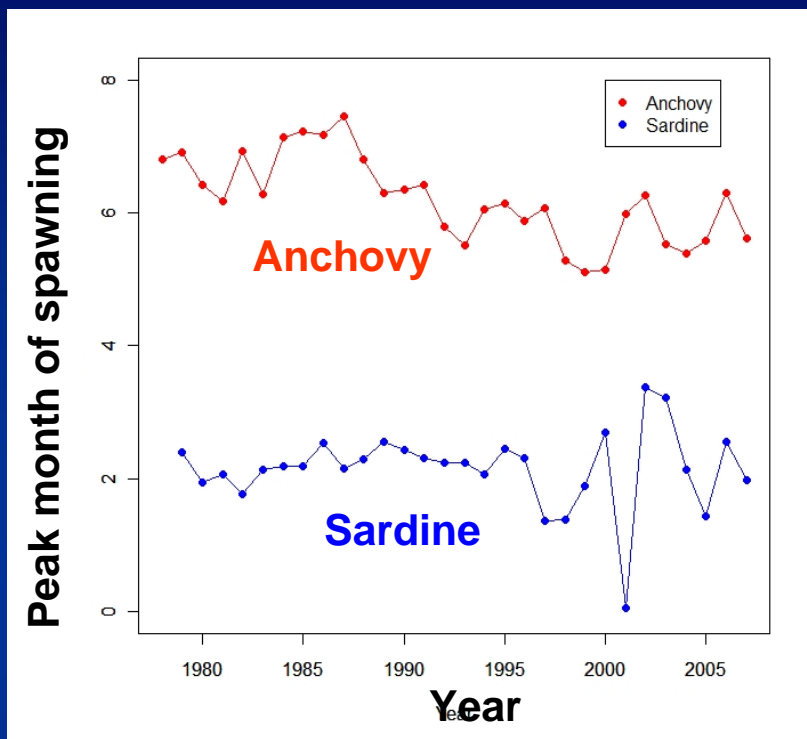
Climate changes and species alternations

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Phenology



Shifts of peak months of anchovy and sardine spawning and zooplankton volume in the Kuroshio Current system

- Anchovy spawning peak and plankton bloom shifted to be earlier, while sardine spawning peak did not so, during the last 30 years, implying potential differences in climate effects on spawning phenology.

Future

- These species-specific biological responses would constitute a key in understanding mechanisms of species alternations through differential climate effects on congeneric species.

Links to other disciplinary fields

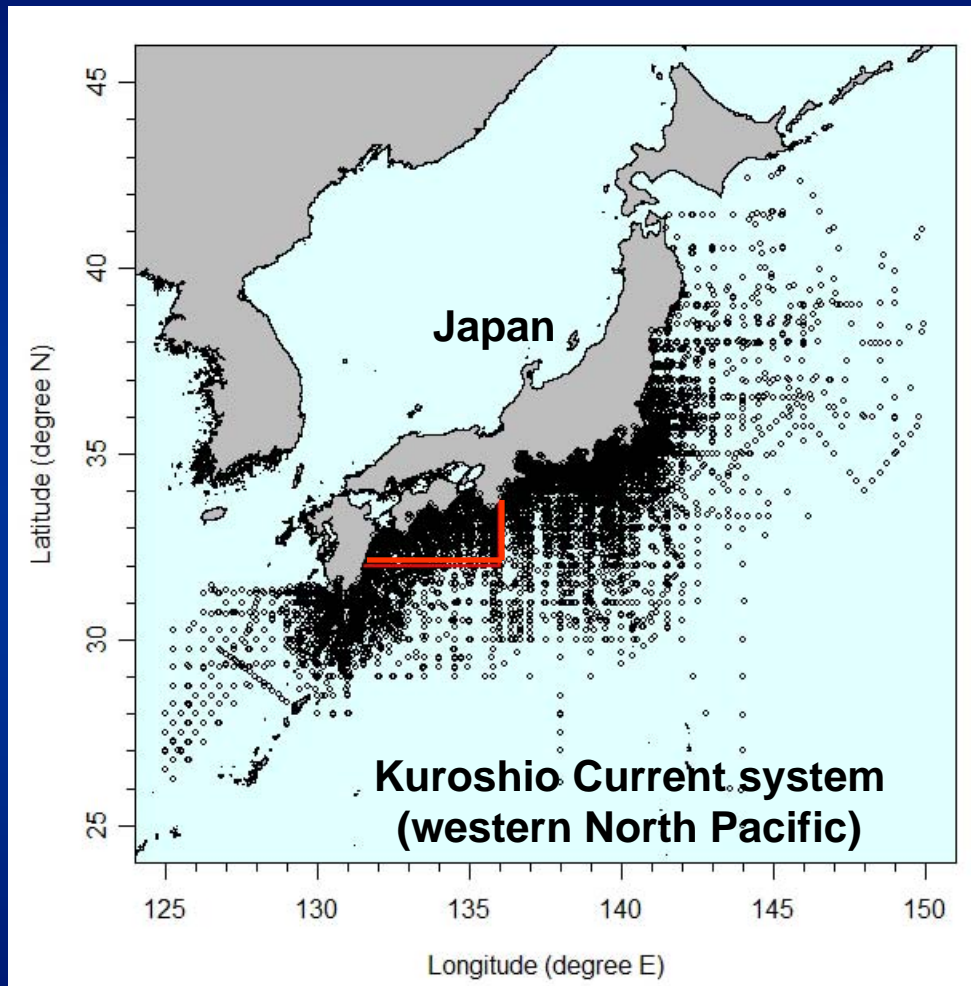
- The biological information will be passed to model studies.
- A suggestion to experimental study designs.

Next study design

- Historical fluctuations of spawning habitats relative to species-specific optimal environments.

Data set

Long-term data set of monthly egg surveys (Japan data)



Spatially and temporally limited:

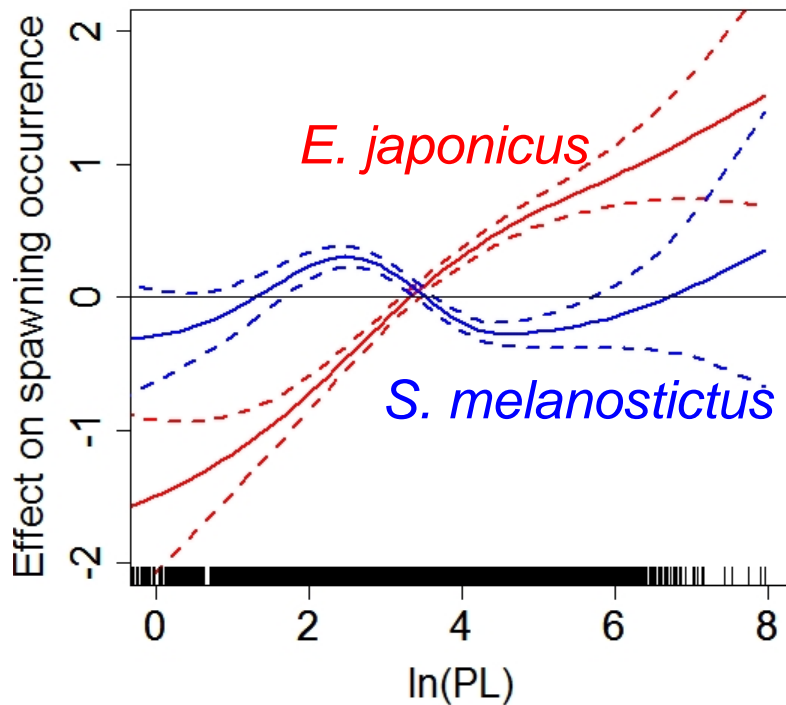
- **Tosa Bay area**
Overlapping spawning area
- **February to April**
Overlapping spawning months

Sampling stations in the monthly egg surveys off the Pacific coast of Japan from 1978 to 2007.

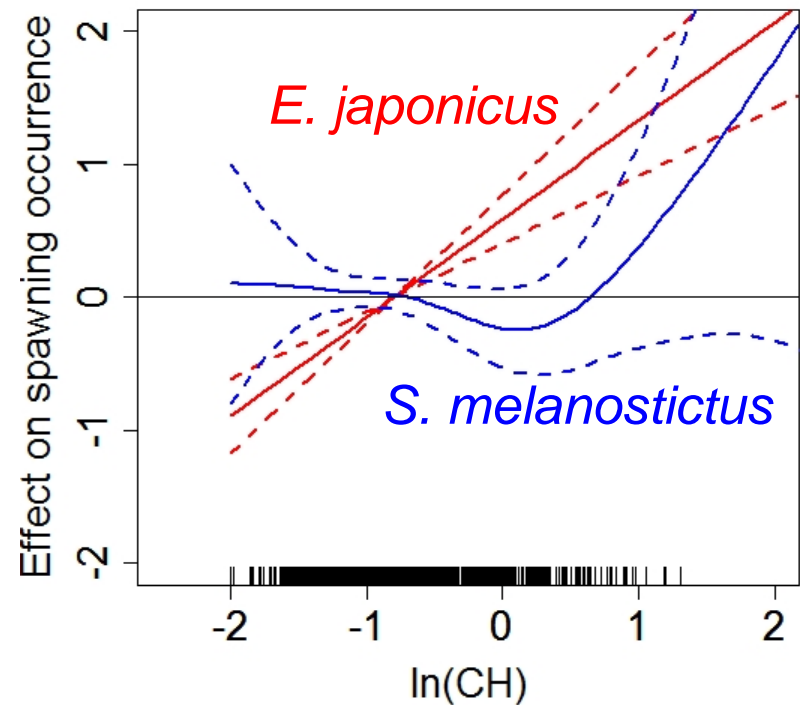
Spawning responses

Tosa Bay area
February to April

Zooplankton volume



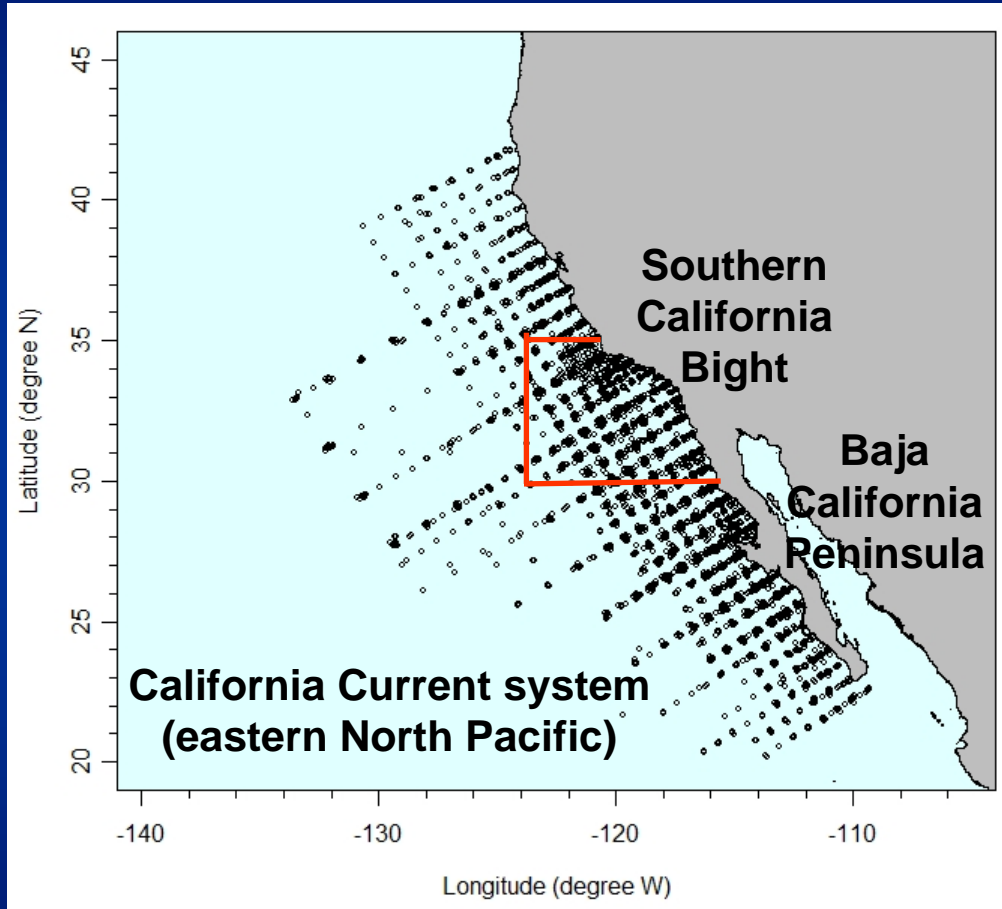
Chlorophyll-a concentration



Smoothed effects of environmental factors on spawning probability by the GAMs in the Tosa Bay area from February to April.

Data set

Long-term data set of CalCOFI surveys (CalCOFI data)



Spatially and temporally limited:

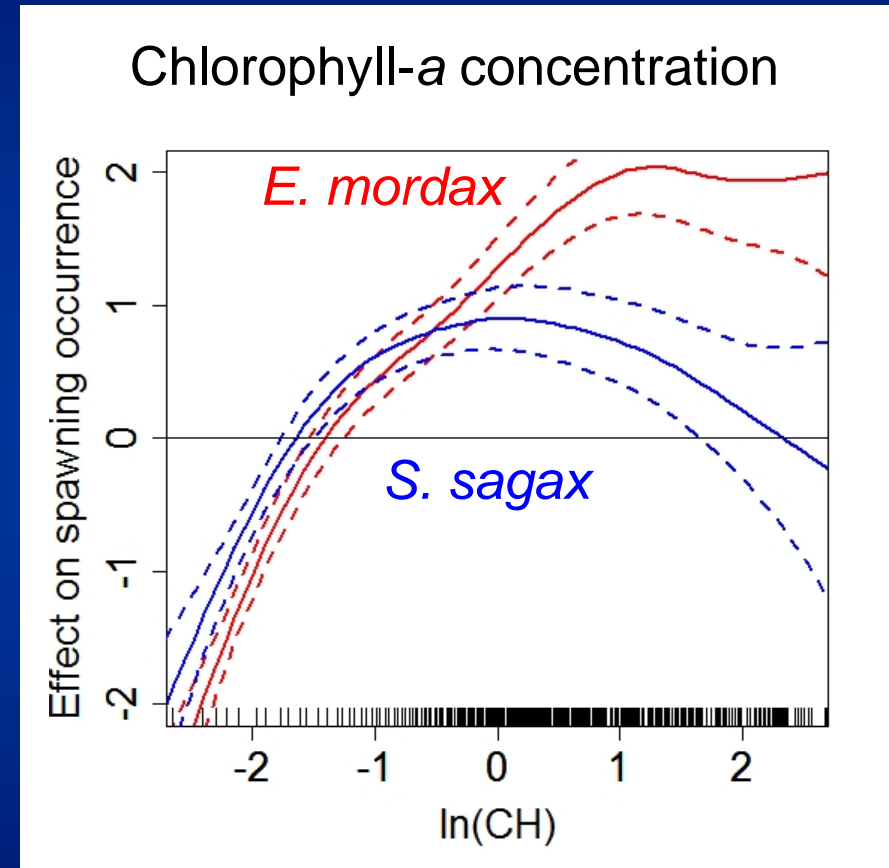
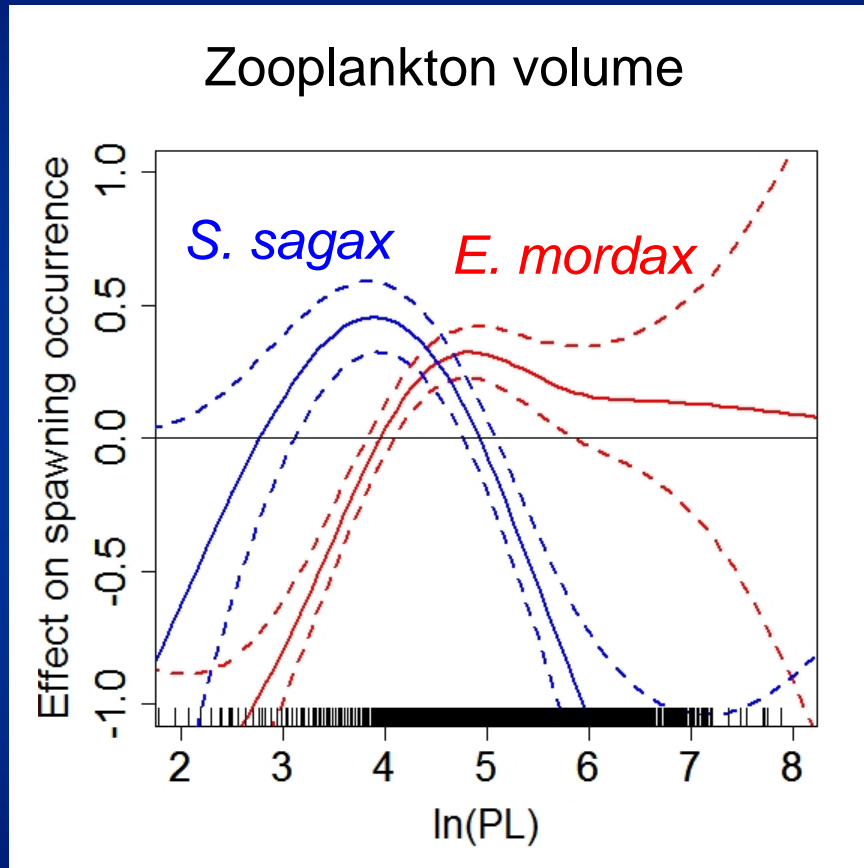
➤ Southern California Bight

➤ February to April
Overlapping spawning months

Sampling stations in the CalCOFI surveys off California and Baja California from 1951 to 2008.

Spawning responses

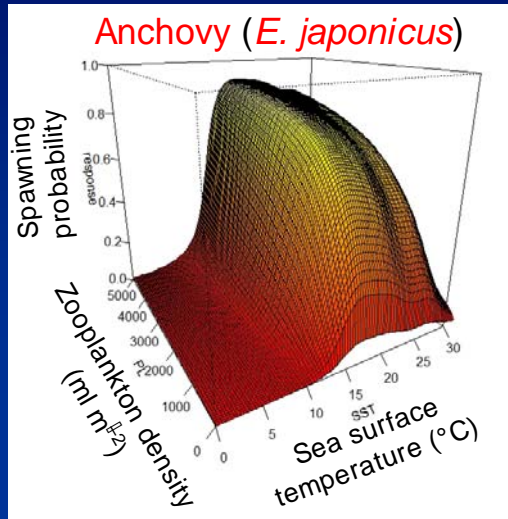
Southern California Bight February to April



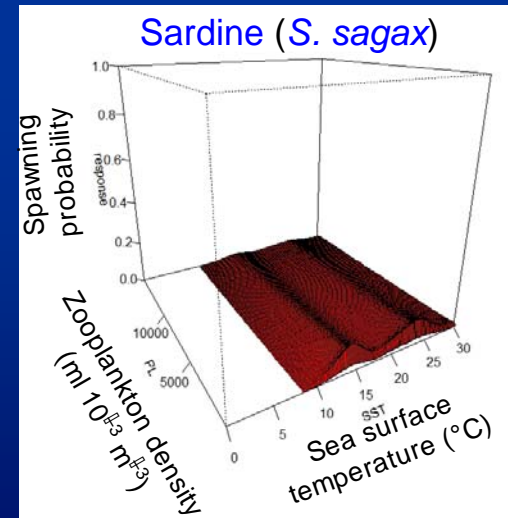
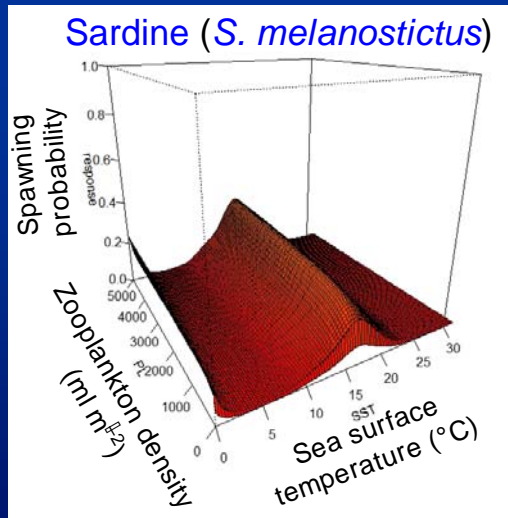
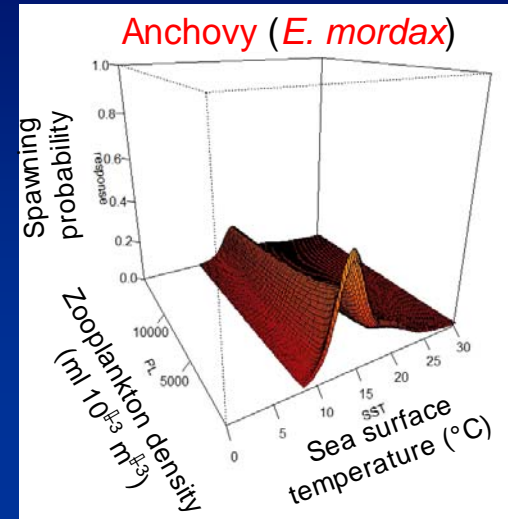
Smoothed effects of environmental factors on spawning probability by the GAMs in the Southern California Bight from February to April.

Comparison (example)

Kuroshio



California



Probability of spawning in relation to **SST** and **plankton volume** in the GAMs applied to the data subsets with all the variables available.