

# Differential optimal temperatures for growth of larval anchovy and sardine: A potential mechanism for regime shifts?



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## *Preliminary question*

**Why does a subtle environmental change trigger a drastic fish regime shift?**



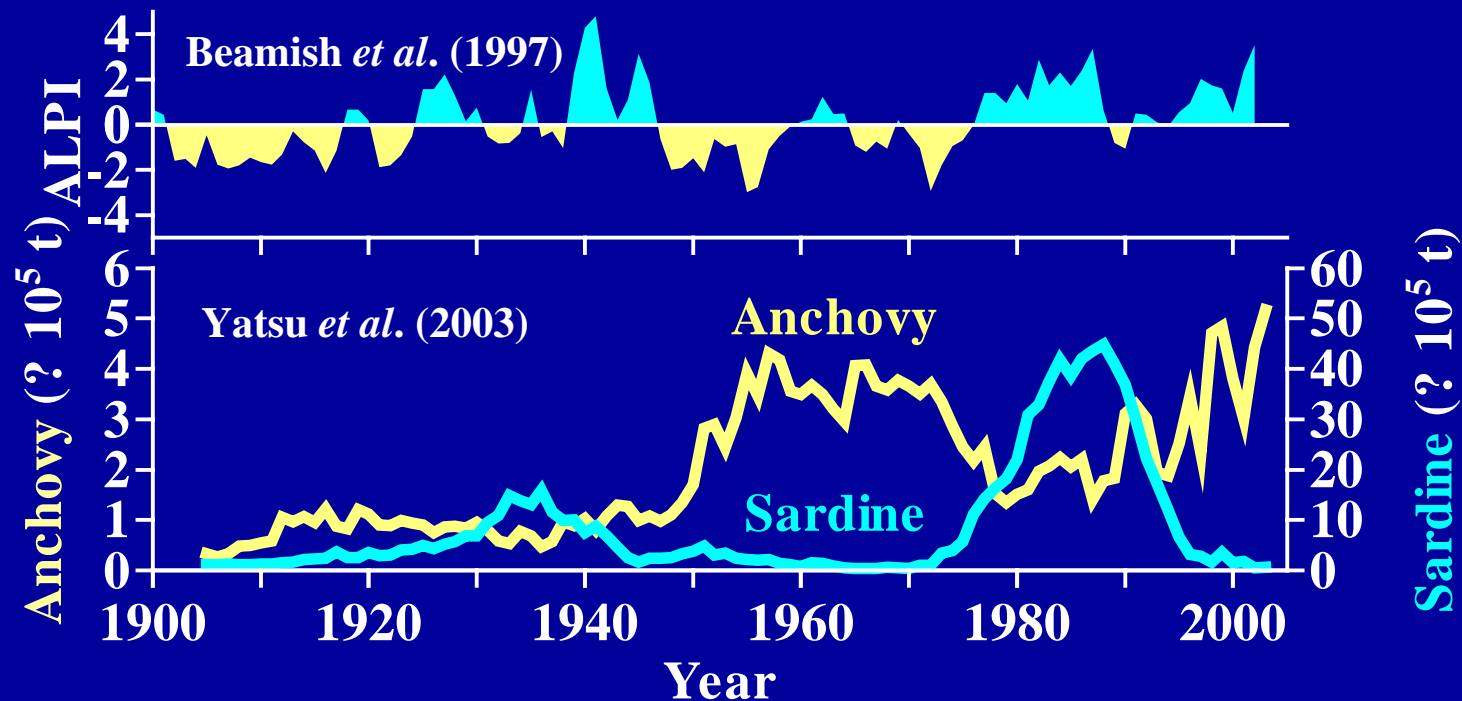
## *Key question*

**Why do anchovy flourish and sardine collapse during the same ocean regime and vice versa?**

# Fish regime shift

## Climate and fish regime shift

- Climate impacts fisheries.
- A mystery of the ocean is the out-of-phase stock oscillations between **sardine** and **anchovy**.
- ‘Fish regime shift’ has been attributed to ‘ocean regime shift’.



Catch histories of **Japanese anchovy** *Engraulis japonicus* and **Japanese sardine** *Sardinops melanostictus*, corresponding to Aleutian low pressure index.

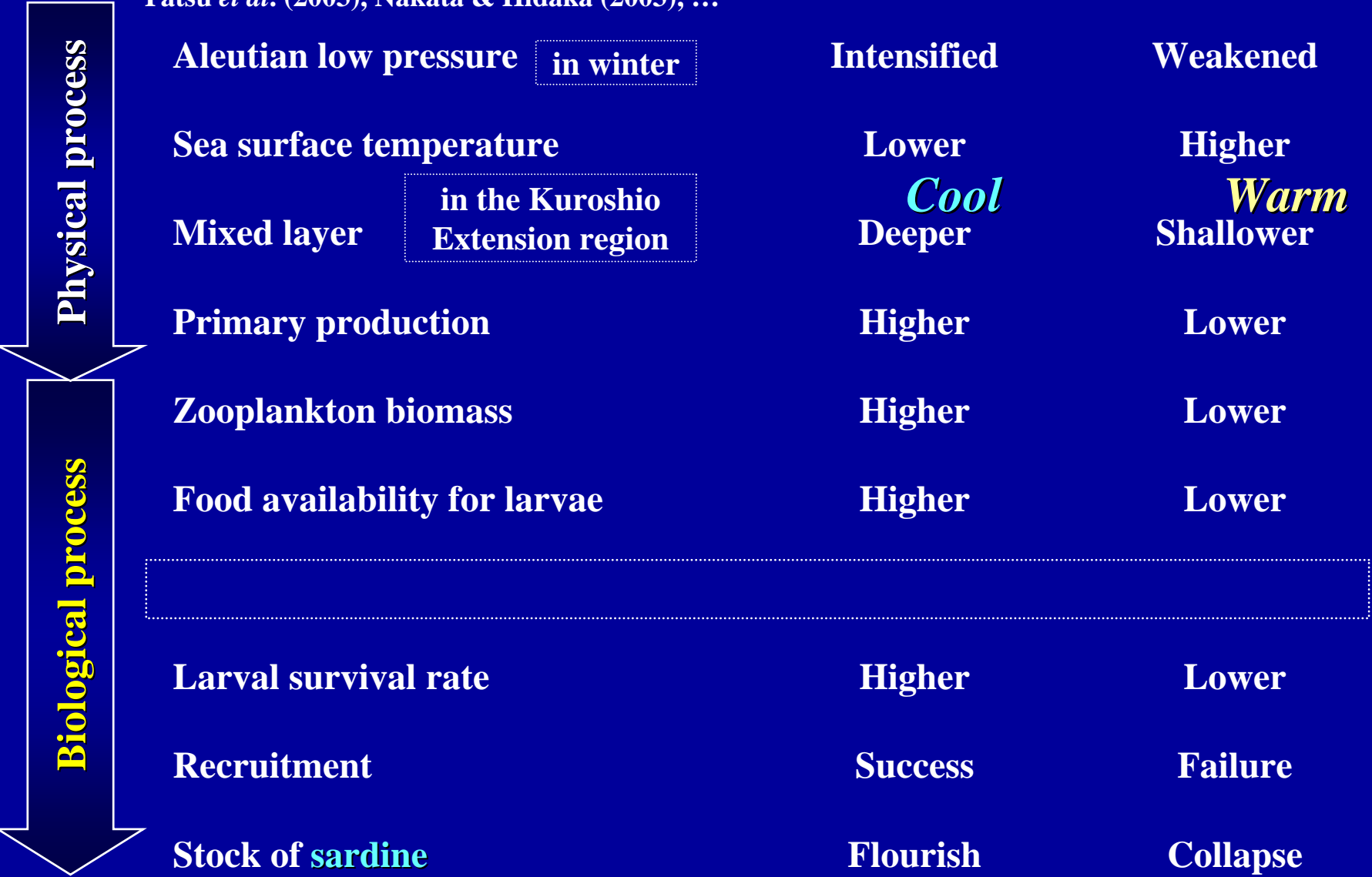
# Climate cascade

## Scenario for sardine

Noto & Yasuda (1999, 2003), Yasuda *et al.* (1999),  
Yatsu *et al.* (2003), Nakata & Hidaka (2003), ...

## Sardine's flourish Sardine's collapse

(Sardine regime) (Anchovy regime)



## *Preliminary question*

**Why does a subtle environmental change trigger a drastic fish regime shift?**



## *Key question*

**Why do anchovy flourish and sardine collapse during the same ocean regime and vice versa?**

# Growth–survival

## *‘Growth–survival’ paradigm during early life stages*

- ‘Growth–mortality’ hypothesis (Anderson 1988)
- Faster growing larvae are more likely to survive in the sea.

## *Three growth-related mechanisms*

- ‘**Bigger is better**’ hypothesis (Miller *et al.* 1988)  
Size: negative size-selective mortality
- ‘**Stage duration**’ hypothesis (Chambers & Leggett 1987, Houde 1987)  
Time: high mortality larval stage duration
- ‘**Growth-selective predation**’ hypothesis (Takasuka *et al.* 2003, 2004)  
Growth rate (*per se*): direct impacts on vulnerability to predation

## *In theory, ...*

- These are independent of and synergistic with one another.
- Even subtle variations in growth rates potentially cause extreme fluctuations in survival probability and recruitment.

# Climate cascade

## Scenario for sardine

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## Sardine's flourish Sardine's collapse

(Sardine regime) (Anchovy regime)

Aleutian low pressure in winter

Intensified

Weakened

Sea surface temperature

Lower

Higher

Mixed layer

in the Kuroshio  
Extension region

Cool  
Deeper

Warm  
Shallower

Primary production

Higher

Lower

Zooplankton biomass

Higher

Lower

Food availability for larvae

Growth rate

Amplifier

‘Growth–survival’ paradigm

➤ ‘Bigger is better’

➤ ‘Stage duration’

➤ ‘Growth-selective predation’

Larval survival rate

Recruitment

Success

Failure

Stock of sardine

Flourish

Collapse

Physical process

Biological process

Relationship between growth rates during early life history stages and sea temperature was examined for **Japanese anchovy** and **Japanese sardine**.



*Engraulis japonicus*

VS



*Sardinops melanostictus*

**‘Growth-optimal temperature’** hypothesis:  
A potential mechanism for fish regime shift?

# Materials and Methods

## *Samples*

### ➤ Larval Japanese anchovy *Engraulis japonicus*



- A portion of samples are identical to those in the previous studies: Aoki & Miyashita (2000), Takasuka & Aoki (2002), Takasuka *et al.* (2003, 2004, 2004), Takasuka & Aoki (in review)

### ➤ Larval Japanese sardine *Sardinops melanostictus*



- A portion of samples are identical to those in the previous study: Oozeki & Zenitani (1996)
- Supplemented by Hiroya Sugisaki (Tohoku National Fisheries Research Institute)

## *Growth rates*

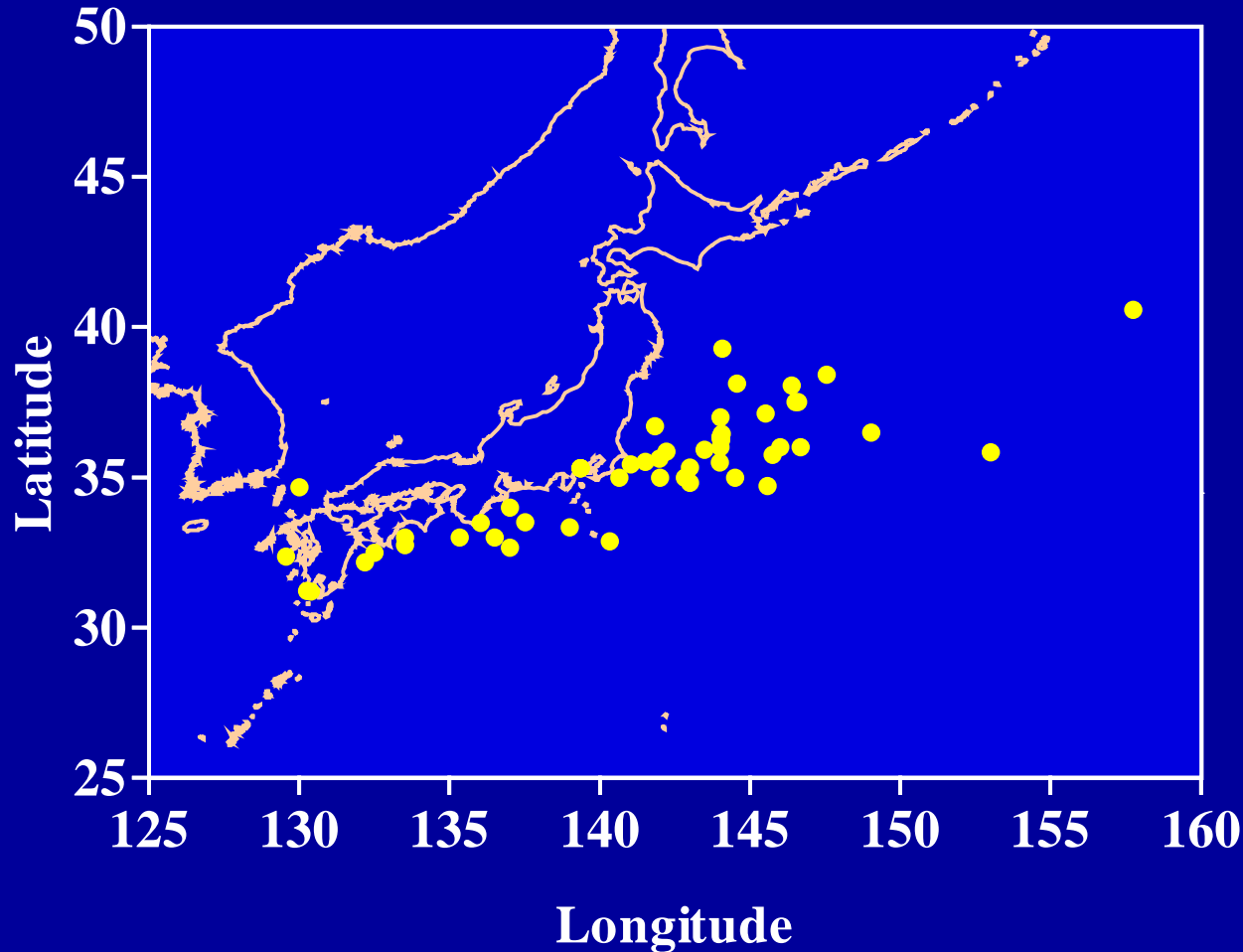
- Sagittal otolith microstructure analysis
- Recent 3 day mean growth rates directly before capture
- Back-calculation by the biological intercept method



Relationship between recent growth rates and  
sea surface temperature at the time of capture

# Samples

50 stations in total, 1990–2004



## Larval anchovy



- All seasons
- 34 samples
- 2041 larvae
- 6–35 mm SL

## Larval sardine



- Jan.–Jun.
- 30 samples
- 766 larvae
- 8–35 mm SL

Sampling areas and stations for larval **Japanese anchovy** and **Japanese sardine**.

# Materials and Methods

## *Samples*

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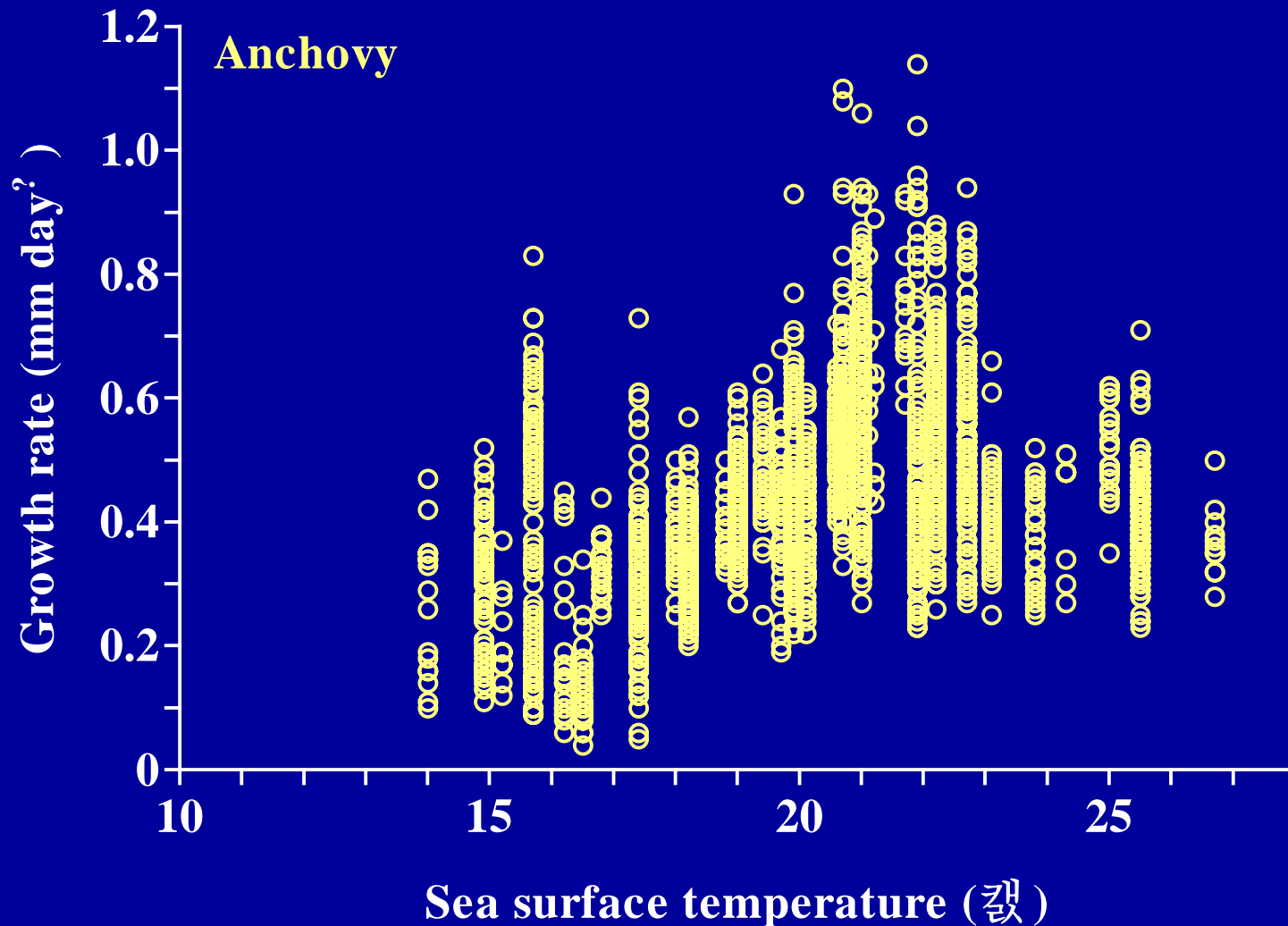
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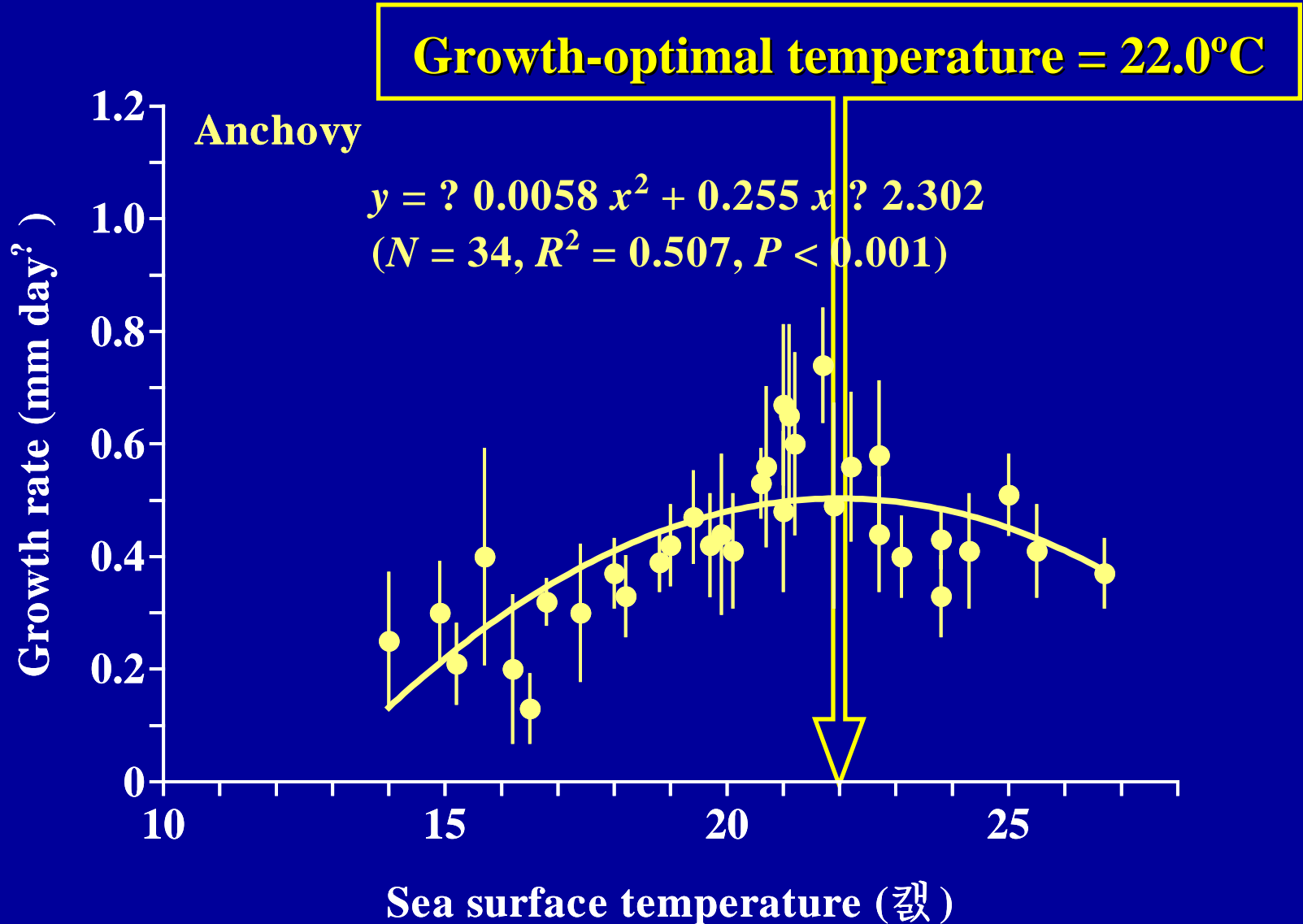
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# Growth–SST for anchovy



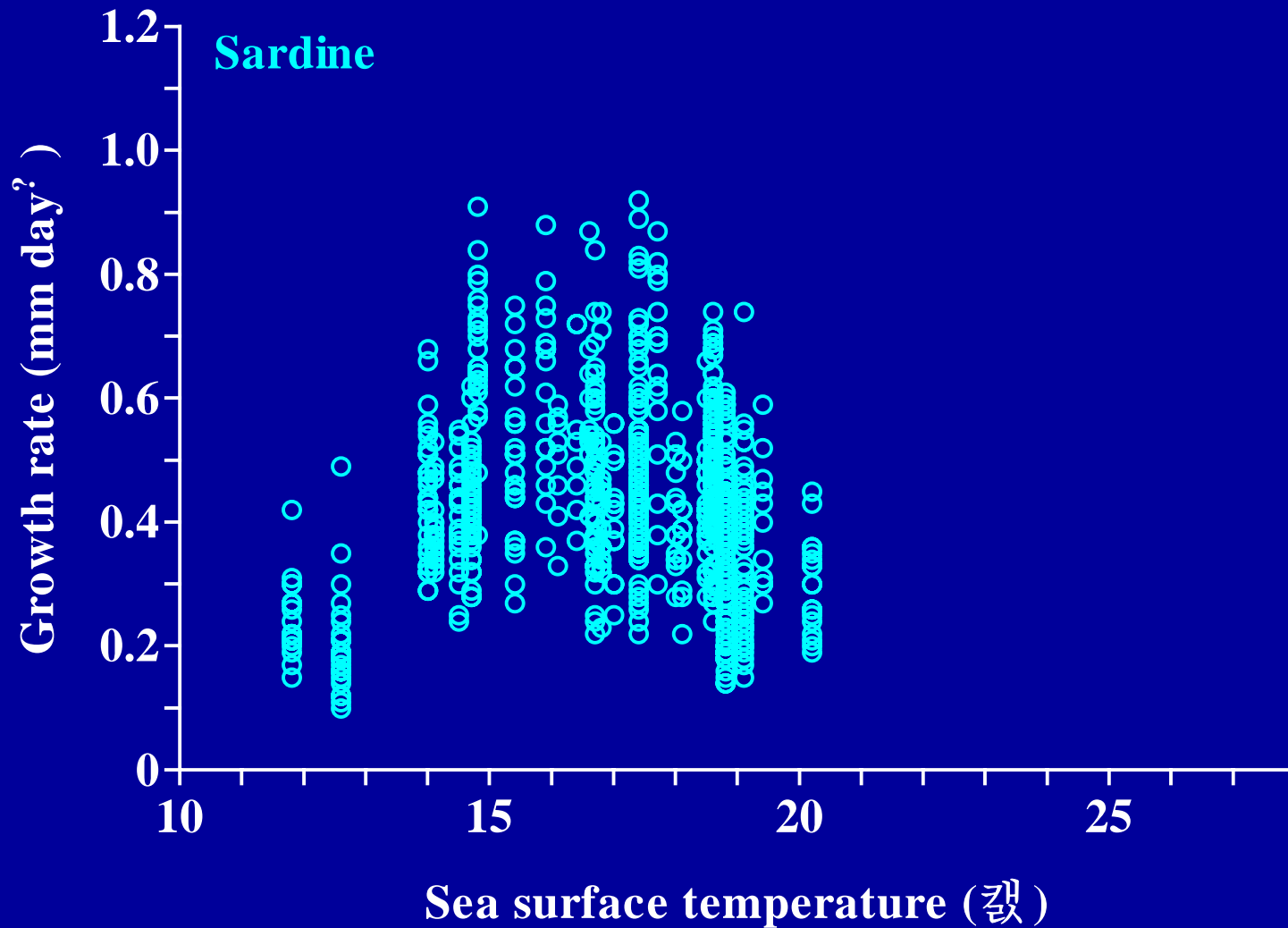
Relationship between recent 3 day mean growth rates and sea surface temperature for larval **Japanese anchovy**.

# Growth–SST for anchovy



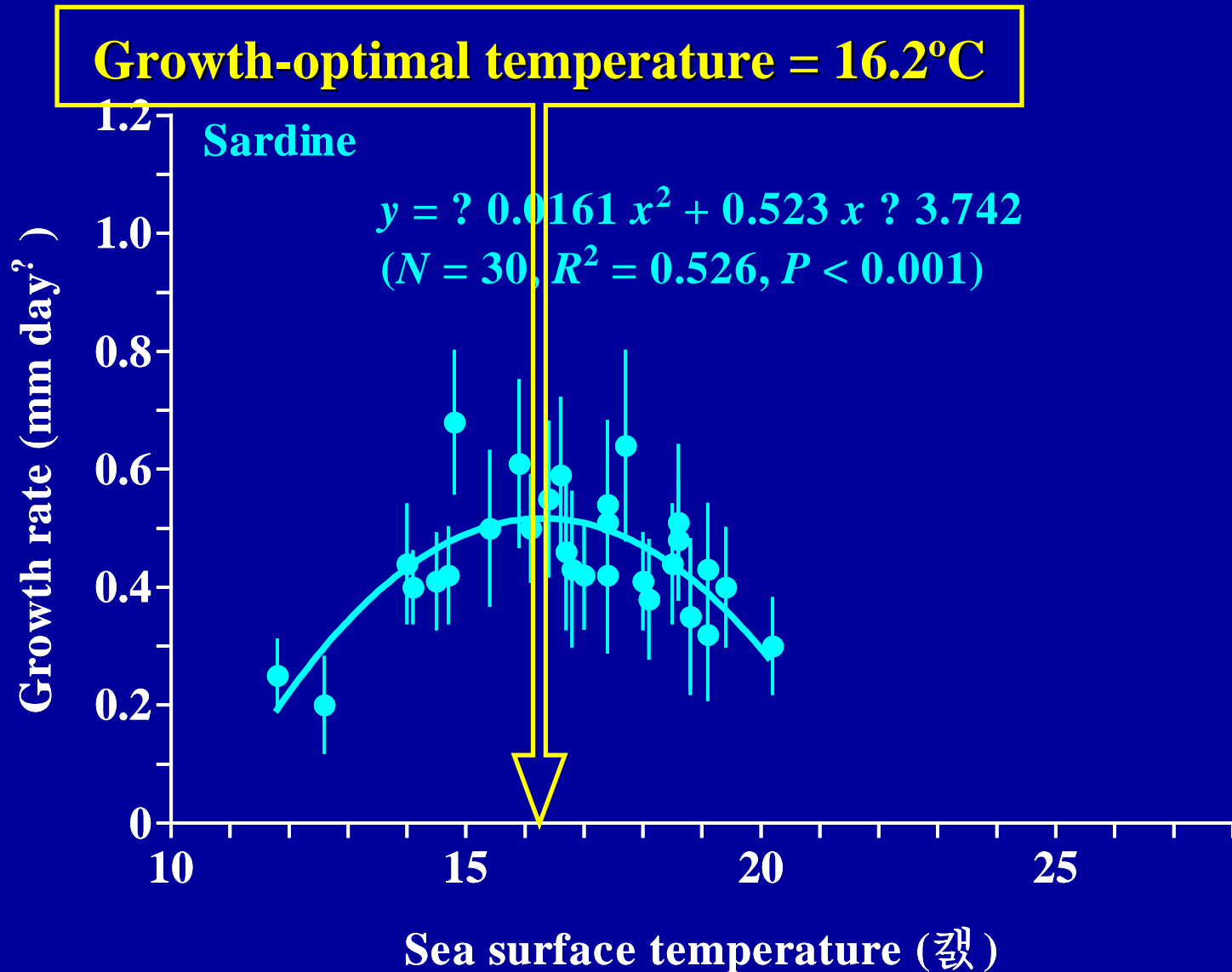
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# Growth–SST for sardine



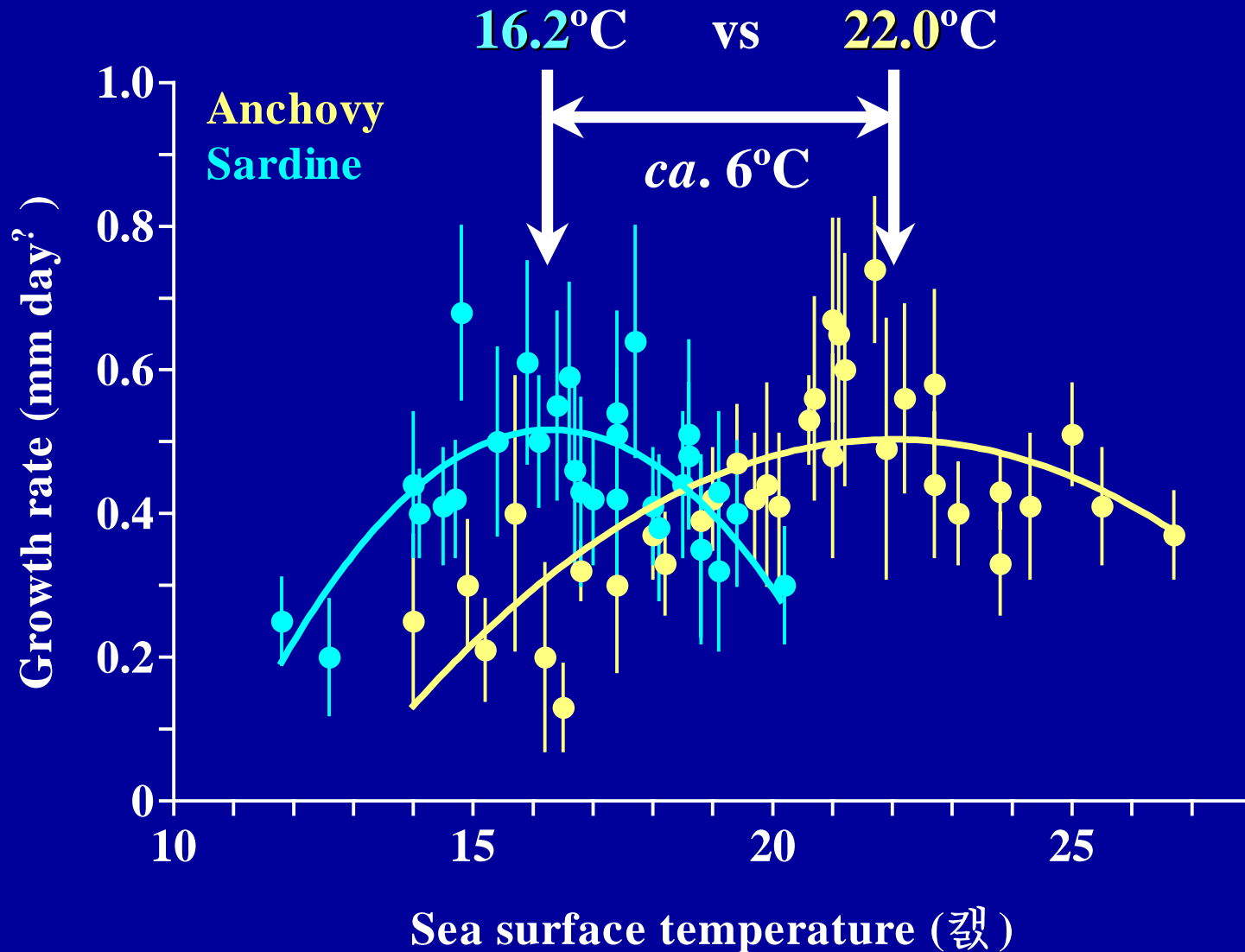
Relationship between recent 3 day mean growth rates and sea surface temperature for larval **Japanese sardine**.

# Growth–SST for sardine



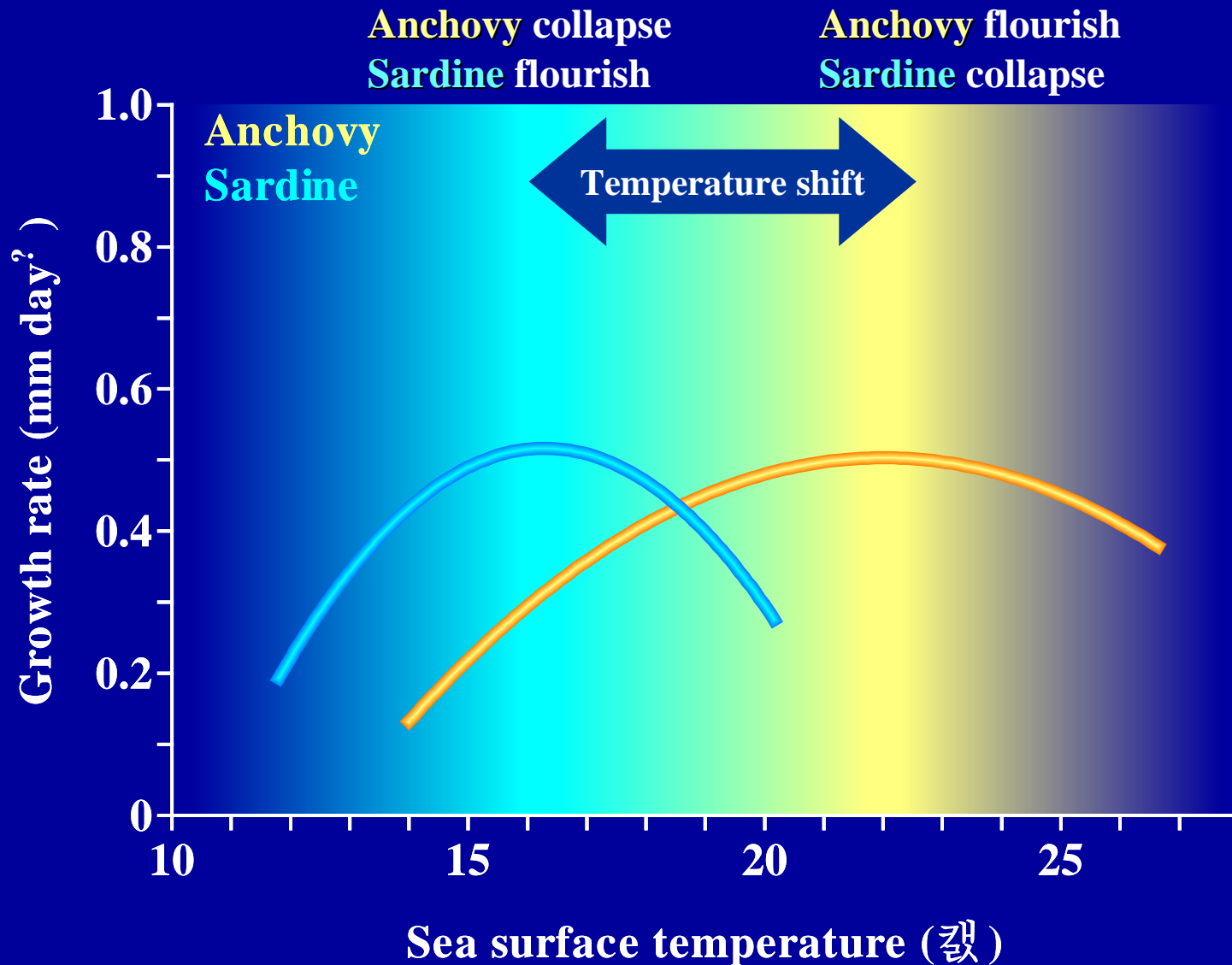
Relationship between recent 3 day mean growth rates and sea surface temperature for larval **Japanese sardine**.

# Anchovy vs Sardine



Relationship between recent 3 day mean growth rates and sea surface temperature for larval **anchovy** and **sardine**.

# Mechanism



Conceptual framework of a potential mechanism for fish regime shift by the differential growth-optimal temperatures.

# Issues raised

## *In summary, ...*

- In the western North Pacific, the **warm anchovy regime** has shifted to the **cool sardine regime** and back (e.g. McFarlane, *et al.* 2002).
- Differential optimal temperatures for larval growth rates can explain the fish regime shift at least theoretically, **if they experience exactly the same environments.**

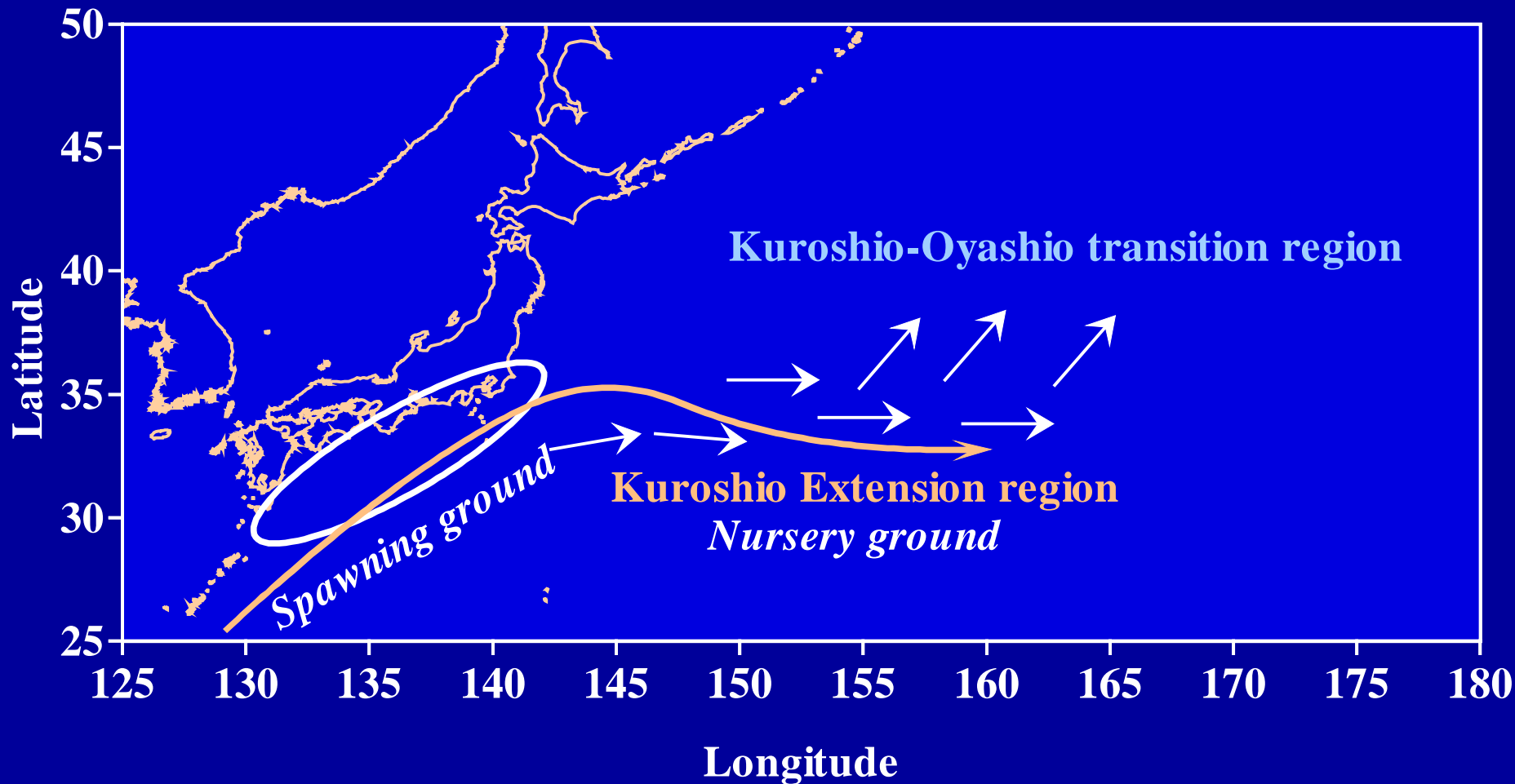
## *However, ...*

- The spawning seasons differ between **anchovy** and **sardine**.
- The SST ranges differed in the present samples.

**What temperatures are they likely to experience?**

**Is the difference in growth-optimal temperatures  
(*ca.* 6°C) really significant?**

# General early life history

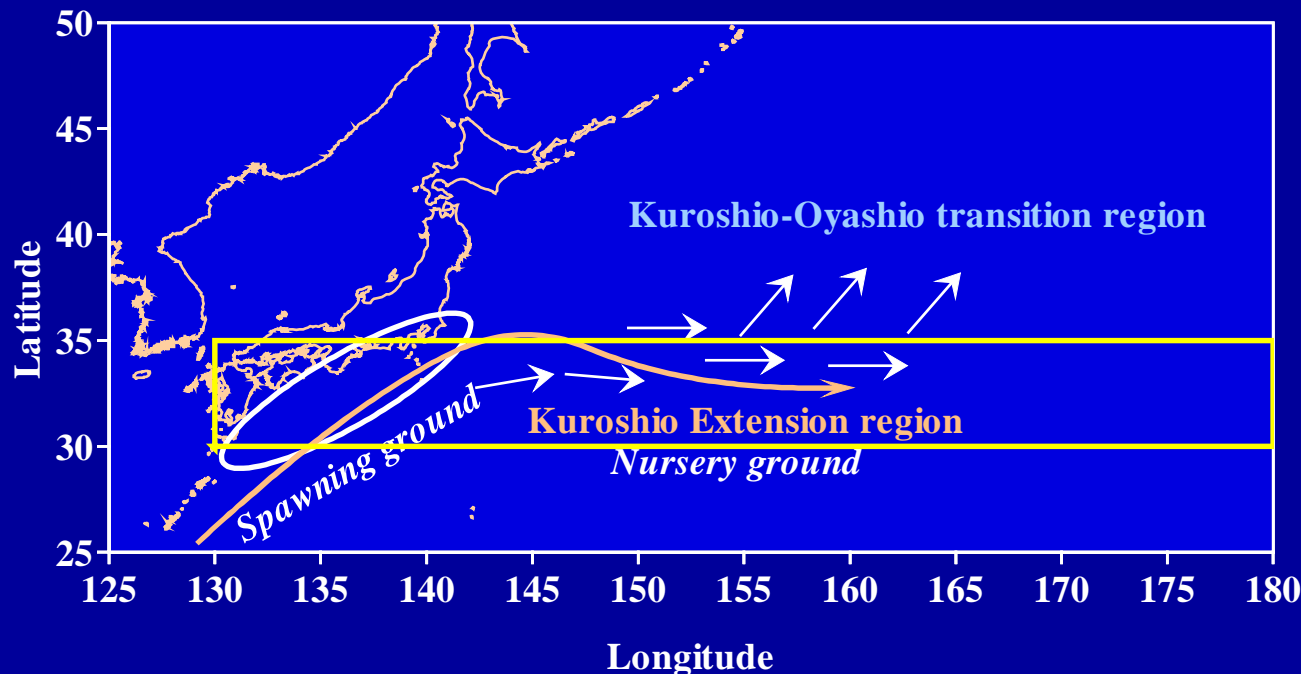


Conceptual diagram of the general pattern of spawning ground, transport and migration for **anchovy** and **sardine**.

# Sea surface temperature

## *Nursery ground*

- *Consideration:* Offshore transport  
Different peaks of hatching
- *Assumption:* Spawning seasons are invariable annually.  
Larvae are transported physically.
- **Mean SST in the Kuroshio Extension region**  
**(30–35°N, 130–180°E)** (prepared by Tomowo Watanabe)



30–35°N  
130–180°E

## **Larval anchovy**

- **Apr.–May**

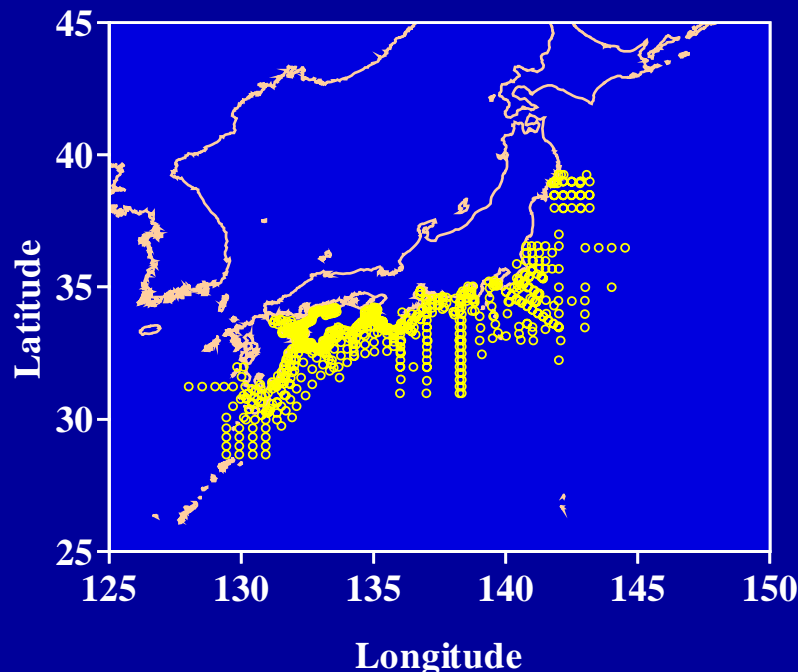
## **Larval sardine**

- **Feb.–Mar.**

# Sea surface temperature

## *Spawning ground*

- **Consideration:** Temporal and spatial dynamics of the SST at the time of hatching
- **Assumption:** Temperatures in the spawning ground regulate growth rates after hatching.
- **Egg-density-weighted mean SST** from a newly developed database.



Egg sampling

Larval anchovy

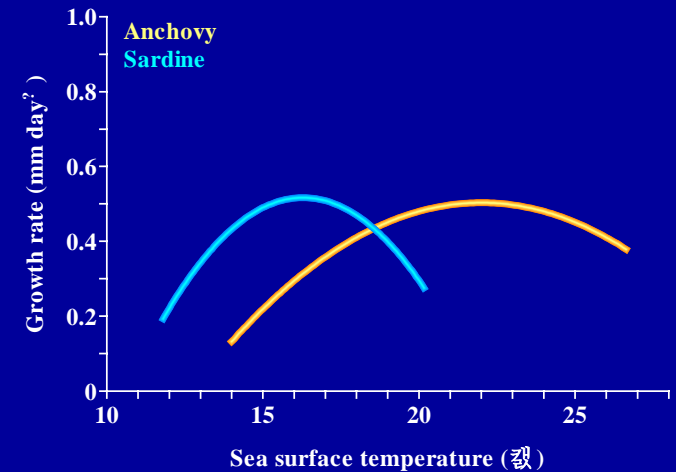
Larval sardine

- All seasons
- All stations
- Annual mean

# Retrospective test

## *Growth rate conversion*

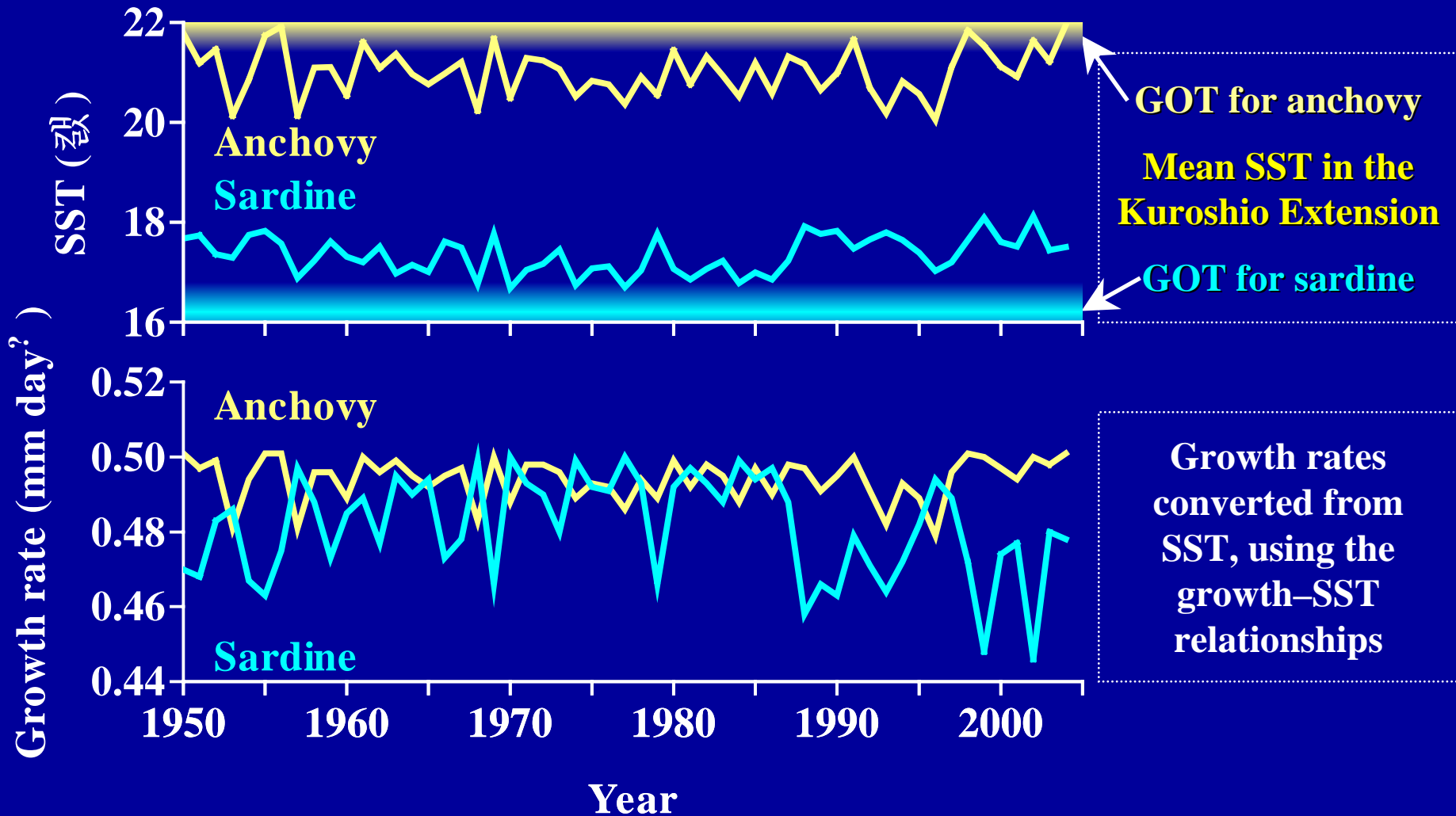
- Larval growth rates were converted from SST data, using the growth–SST relationships, for **anchovy** and **sardine**.
- Temporal shifts of the converted growth rates were compared with Catch history data and RPS data.



## *Time series data*

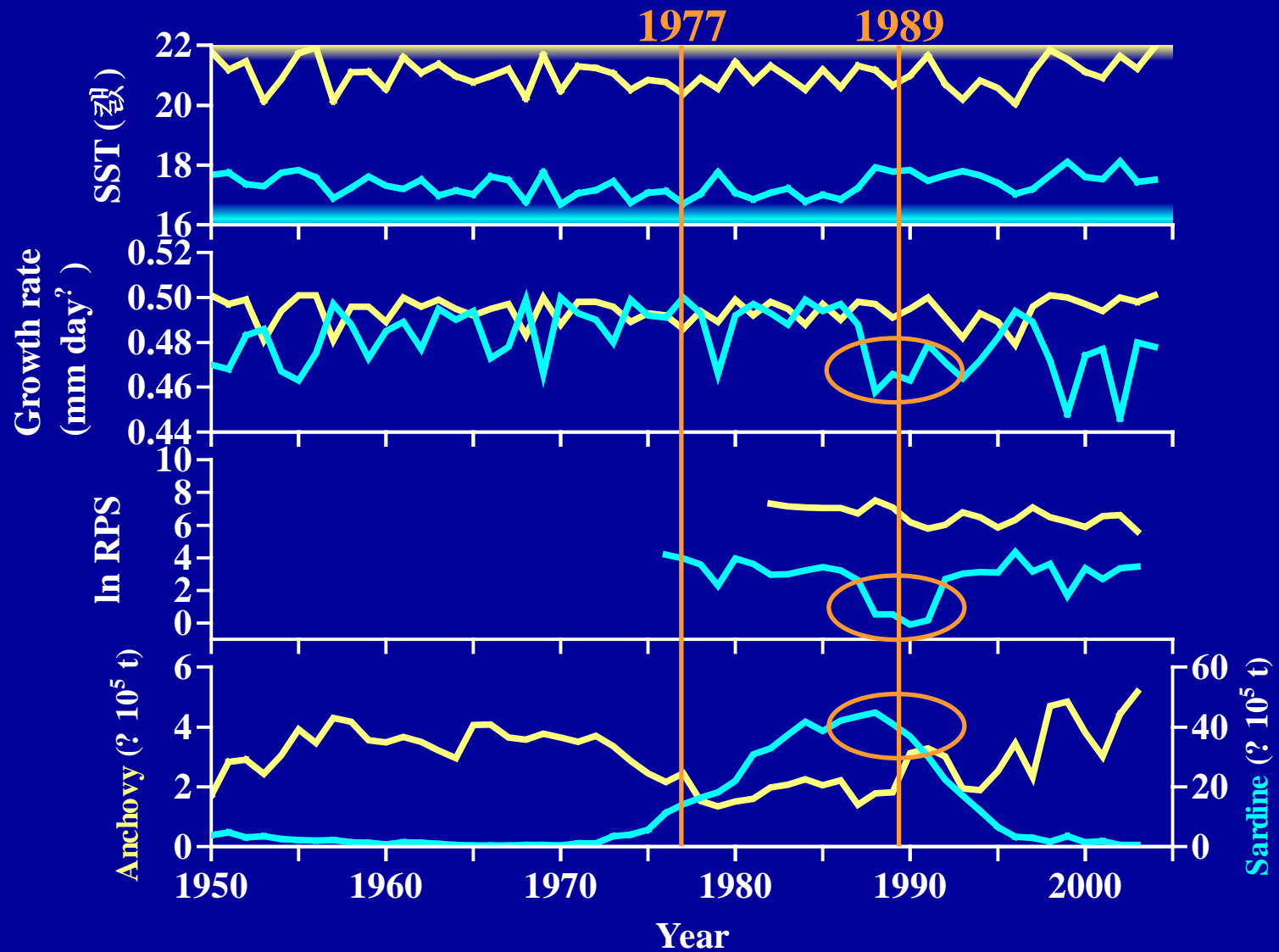
- Catch history (1905–2003) (arranged by Akihiko Yatsu)
- Recruitment per spawning biomass (RPS) (1976–2003)  
(from the stock assessment reports)

# Nursery ground



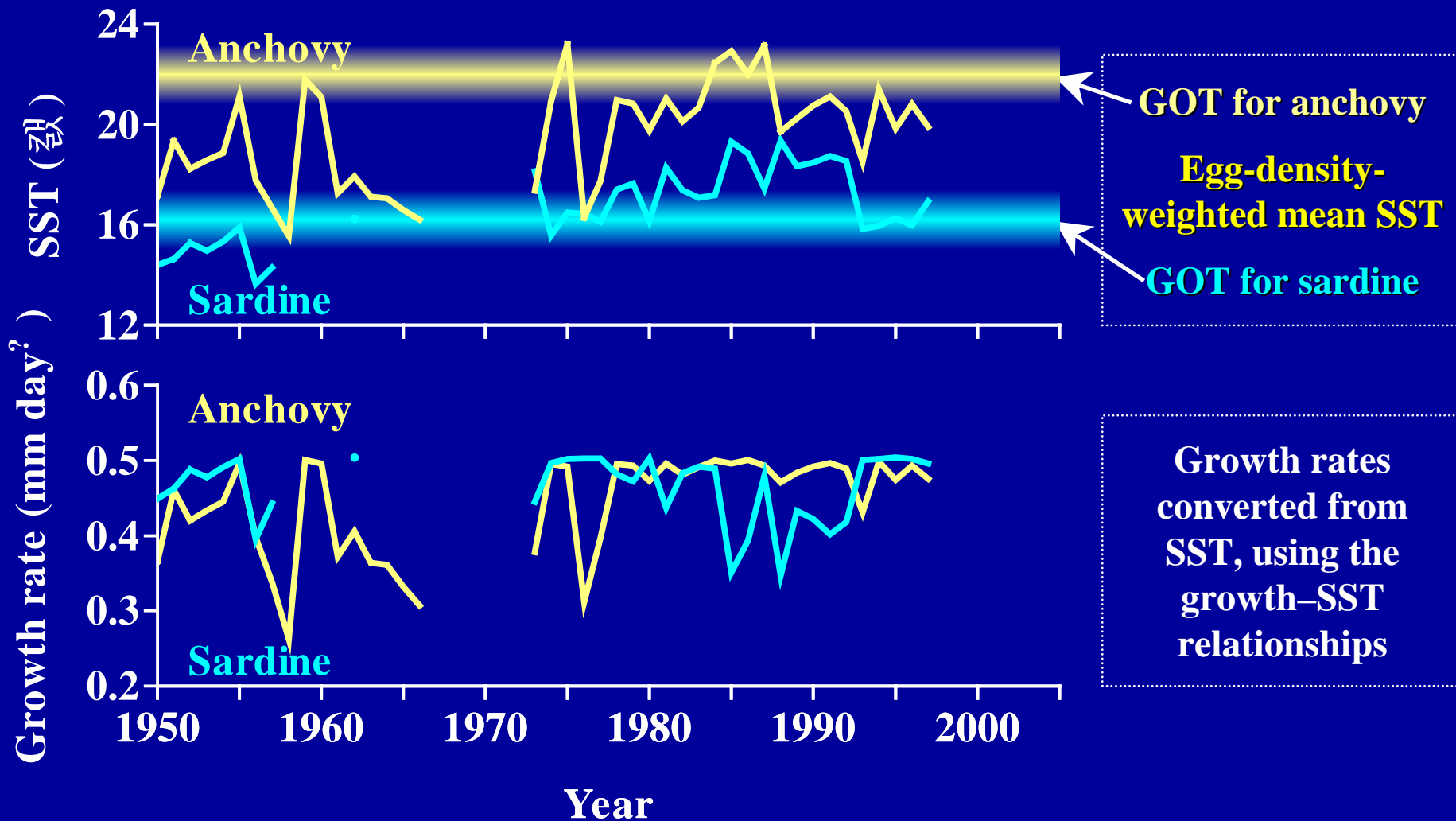
**Mean SST in the Kuroshio Extension region and the converted growth rates for larval anchovy and sardine.**

# Time series data



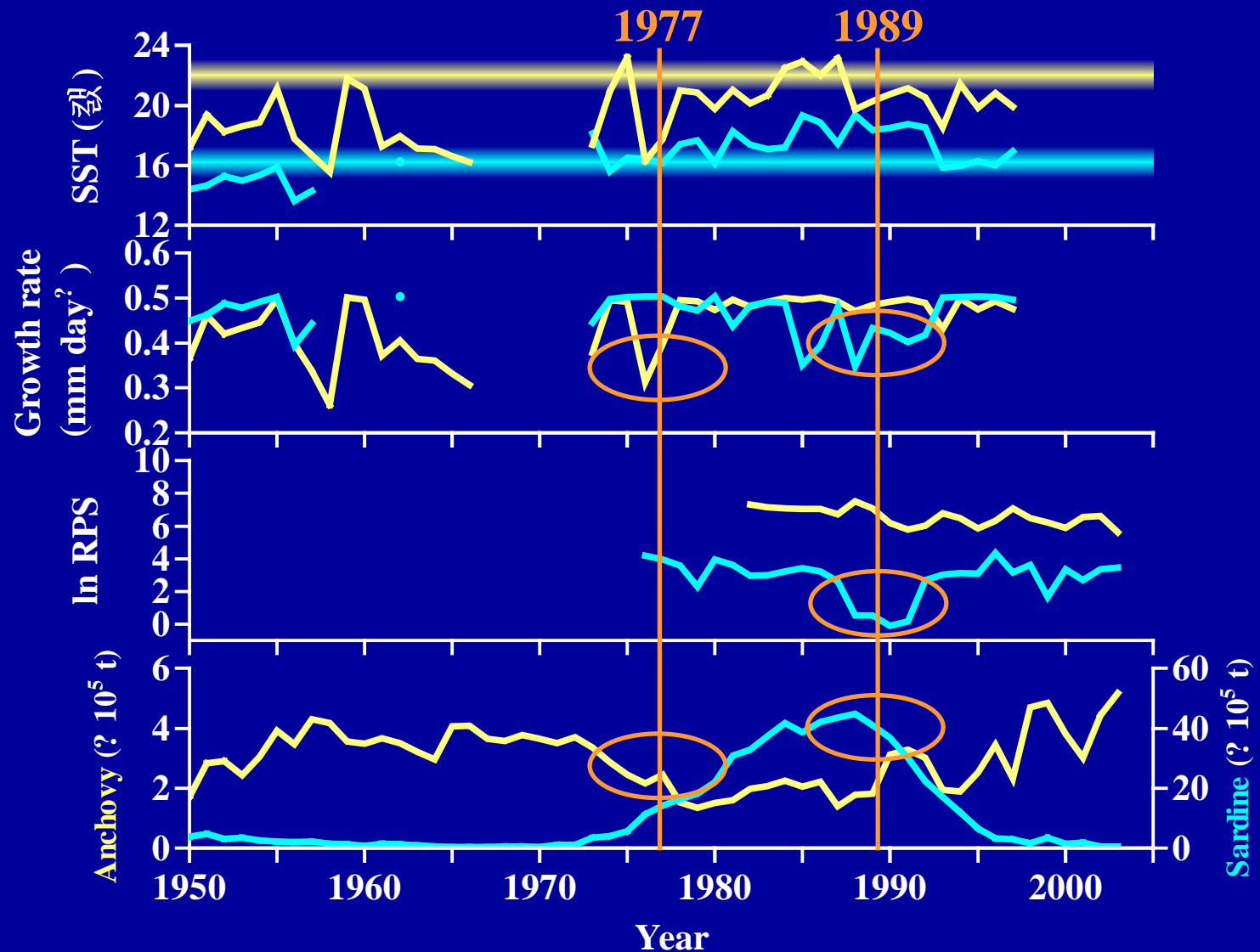
Times series data of **mean SST in the Kuroshio Extension region**, larval growth rates converted from SST, RPS and catch history for anchovy and sardine.

# Spawning ground



**Egg-density-weighted mean sea surface temperature** and the converted growth rates for larval **anchovy** and **sardine**.

# Time series data



Times series data of **egg-density-weighted mean SST**, larval growth rates converted from SST, RPS and catch history for **anchovy** and **sardine**.

# Preliminary question

**Why does a subtle environmental change trigger a drastic fish regime shift?**

## *Theoretical solution*

- The ‘growth–survival’ paradigm has been incorporated into the the ‘climate cascade’.
- Even a subtle temperature shift potentially trigger a drastic fish regime shift.
- The growth-related mechanisms serve as an amplifier.

## Key question

**Why do anchovy flourish and sardine collapse during the same ocean regime and vice versa?**

### *Differential optimal temperatures for larval growth rates*

- Differential optimal temperatures for growth rates were demonstrated between larval Japanese **anchovy** (22°C) and larval Japanese **sardine** (16°C).
- Temperatures which larvae are assumed to experience have fluctuated mainly between 16 and 22°C.
- Temporal shifts of the growth rates converted from such temperatures seemed to correspond to fish regime shifts at least to some extent.

# Hypothesis proposed

## **‘Growth-optimal temperature’ hypothesis**

- Potential biological mechanism for fish regime shift
- The theory is independent of and synergistic with the existing hypotheses.

- I.** ‘Growth–survival’ paradigm
- II.** Direct temperature impacts
- III.** Differential growth-optimal temperatures

A possibility of collaboration:

Reversed growth-optimal temperatures in the eastern North Pacific?

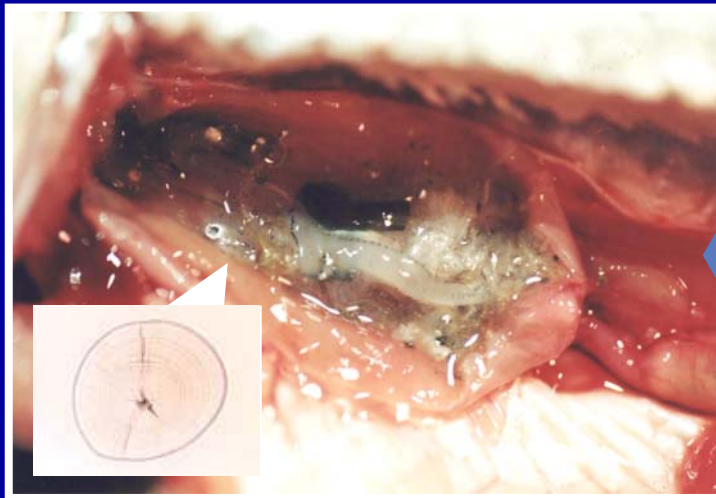
East meets West in the fish regime shift?

## Is a slower growing larval Japanese anchovy actually removed by predation at a given moment in the sea?

(Takasuka *et al.* 2003, 2004, 2004)

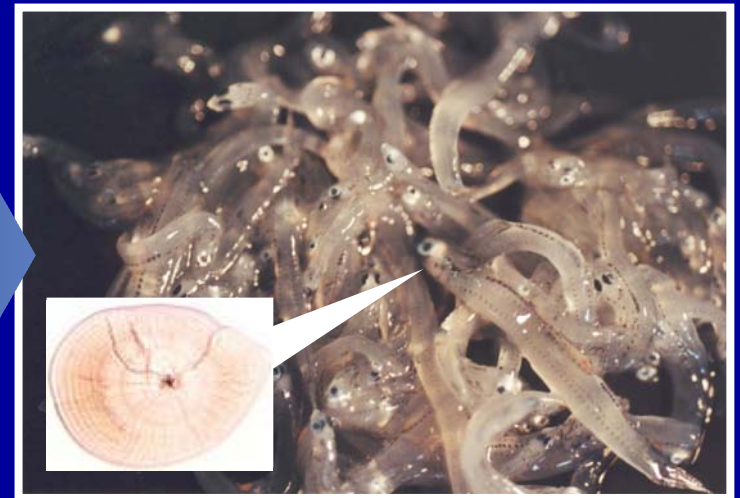
- Growth rates were compared between the larvae dissected from the stomach contents of the predators and the larvae captured simultaneously with the predators.

**Ingested larvae**



*Comparison*

**Surviving larvae**



- The **ingested larvae** had lower growth rates than the **surviving larvae** even at the same size at a given moment in the sea.

# Growth–survival

How strongly do growth rates influence survival?

## *Functional mechanisms of the paradigm*

‘**Bigger is better**’ (but we know ‘bigger is not always better’)

- In specific conditions, the selection is intensive.

‘**Stage duration**’

- Simulation studies by Houde (1987, 1989) suggested that 0.2–0.3 mm day<sup>-1</sup> growth variation can cause over 100-fold survival probability (accumulated effects).

‘**Growth-selective predation**’

- Our previous studies and preliminary analysis suggested that declines in growth rates can lead to 2–5 times vulnerability to predation (at maximum) at a given moment.
- Predation is the primary and direct source of mortality.
- All of the mechanisms should be predator-specific.
- Substantial quantitative data will be required.

## Incidental question

Why does the stock of sardine fluctuate greater than that of anchovy?

### *Response of growth rates to temperature*

- Responses of growth rates to sea temperature seemed drastic for larval **sardine** and moderate for larval **anchovy**.
- Larval **sardine** may be more susceptible to temperature shift than larval **anchovy**.
- This seems consistent with the fact that the stock of **sardine** has fluctuated about 10-fold greater than that of **anchovy** around Japan.
- ✧ Further studies will be required to prove the above.
- ✧ Are differences in longevity more important?

# Recent EWMT

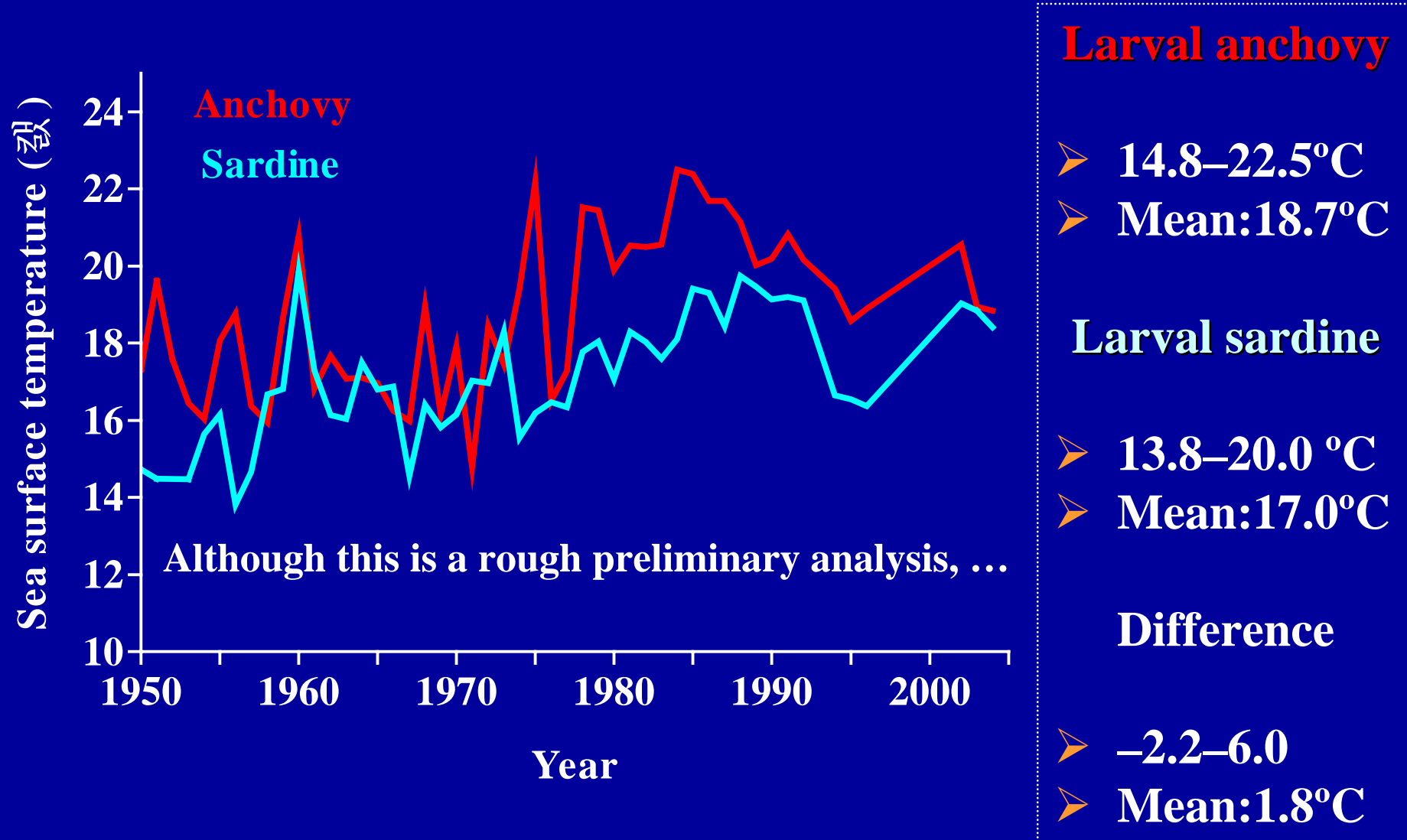
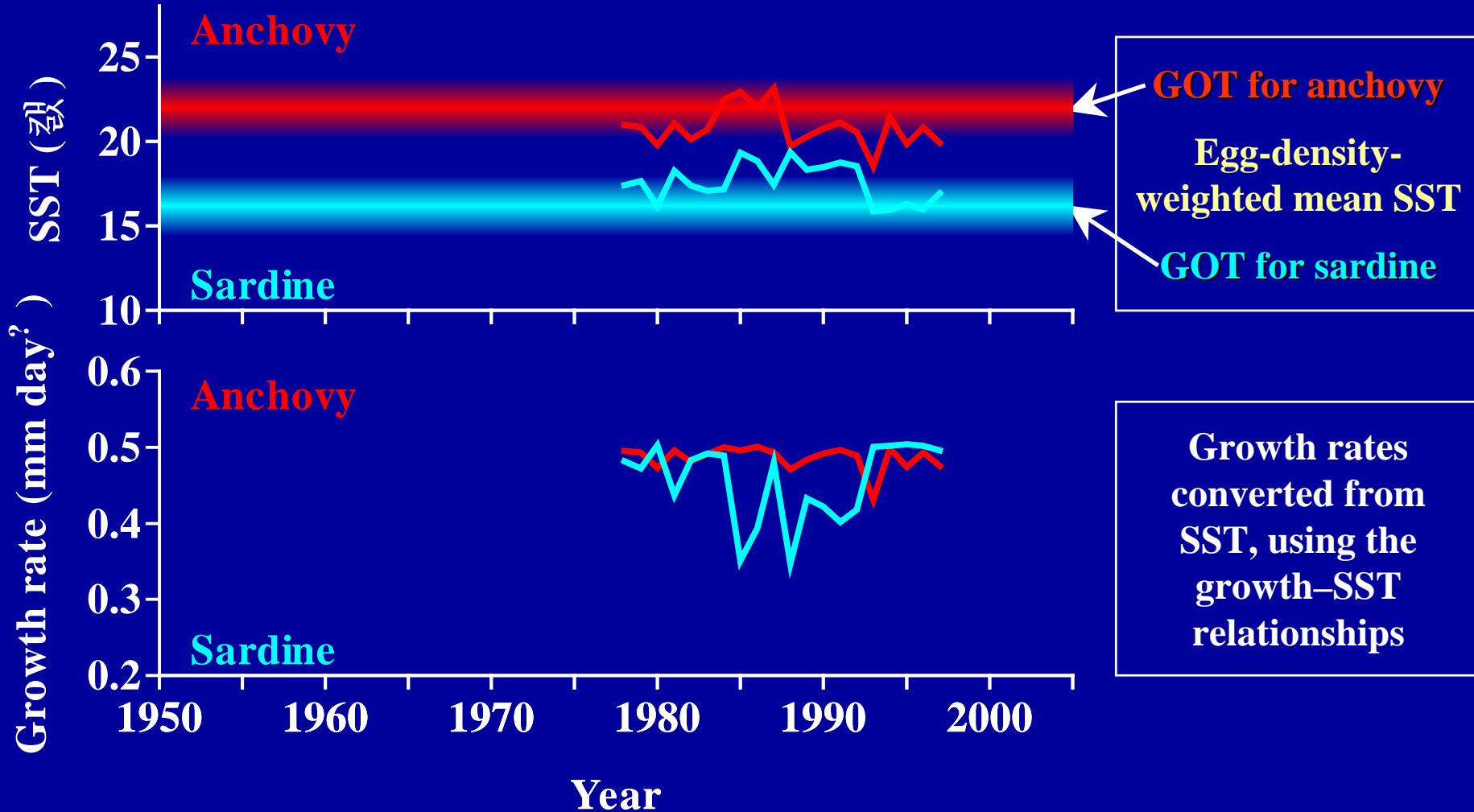


Fig. 7. Time series data of egg-density-weighted mean sea surface temperature for larval **anchovy** and **sardine**.

# Recent EWMT

Preliminary analysis



**Fig. 10. Egg-density-weighted mean sea surface temperature and the converted growth rates for larval **anchovy** and **sardine**.**

# Recent EWMT

Preliminary analysis

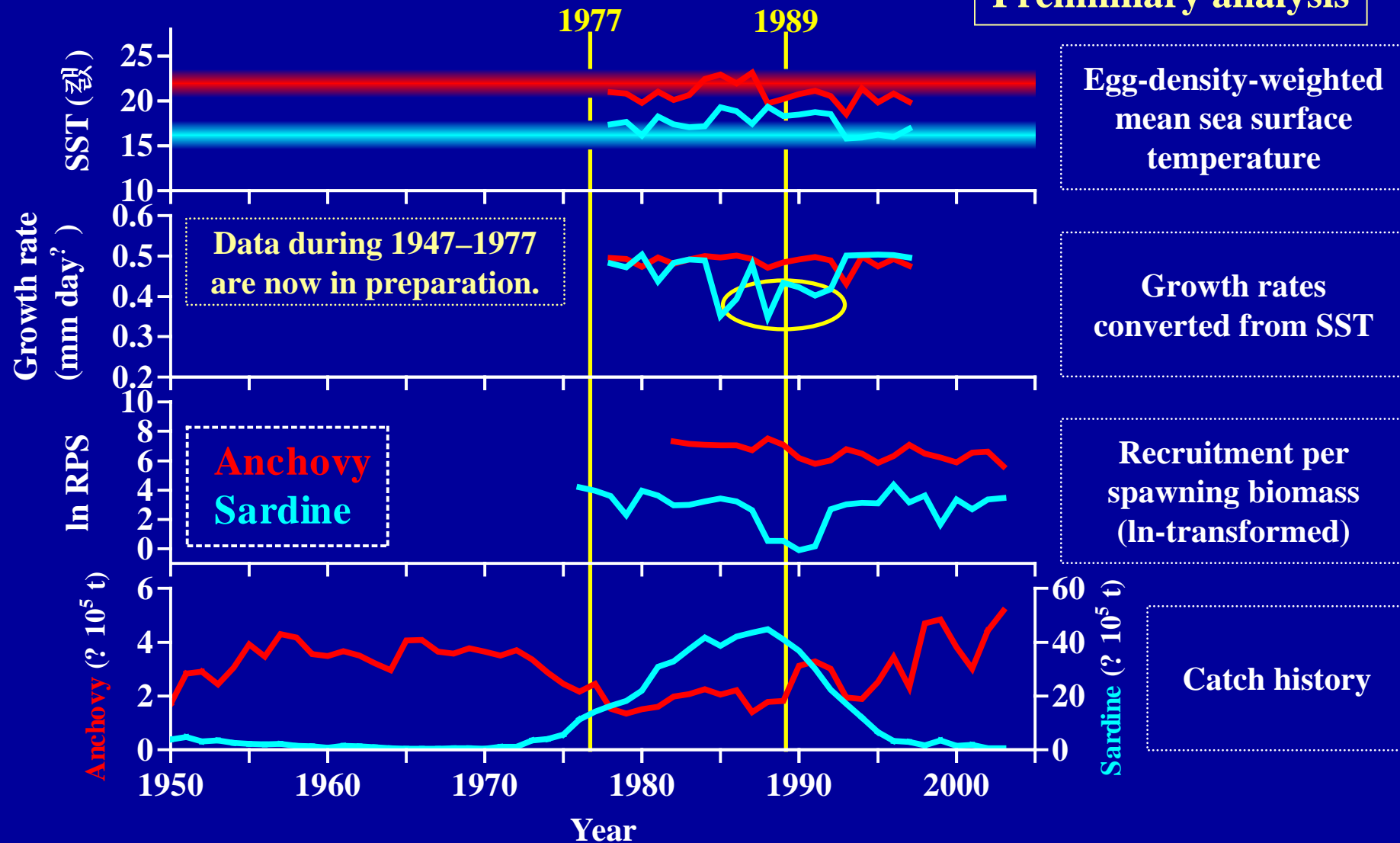


Fig. 11. Times series data of egg-density-weighted mean SST, larval growth rates converted from SST, catch and RPS for **anchovy** and **sardine**.