Density-dependent egg production in small pelagic fish: a key to life cycle closure

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Paradigm

A paradigm of fisheries science

"Spawner biomass is a suitable proxy for reproductive potential of a fish stock."

Leggett & Frank (2008) "Paradigms in fisheries oceanography"

Oceanography and Marine Biology: An Annual Review

"SSB–TEP proportionality" paradigm

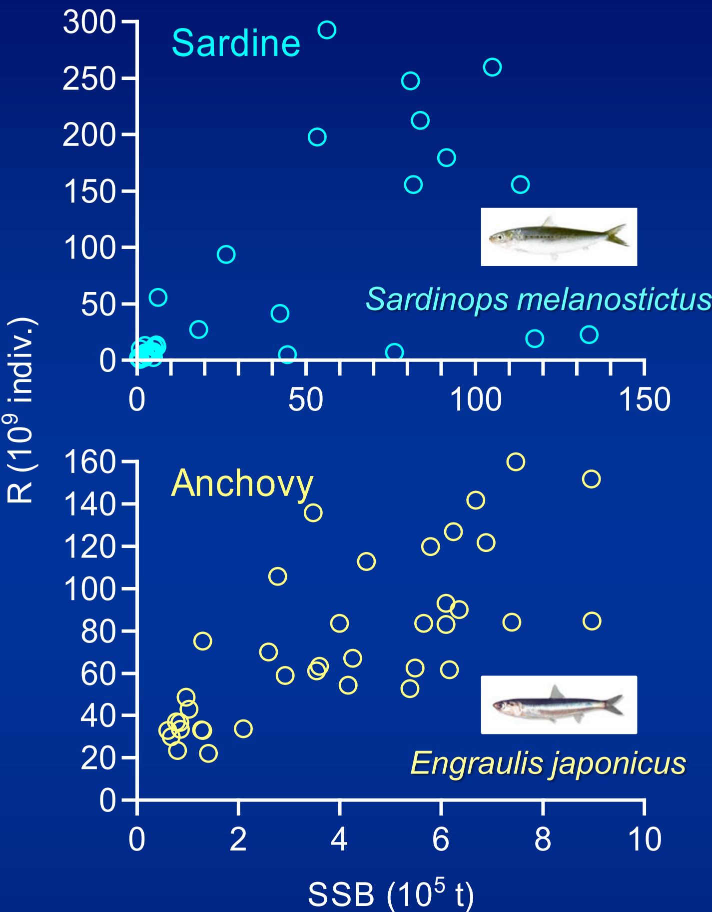
"Spawning stock biomass (SSB) and total egg production (TEP) are proportional to each other."

A basic premise underlying the spawner–recruitment models for fisheries management and studies on recruitment mechanisms of fish.

Ricker (1954), Beverton & Holt (1957), Barrowman & Myers (2000)

Takasuka *et al*.

Spawner–recruitment



Reproductive potential

Total egg production (TEP)

Spawning stock biomass (SSB)

Spawner–recruitment relationships:

usually, recruitment (R) versus spawning stock biomass (SSB)

In theory

- The asymptotic pattern represents density-dependent effects on recruitment (i.e. self-regulating processes).
- Any variability from the asymptotic pattern represents density-independent effects on recruitment (i.e. environmentally-regulated processes).

Interpretation

- Density-dependent mortality from hatching to recruitment.
- Density-independent mortality from hatching to recruitment.

Paradigm

"SSB–TEP proportionality" paradigm

- Progress in studies on maternal effects on reproductive potential has led to doubt about the paradigm.
  "Bigger, older, fatter, and repeat spawners produce larger and more eggs"
- Nonetheless, a direct test of the paradigm at multidecadal scales has been difficult because of data limitations in the stock assessment systems worldwide.
- It is difficult to prepare TEP data independent of SSB data.

In the present study, …

- We directly tested the paradigm based on a combination of two independent time series (SSB and TEP), using sardine and anchovy as model species.
- To show that the "SSB–TEP proportionality" is partially distorted by density-dependent egg production.

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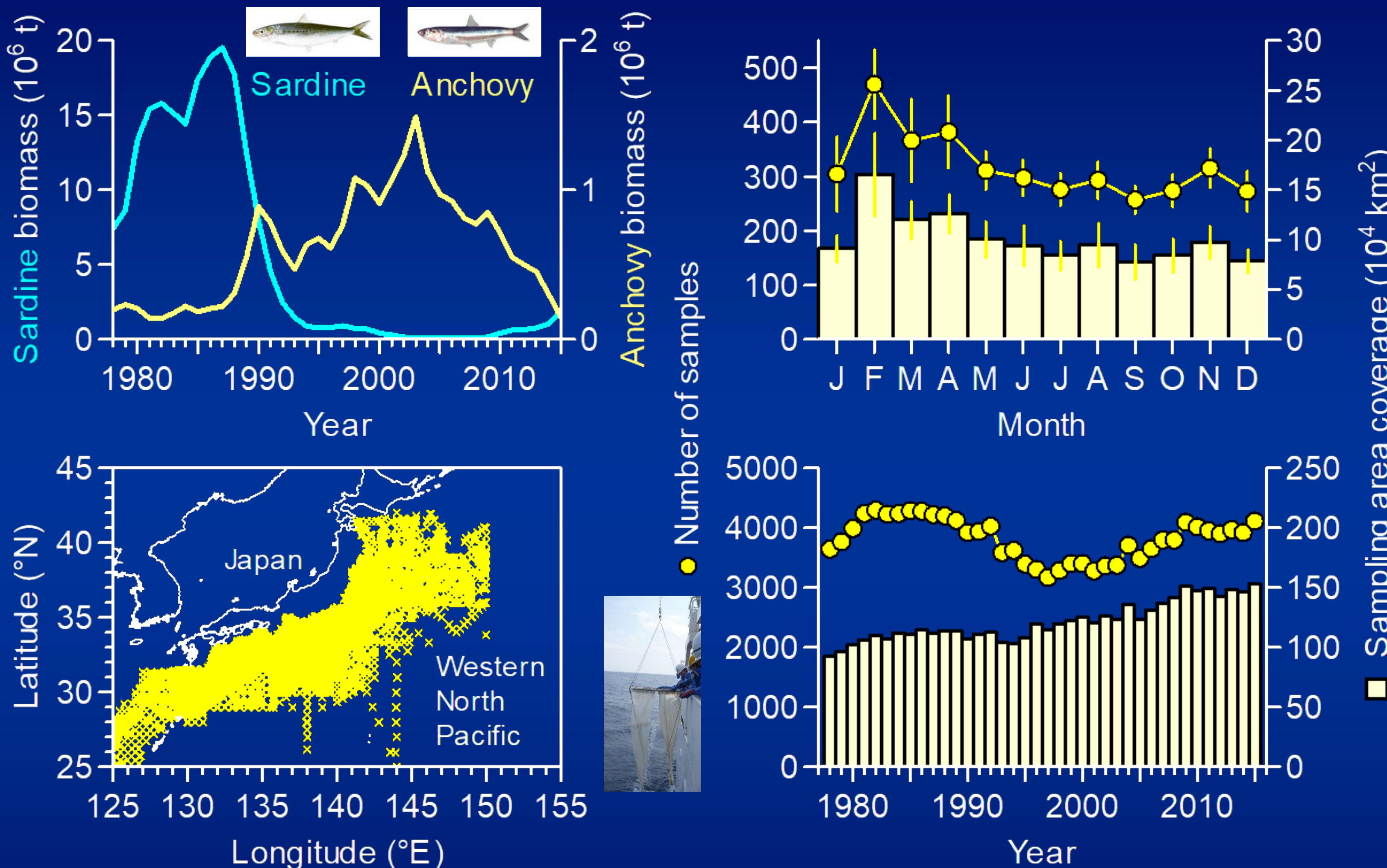
Egg surveys



Egg surveys covering the spawning grounds during the high- and low-biomass periods of sardine and anchovy in the western North Pacific from 1978 to 2015 (38 years). The data set includes a total of 145,157 vertical tows of plankton nets.

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   - Evidence of density-dependent egg production through a direct test of the paradigm of fisheries science
2. Disentangling density-dependent effects
   - Disentangling density-dependent effects on egg production and survival from egg to recruitment
3. Application to recruitment studies
   - Revisiting sardine recruitment hypotheses by an egg-production-based survival index

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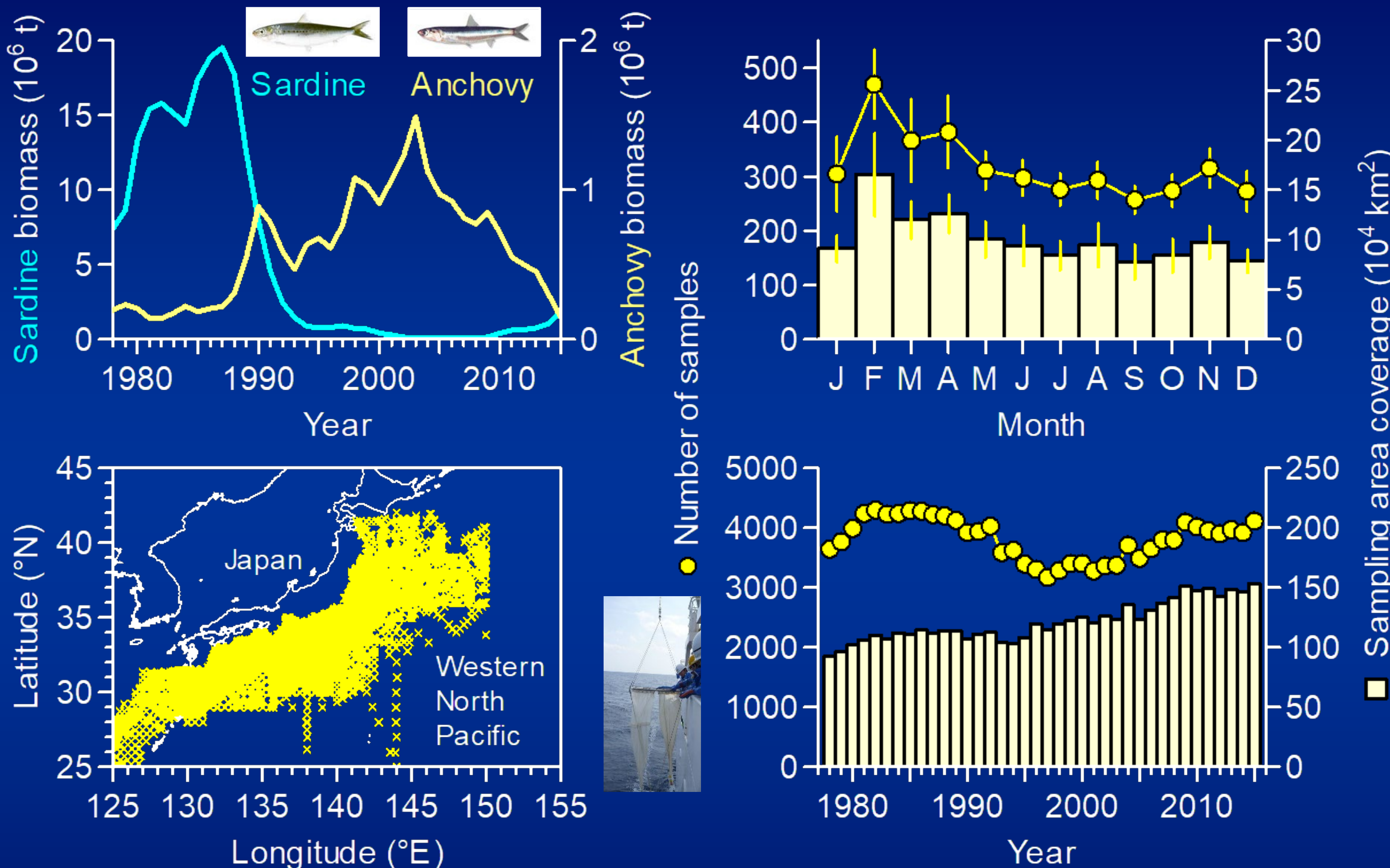
Egg surveys

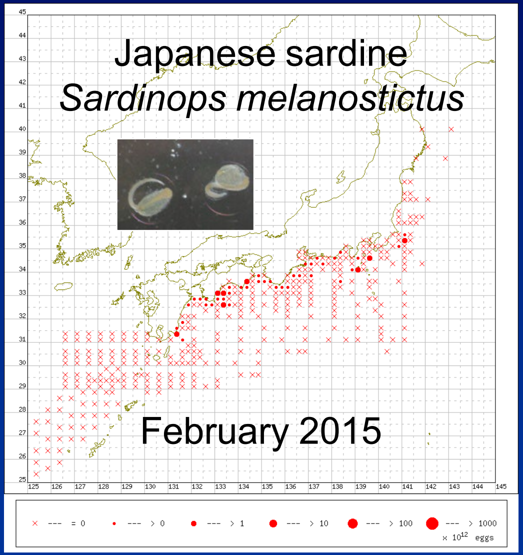


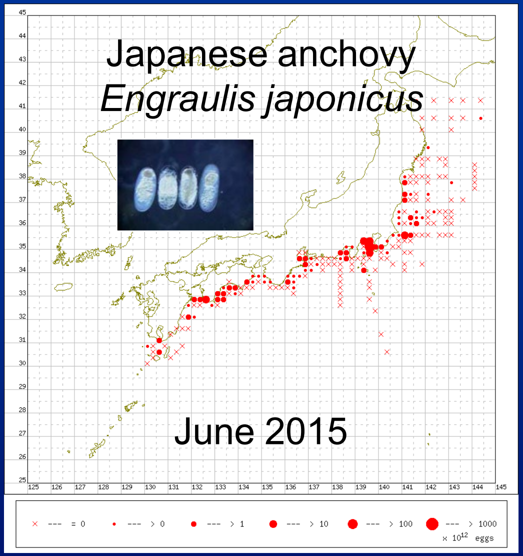
Egg surveys covering the spawning grounds during the high- and low-biomass periods of sardine and anchovy in the western North Pacific from 1978 to 2015 (38 years). The data set includes a total of 145,157 vertical tows of plankton nets.

Egg production

Annual total egg production (TEP)

1. Monthly mean egg density for each 15’ × 15’ (latitude × longitude) square
2. Monthly egg abundance for each square
   = monthly mean egg density for each square × square area
3. The parameters considered to realistically assess the quantitative data:
   - Egg developmental stage
   - Egg incubation time (a function of temperature)
   - Egg survival rate
4. Monthly egg abundance
   = sum of monthly egg abundance for all the squares
5. Annual total egg production (TEP)
   = sum of monthly egg abundance for all the months
   - Sardine: October of the previous year to September of the year
   - Anchovy: January to December of the year





Examples of distributions of monthly egg production.

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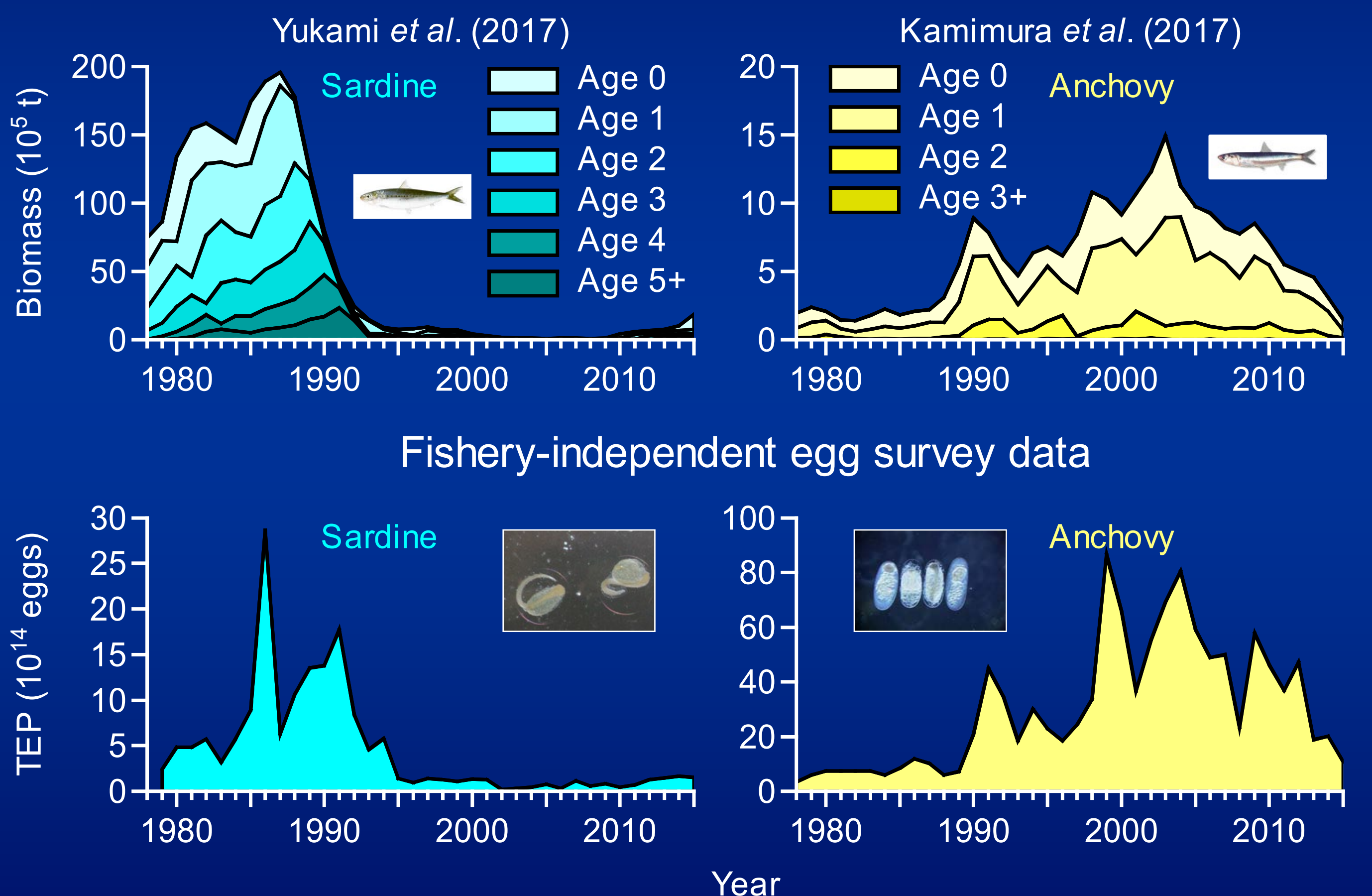
Biomass and TEP

A combination of two independent 38-year time series

Fishery-dependent stock assessment data
(derived from stock assessment reports)



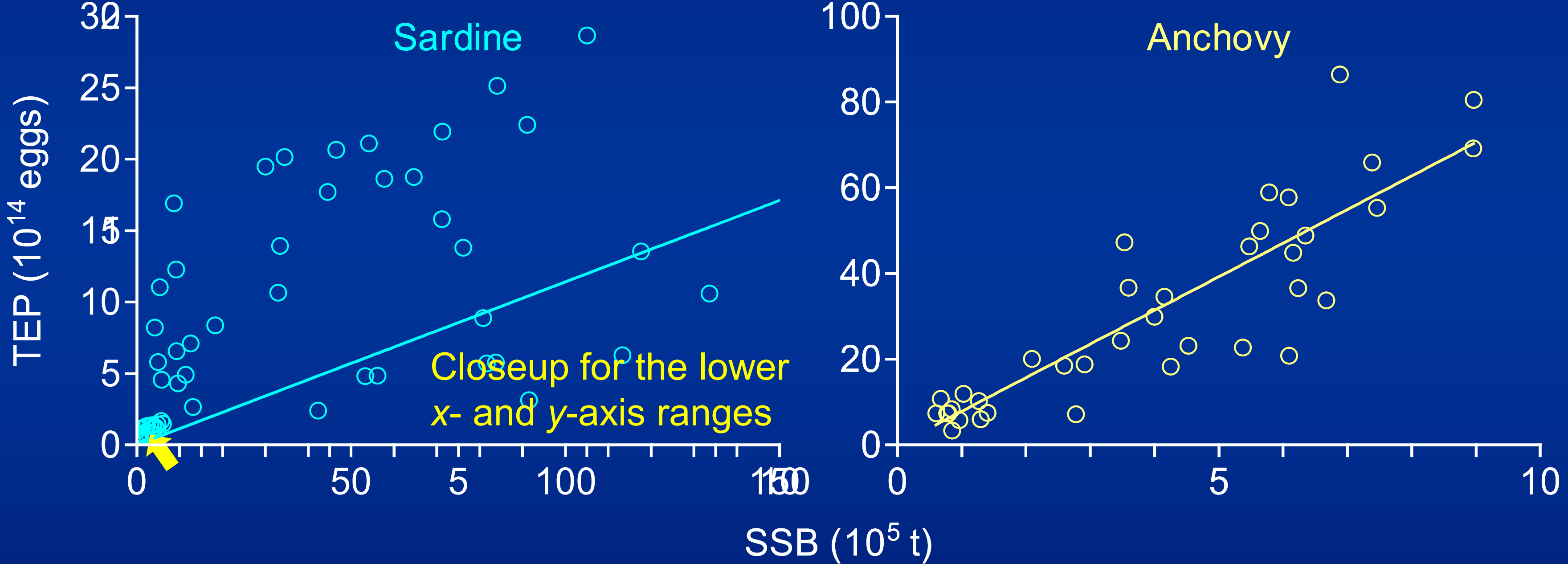
Multidecadal changes in biomass and annual total egg production (TEP) of the Pacific stocks of sardine and anchovy.

Takasuka *et al*.

TEP vs SSB

Direct test of the "SSB–TEP proportionality" paradigm based on a combination of two independent 38-year time series

- Spawning stock biomass (SSB): fishery-dependent stock assessment data
- Annual total egg production (TEP): fishery-independent egg survey data



$y = 114 \times 10^6 x$
(n = 37, R^2 = 0.636, $p < 0.001$)

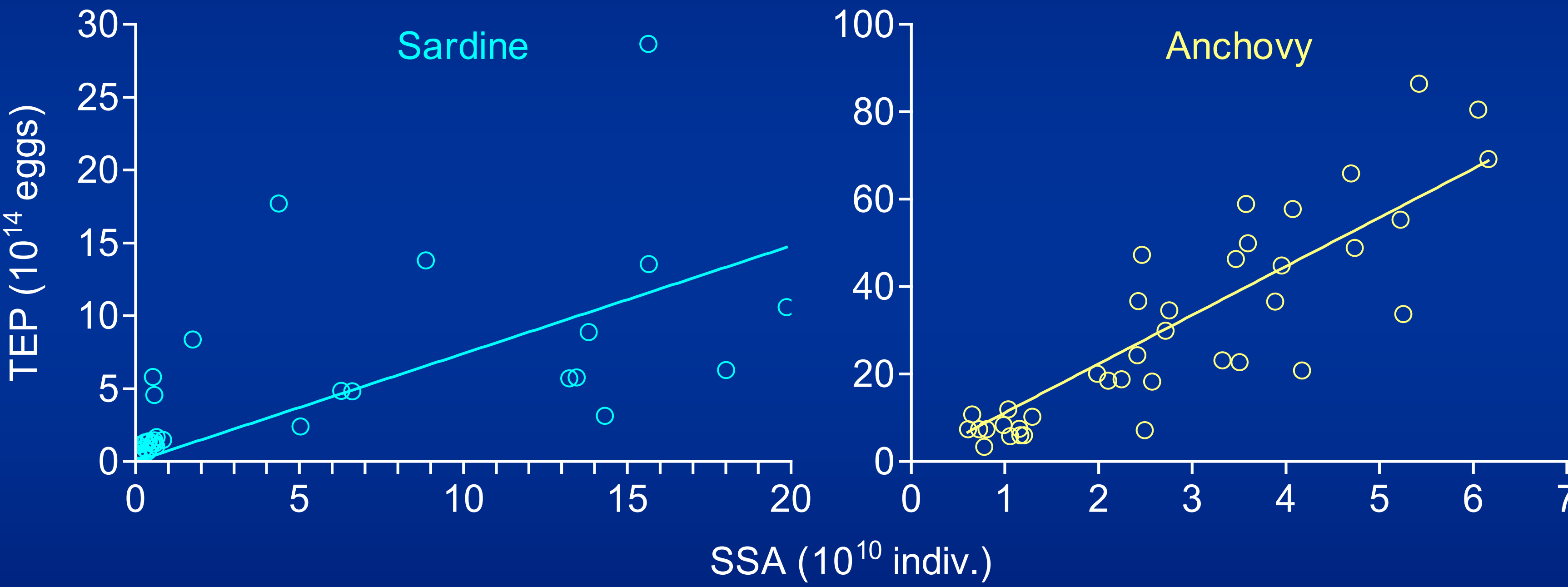
$y = 7792 \times 10^6 x$
(n = 38, R^2 = 0.917, $p < 0.001$)

Relationships of annual total egg production (TEP) to spawning stock biomass (SSB) for sardine and anchovy.

TEPPS

Annual total egg production per spawner individual (TEPPS)

= Annual total egg production (TEP) / spawning stock abundance (SSA)
= How many eggs are produced from an individual spawner for a year
= Annual realized fecundity (integrating batch fecundity, spawning fraction, etc.)



$y = 7{,}400 \times x$
($n = 37$, $R^2 = 0.353$, $p < 0.001$)

$y = 111{,}605 \times x$
($n = 38$, $R^2 = 0.754$, $p < 0.001$)

Relationships of annual total egg production (TEP) to spawning stock abundance (SSA) for sardine and anchovy.

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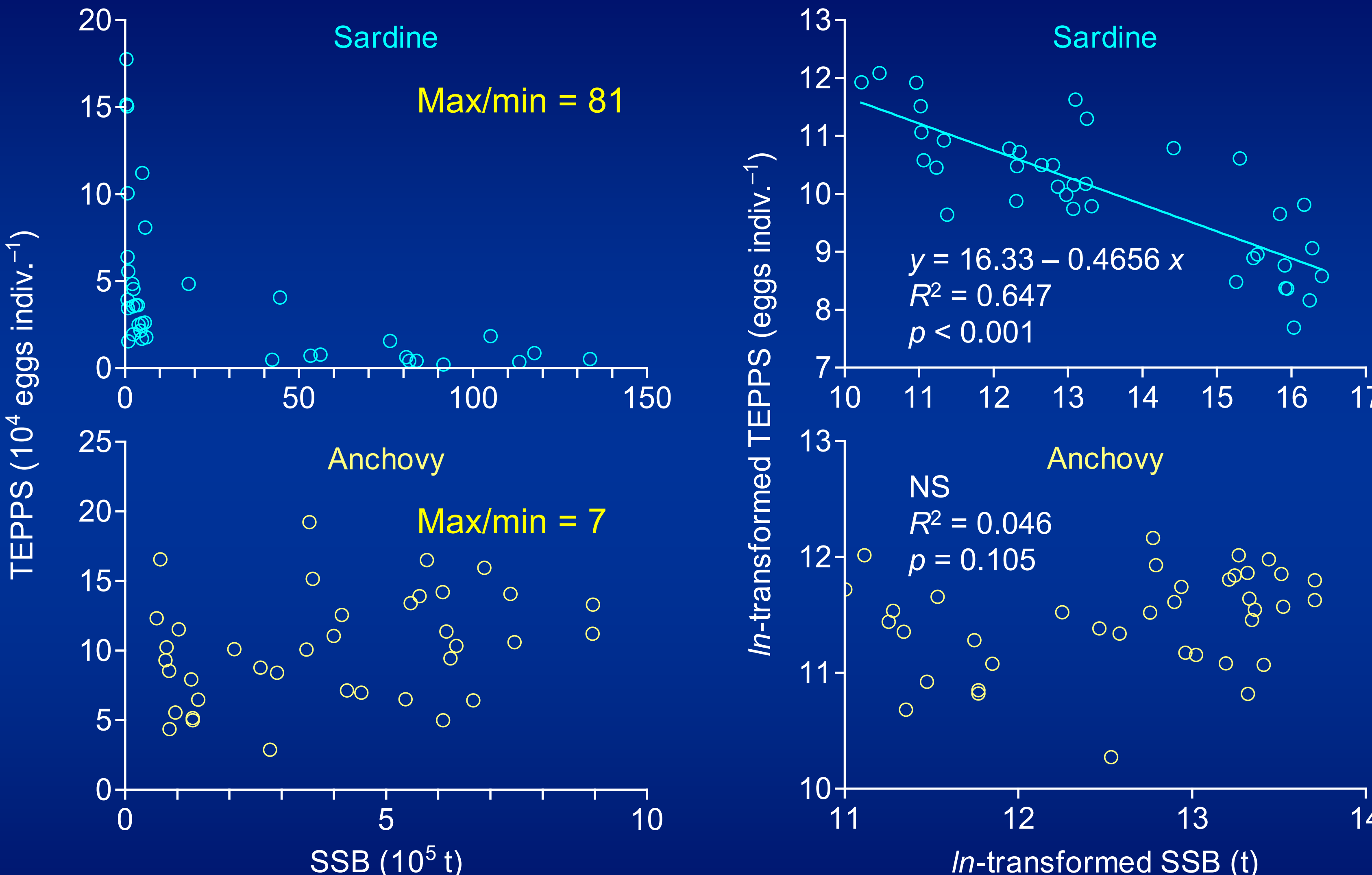
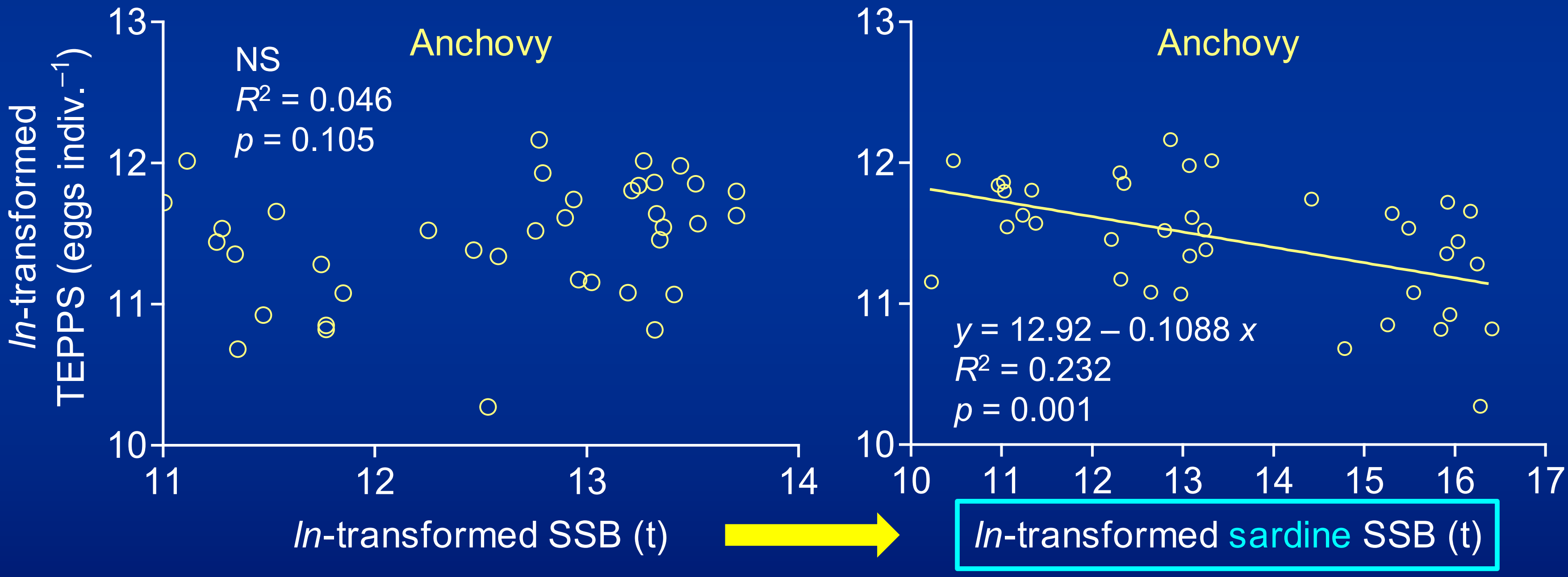
TEPPS vs SSB



Relationships of annual total egg production per spawner (TEPPS) to spawning stock biomass (SSB) for sardine and anchovy.

TEPPS vs SSB

- A significantly negative relationship appeared when anchovy TEPPS was related to sardine SSB.
- Hypothesis: Anchovy TEPPS is influenced by sardine biomass.
- Analysis: seasonal/regional anchovy TEPPS versus sardine SSB.



Relationships of annual total egg production per spawner (TEPPS) of anchovy to spawning stock biomass (SSB) of sardine.

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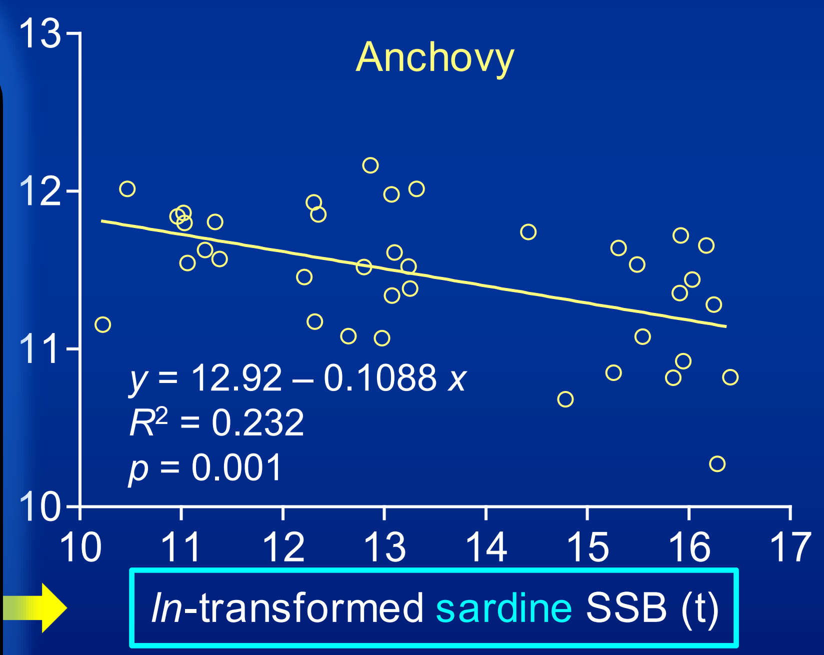
TEPPS vs SSB

- A significantly negative relationship appeared when anchovy TEPPS was related to sardine SSB.
- Hypothesis: Anchovy TEPPS is influenced by sardine biomass.
- Analysis: seasonal/regional anchovy TEPPS versus sardine SSB.

- The negative relationship of anchovy TEPPS to sardine SSB became stronger under the intensive spawning overlap between sardine and anchovy (in the coastal waters from winter to spring).
- The relationship became weaker under the less spawning overlap.
- The relationship disappeared under no spawning overlap.

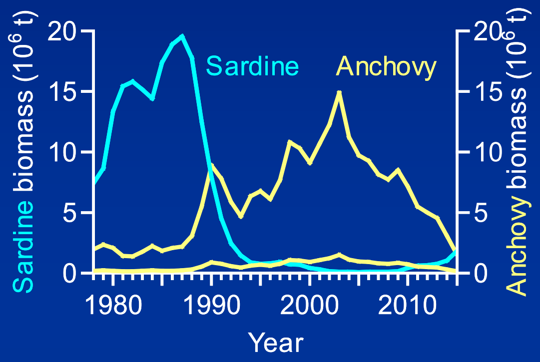


a... ...ction per spawner (TEPPS) of ... (SSB) of sardine.

Summary

Direct test of the paradigm

- We directly tested the "SSB–TEP proportionality" paradigm based on a combination of two independent time series.
- The proportionality is partially distorted by density-dependent egg production.



Density-dependent egg production

- Marked difference between the species.
  Sardine: intraspecific (self-density-dependent)
  Anchovy: interspecific (sardine-density-dependent)
- The phenomena would be attributable to maternal effects through intraspecific and interspecific competition for food resources required as energy for reproduction.
- Density-dependent egg production was previously unaccounted for in spawner–recruitment relationships.
- How does the existence of density-dependent egg production change the current understanding of density-dependent processes in the life history of fish?

Density-dependent egg production in small pelagic fish: a key to life cycle closure

1. Density-dependent egg production

- Evidence of density-dependent egg production through a direct test of the paradigm of fisheries science

2. Disentangling density-dependent effects

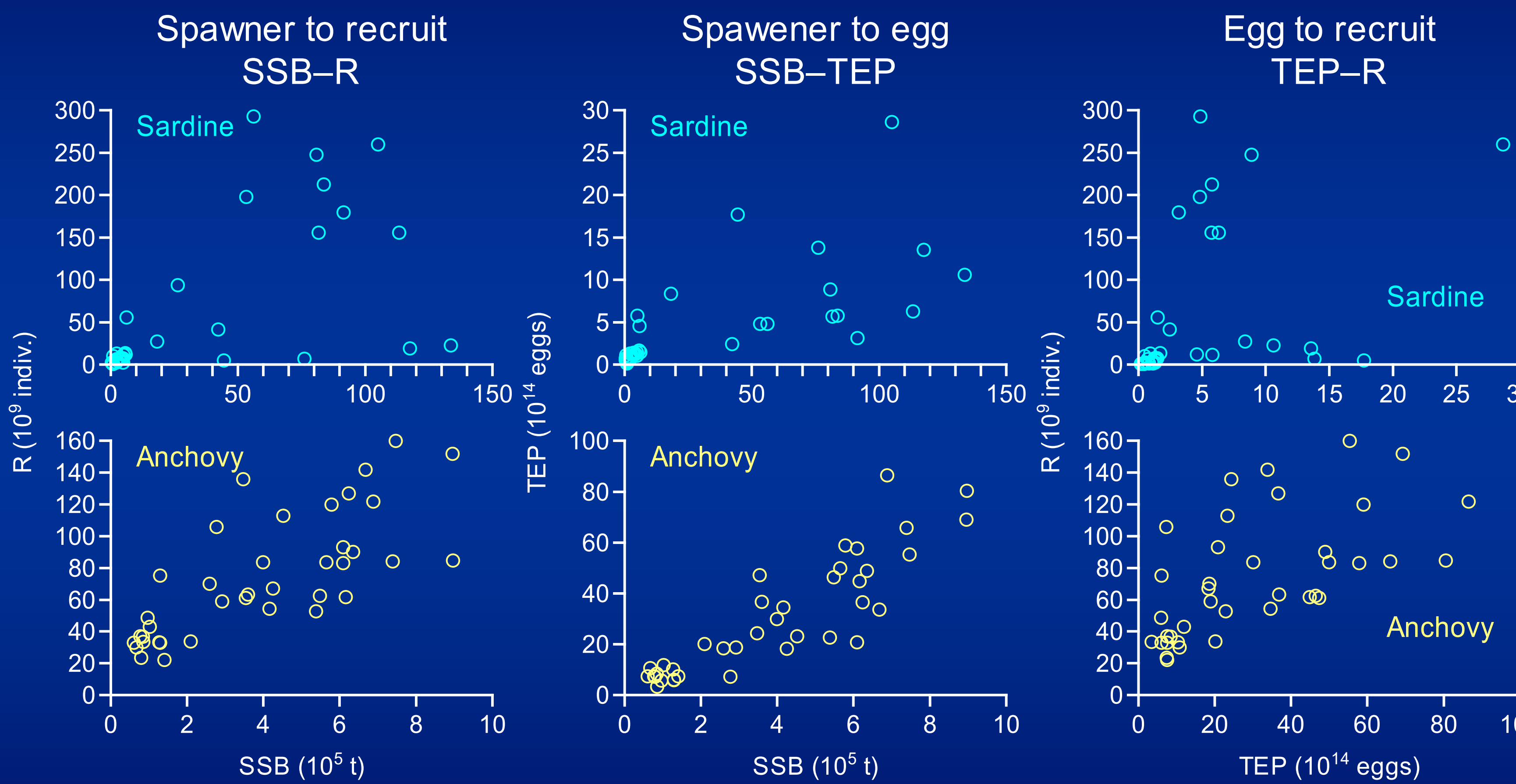
- Disentangling density-dependent effects on egg production and survival from egg to recruitment

3. Application to recruitment studies

- Revisiting sardine recruitment hypotheses by an egg-production-based survival index

Disentangling

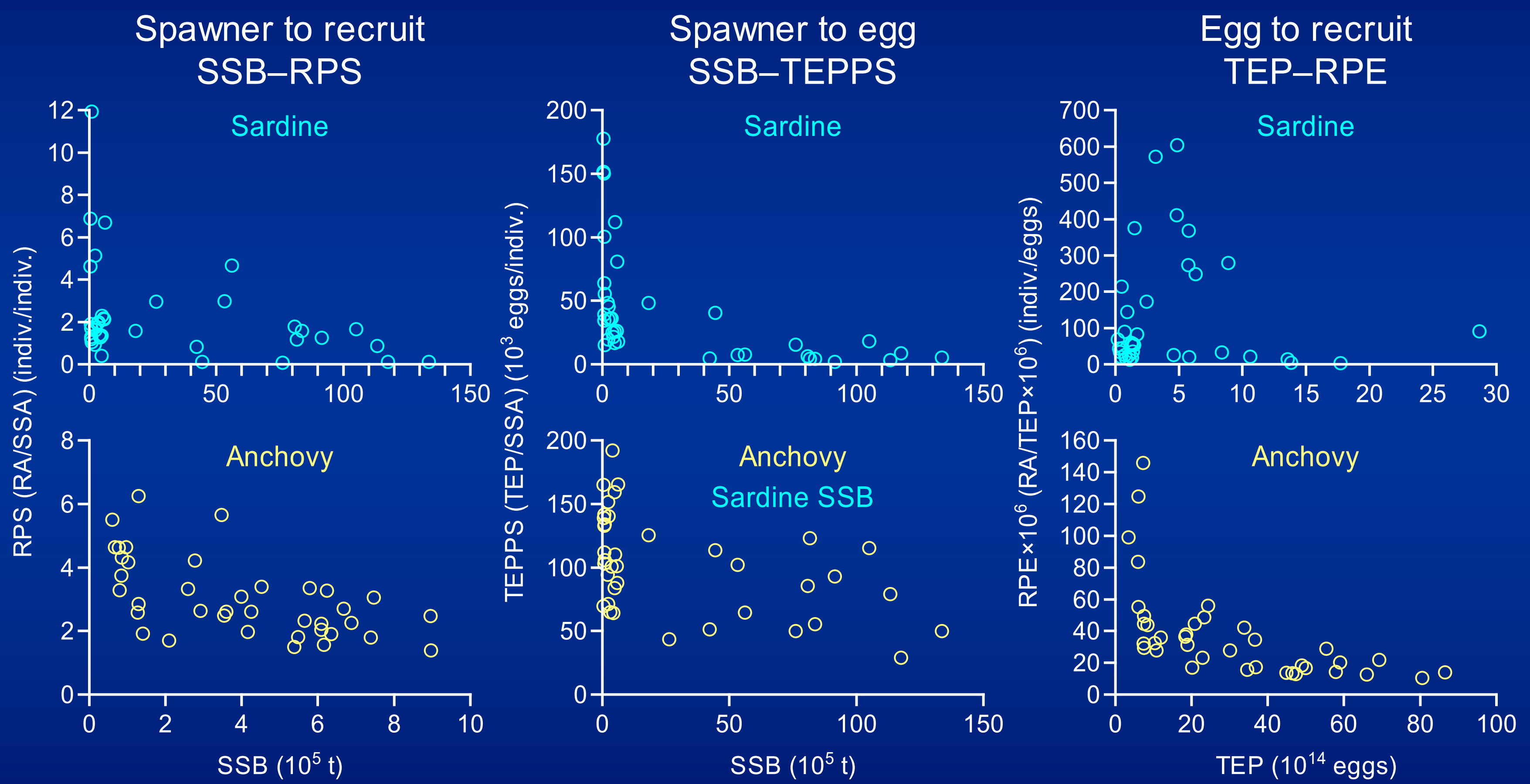
Disentangling density-dependent effects on egg production and survival from egg to recruitment



Relationships among spawning stock biomass (SSB), annual total egg production (TEP), and recruitment (R) for sardine and anchovy.

Disentangling

Disentangling density-dependent effects on egg production and survival from egg to recruitment

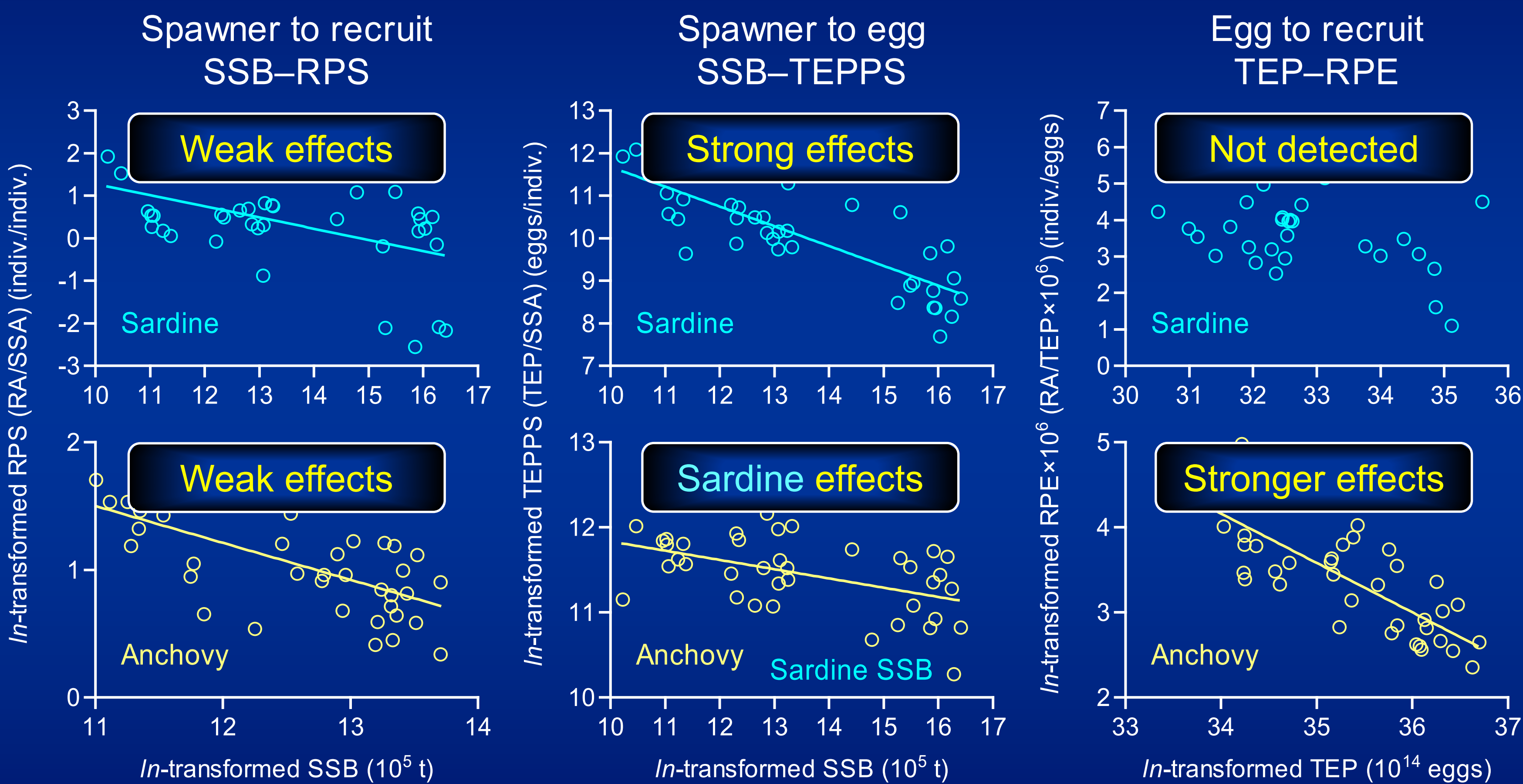


Relationships of recruitment per spawning stock abundance (RPS), annual total egg production per spawner (TEPPS), and recruitment per total egg production (RPE) to spawning stock biomass (SSB) and total egg production (TEP).

Takasuka *et al*.

Disentangling

Disentangling density-dependent effects on egg production and survival from egg to recruitment



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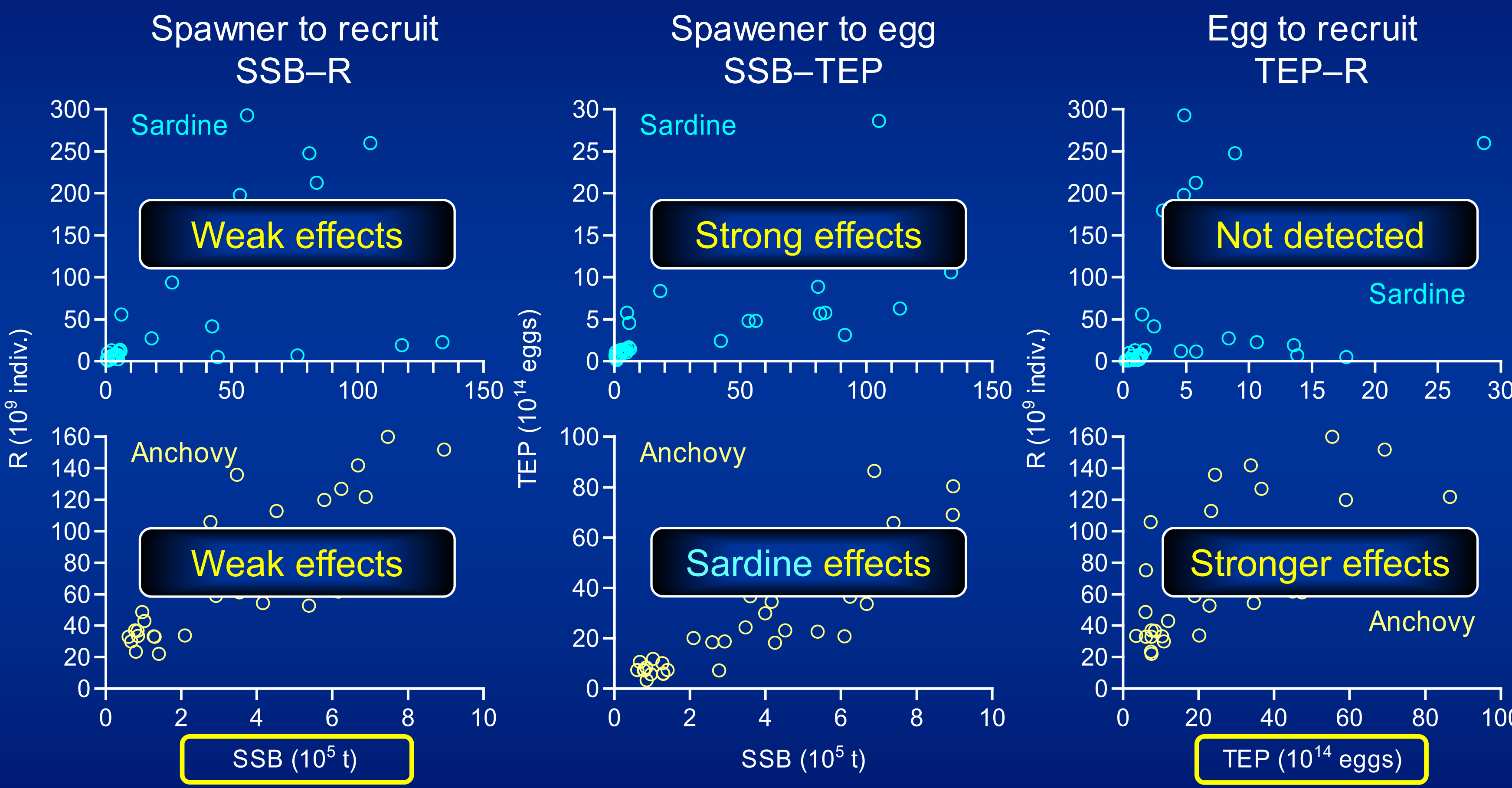


Relationships among spawning stock biomass (SSB), annual total egg production (TEP), and recruitment (R) for sardine and anchovy.

Summary

Disentangling density-dependent effects

- The existence of density-dependent egg production could change the current understanding of density-dependent processes in the life history of fish.
- Proposing to consider a shift from SSB-based to TEP-based strategies.

1. Implications for fisheries management

- Determining biological reference points based on TEP–R relationships rather than SSB–R relationships.
- Considering interspecific interactions in biological reference points.

2. Applications to recruitment studies

- Using TEP-based survival indices for the process from hatching to recruitment.

Perspectives

SSB-based framework

How much spawner biomass should be unexploited to ensure good recruitment?

↓

TEP-based framework

How much egg production is required to ensure good recruitment?

How much spawner biomass should be unexploited to ensure the egg production?

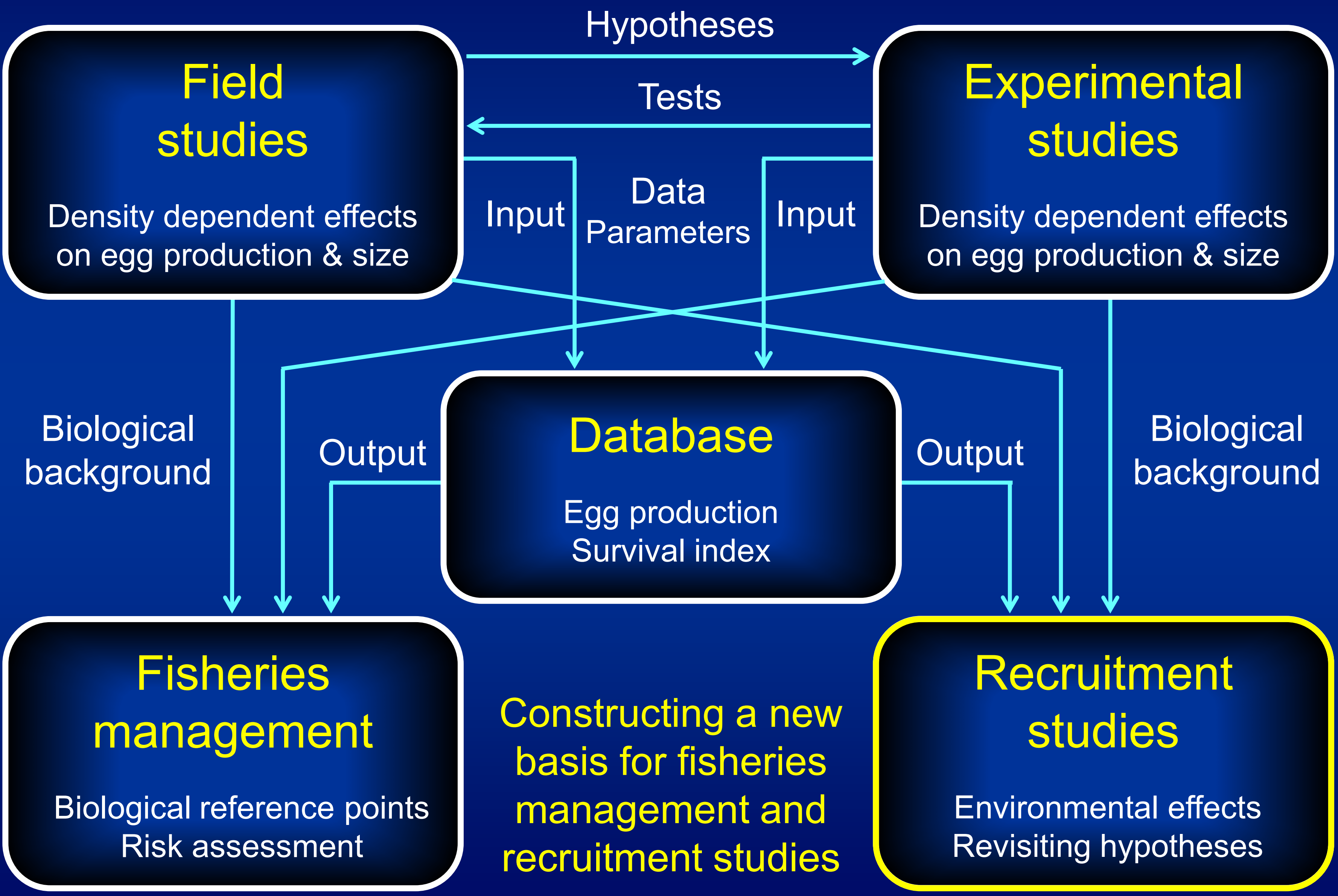
Advantages

1. Biological backgrounds
2. Interspecific interactions

Johan Hjort Symposium

Takasuka *et al*.

Project structure



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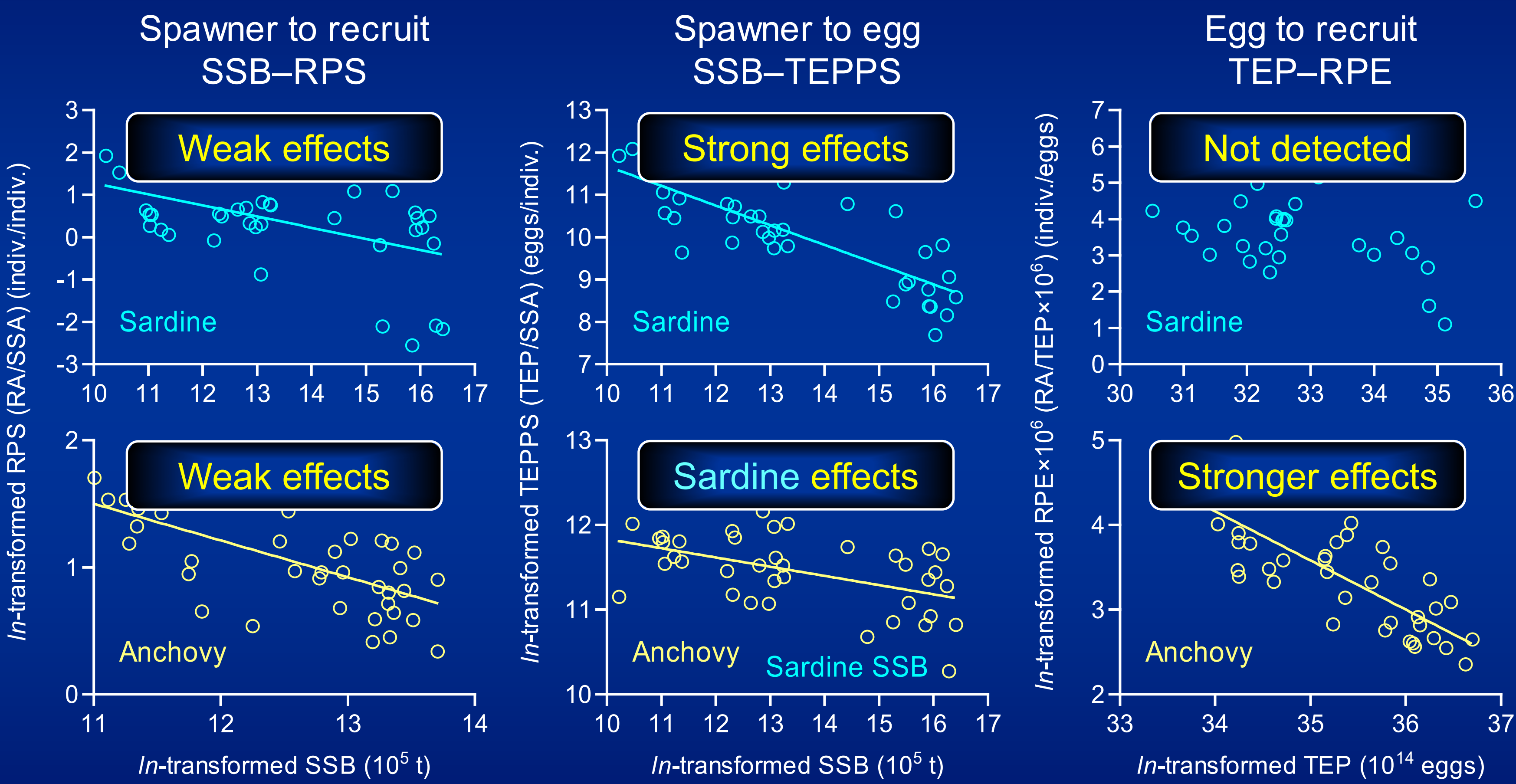

Relationships of recruitment per spawning stock abundance (RPS), annual total egg production per spawner (TEPPS), and recruitment per total egg production (RPE) to spawning stock biomass (SSB) and total egg production (TEP).

Survival indices

- Evidence of density dependence in egg production has led to a need to reconsider the validity of recruitment per spawning stock biomass (RPS), which has been used in previous recruitment studies.

Two indices for survival from hatching to recruitment

RPS
Recruitment per spawning stock biomass

- Traditionally adopted
- SSB-based index
- Based on the "SSB–TEP proportionality" paradigm

VS

RPE
Recruitment per egg production

- Newly proposed
- TEP-based index
- Based on the density dependent egg production

- Revisiting sardine recruitment hypotheses based on the two survival indices by reanalyzing published data for the Pacific stock of Japanese sardine in the Kuroshio Current system at a multidecadal scale.

Hypotheses revisited

Hypothesis	Original source	Data	Period	Hypothetical relationship to survival index
"**Climate index**" Large-scale ocean climate anomaly	Mantua & Hare (2002)	Wintertime Pacific Decadal Oscillation (PDO) index	1979–2015 (37 years)	Positive
"**Ambient temperature**" Ambient temperature in the nursery grounds	Nishikawa (2019)	Sea surface temperature (SST) in the vicinity of the Kuroshio axis during the winter to early spring seasons (Kuroshio SST)	1982–2012 (31 years)	Negative
"**Growth rate**" Growth rate during the early life stages	Takasuka *et al*. (2007)	Growth rate during the larval stage estimated from the Kuroshio SST based on the dome-shaped relationship of larval growth rate to temperature	1982–2012 (31 years)	Positive
	Furuichi *et al*. (2020)	Growth rate during the early juvenile stage estimated through otolith microstructure analysis (samples collected in the Kuroshio–Oyashio transition region during May to June)	1996–2015 (20 years)	Positive

Hypotheses revisited

<table>
<tr><th>Hypothesis</th><th>Original source</th><th>Data</th><th>Problem</th></tr>
<tr><td>“Climate index”
Large-scale ocean climate anomaly</td><td>Mantua & Hare (2002)</td><td>Wintertime Pacific Decadal Oscillation (PDO) index</td><td>Inconsistency between the timings of regime shifts and population dynamics</td></tr>
<tr><td>“Ambient temperature”
Ambient temperature in the nursery grounds</td><td>Nishikawa (2019)</td><td>Sea surface temperature (SST) in the vicinity of the Kuroshio axis during the winter to early spring seasons (Kuroshio SST)</td><td rowspan="3">Lack of significant relationships for periods extending over the high-biomass and low-biomass phases</td></tr>
<tr><td rowspan="2">“Growth rate”
Growth rate during the early life stages</td><td>Takasuka et al. (2007)</td><td>Growth rate during the larval stage estimated from the Kuroshio SST based on the dome-shaped relationship of larval growth rate to temperature</td></tr>
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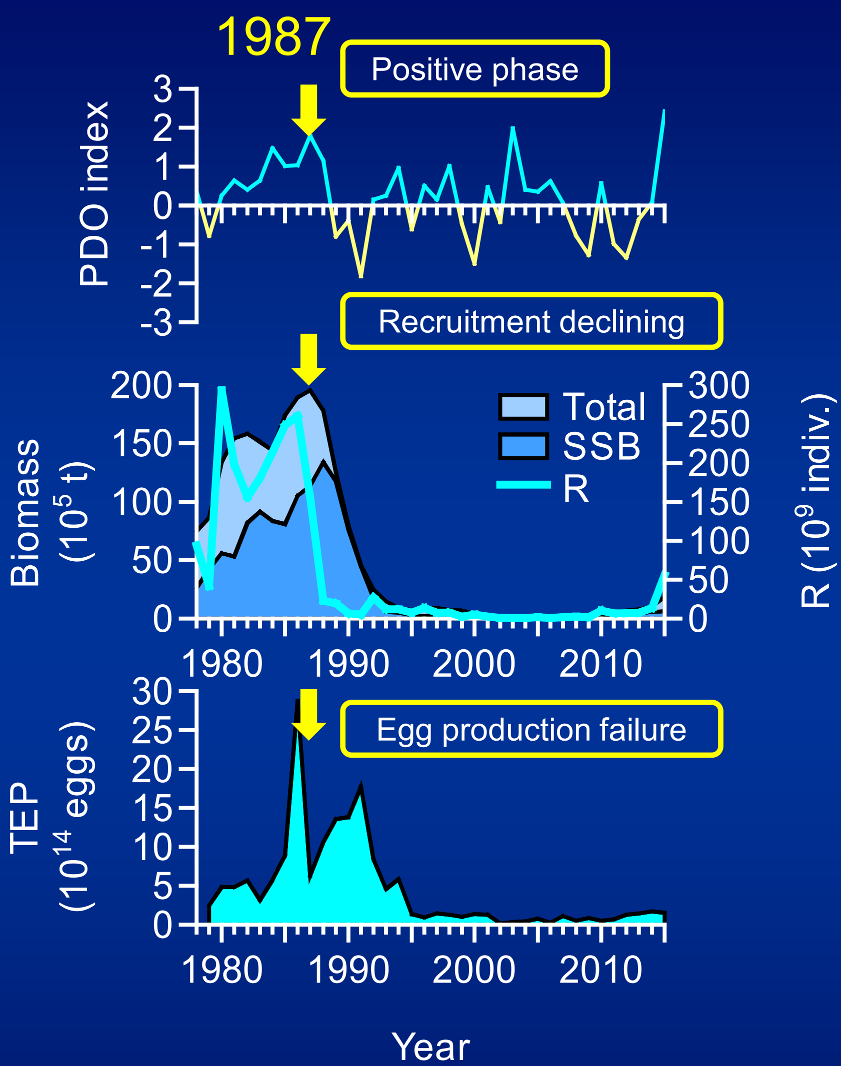
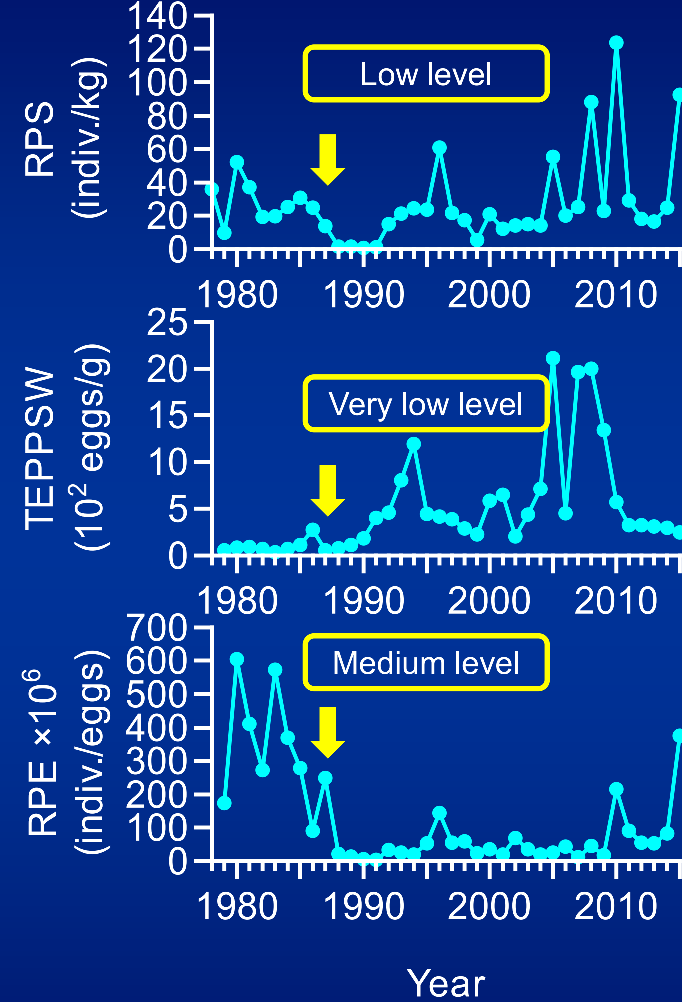
</table>

Takasuka *et al*.

Multidecadal variability

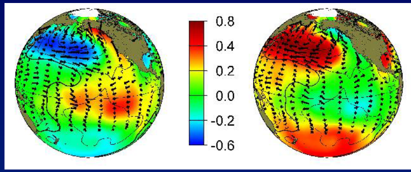




Multidecadal variability of biomass, recruitment, egg production, and production rates in the processes from spawner to recruit, spawner to egg, and egg to recruit for the Pacific stock of sardine under climate variability.

Takasuka *et al*.

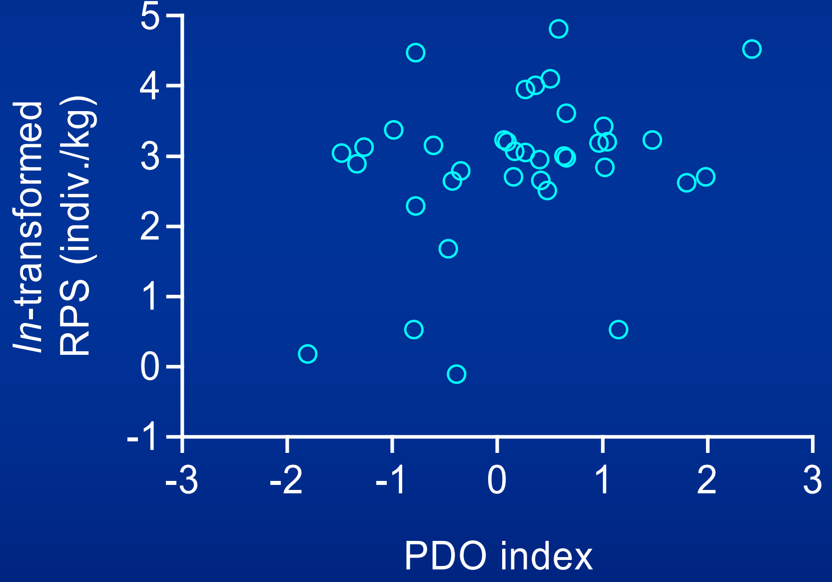
Climate index



"Climate index"

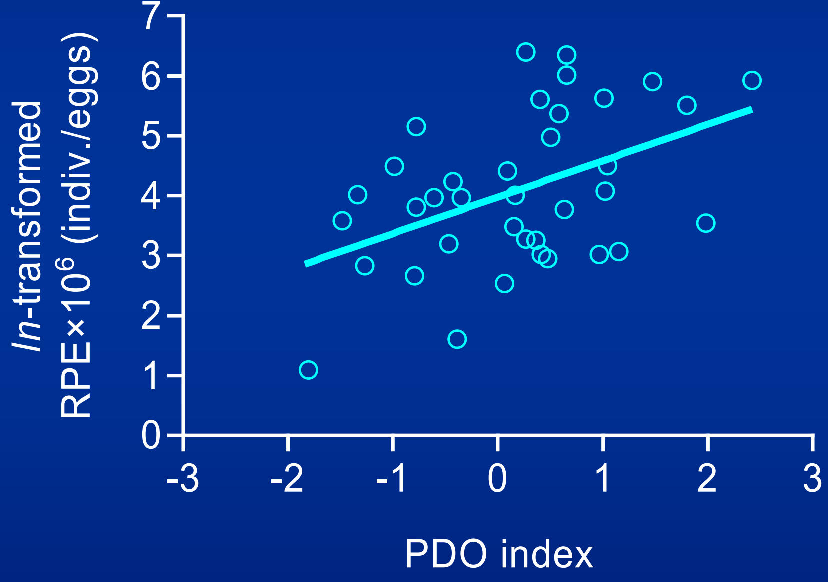
(large-scale ocean climate anomaly)

RPS (SSB-based)



Not significant
(n = 37, R^2 adjusted = 0.063, p = 0.073)

RPE (TEP-based)

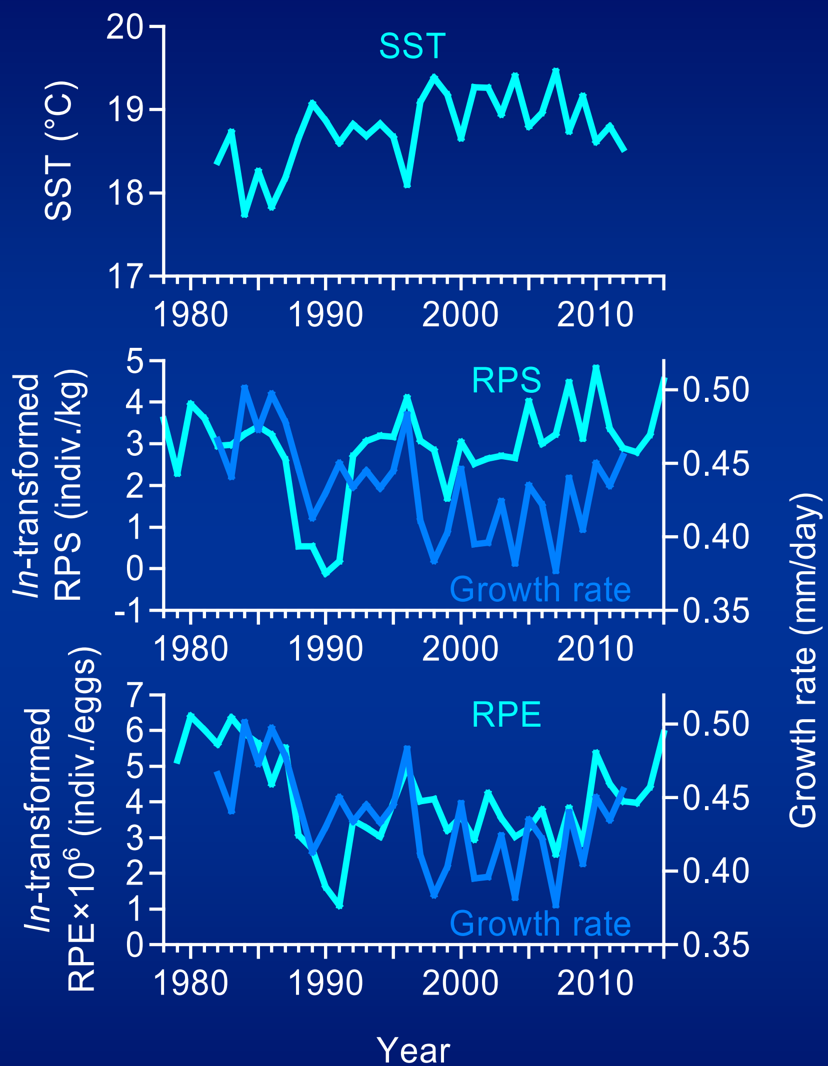


$y = 3.976 + 0.606\,x$
(n = 37, R^2 adjusted = 0.188, p = 0.004)

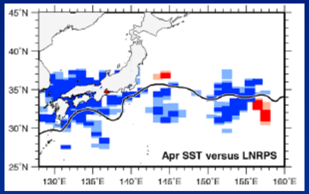
Relationships of survival indices for sardine to wintertime Pacific Decadal Oscillation (PDO) index from 1979 to 2015.

Takasuka *et al.*

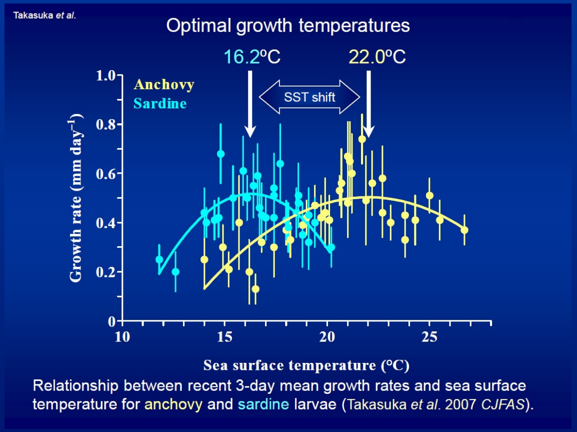
SST and growth rate



Sea surface temperature (SST) in the vicinity of the Kuroshio axis during the winter to early spring seasons (Kuroshio SST)



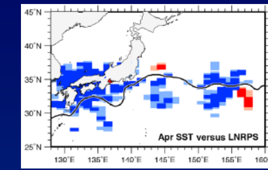
Growth rate during the larval stage estimated from the Kuroshio SST based on the dome-shaped relationship of larval growth rate to temperature



Multidecadal variability of growth rate and survival indices for sardine under temperature variability from 1982 to 2012.

Takasuka *et al.*

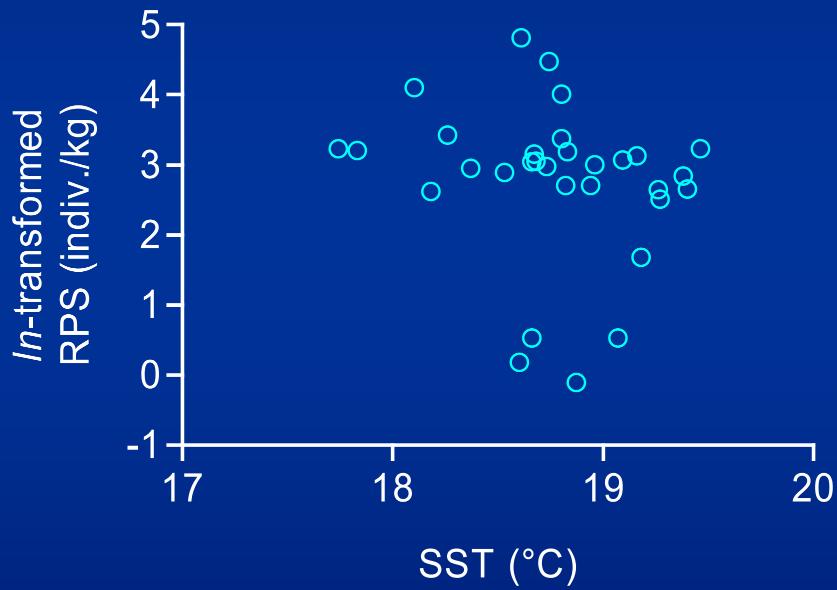
Ambient temperature



"Ambient temperature"

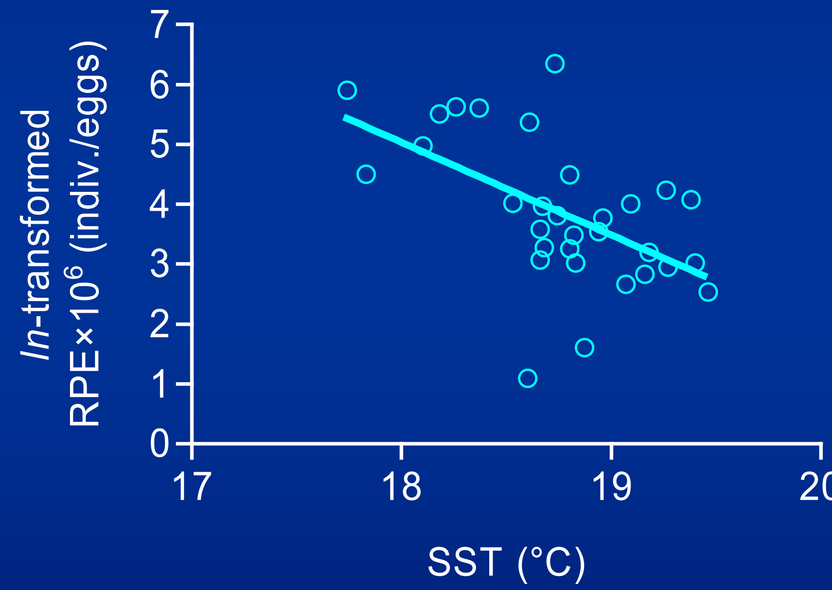
(ambient temperature in the nursery grounds)

RPS (SSB-based)



Not significant
(n = 31, R^2 adjusted = 0.005, p = 0.295)

RPE (TEP-based)



$y = 32.386 - 1.545\,x$
(n = 31, R^2 adjusted = 0.274, p = 0.001)

Relationships of survival indices for sardine to sea surface temperature (SST) in the vicinity of the Kuroshio axis during the winter to early spring seasons (Kuroshio SST) from 1982 to 2012.

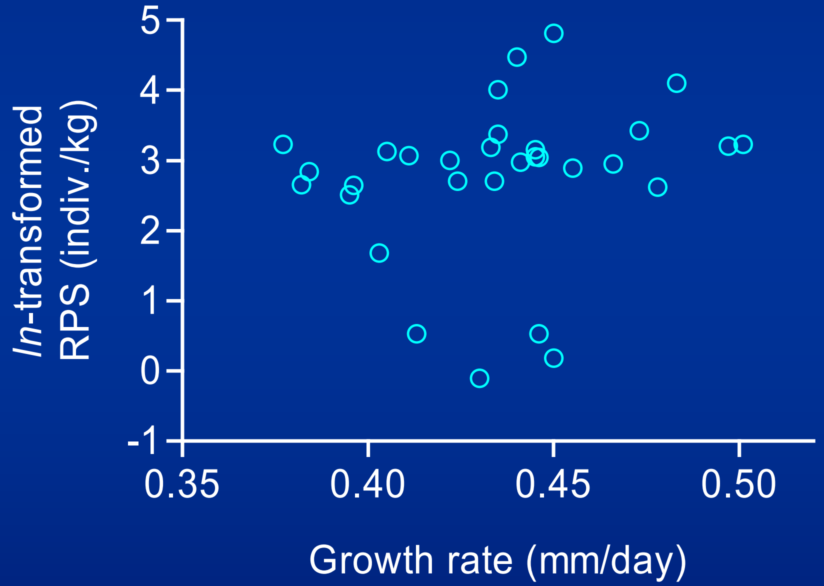
Takasuka *et al*.

Growth rate

"Growth rate" Larvae

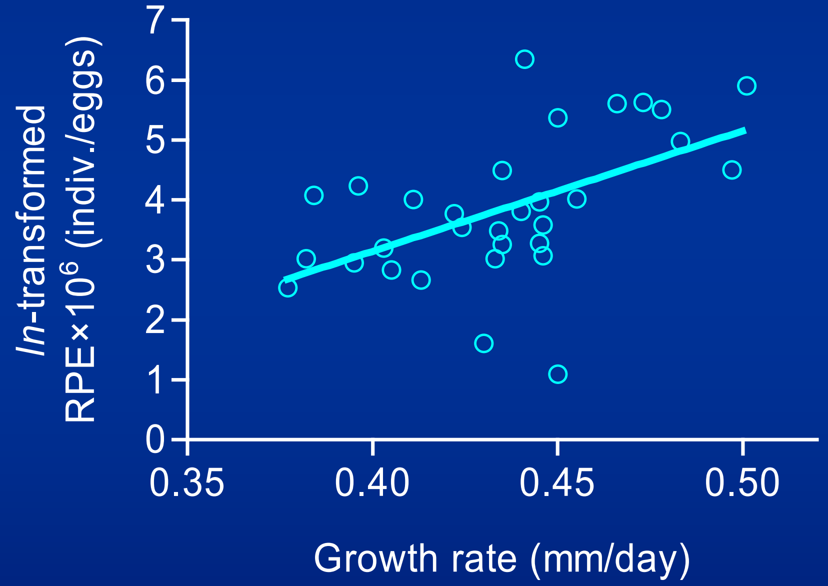
(growth rate during the early life stages)

RPS (SSB-based)



Not significant
(n = 31, R^2 adjusted < 0.001, p = 0.322)

RPE (TEP-based)



$y = -4.896 + 20.096x$
(n = 31, R^2 adjusted = 0.255, p = 0.002)

Relationships of survival indices for sardine to larval growth rate from 1982 to 2012. Larval growth rate was estimated from the Kuroshio SST based on the dome-shaped relationship of larval growth rate to temperature.

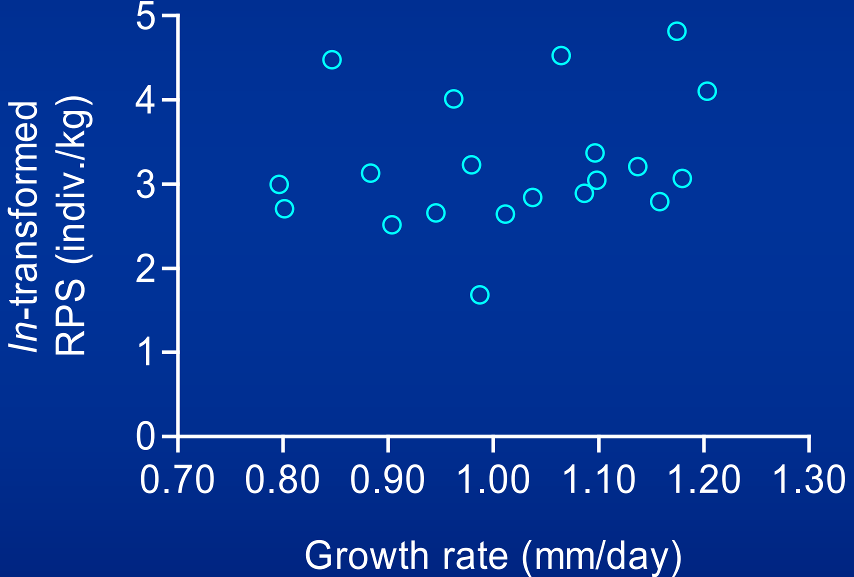
Takasuka *et al*.

Growth rate

“Growth rate” Juveniles

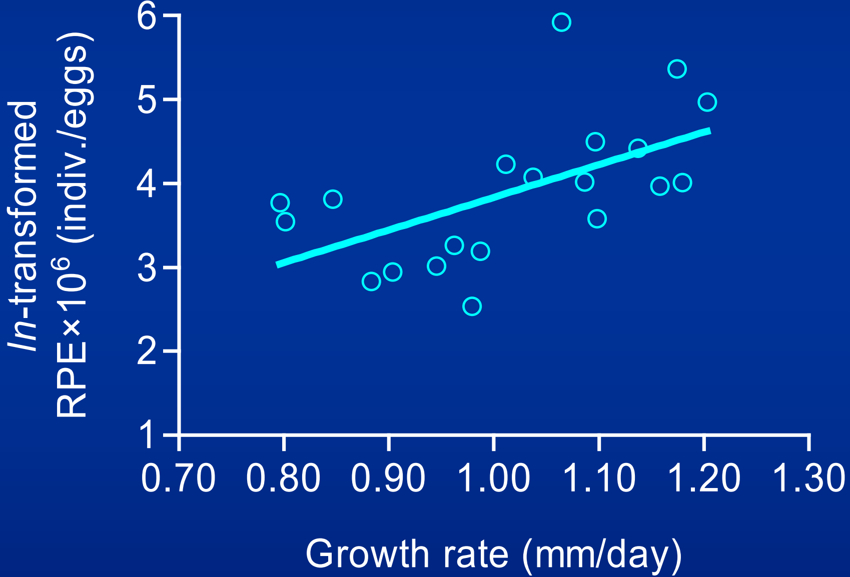
(growth rate during the early life stages)

RPS (SSB-based)



Not significant
(n = 20, R^2 adjusted = 0.003, p = 0.319)

RPE (TEP-based)



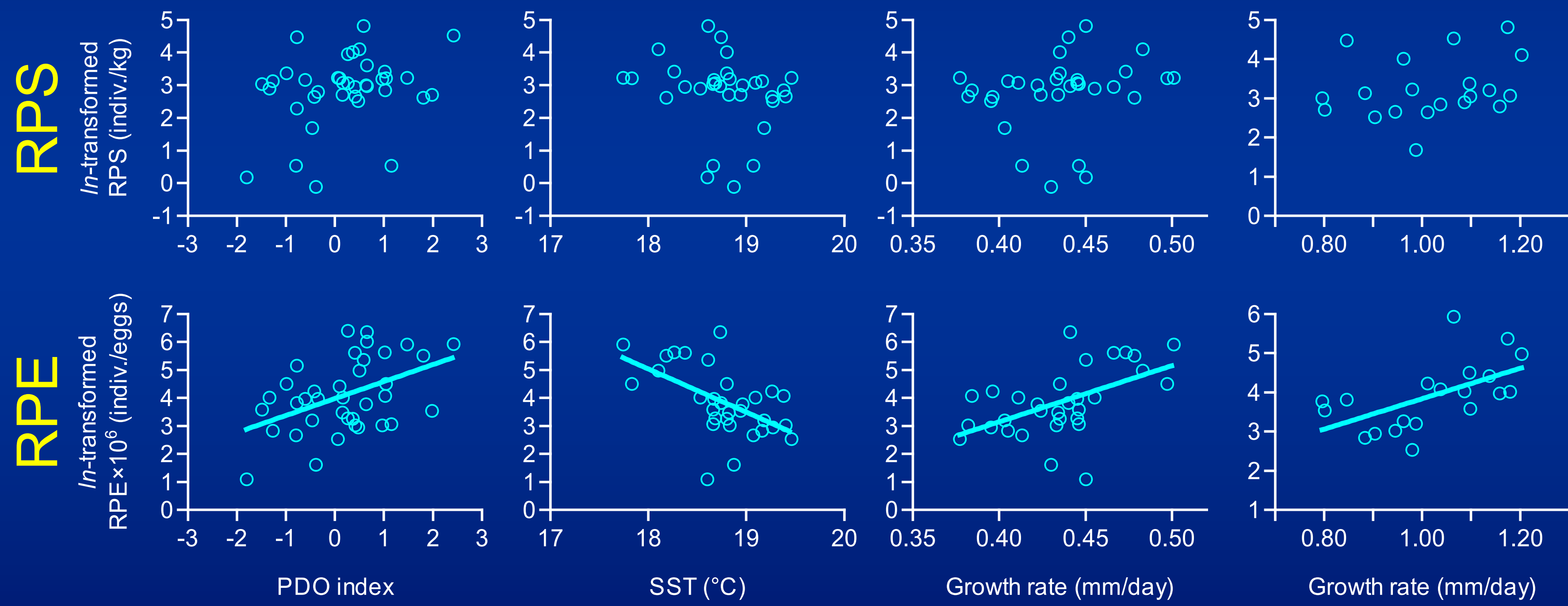
$y = -0.051 + 3.885x$
(n = 20, R^2 adjusted = 0.292, p = 0.008)

Relationships of survival indices for sardine to early juvenile growth rate from 1996 to 2015. Post-metamorphosis growth rate of juveniles was estimated through otolith microstructure analysis.

Takasuka *et al.*

Revisiting hypotheses

"Climate index"	"Ambient temperature"	"Growth rate"	"Growth rate"
Wintertime Pacific Decadal Oscillation (PDO) index	Sea surface temperature (SST) in the vicinity of the Kuroshio axis during winter to early spring (Kuroshio SST)	Larval growth rate estimated from the Kuroshio SST based on the dome-shaped relationship of larval growth rate to SST	Juvenile growth rate estimated through otolith microstructure analysis (the Kuroshio–Oyashio transition region during May to June)



Relationships of survival indices for sardine to climate index (large-scale ocean climate anomaly), ambient temperature (ambient temperature in the nursery grounds), and growth rate (growth rate during the early life stages) at a multidecadal scale.

Summary

Revisiting sardine recruitment hypotheses

- We revisited sardine recruitment hypotheses based on the two survival indices by reanalyzing the published data.
    - Recruitment per spawning stock biomass (RPS): SSB-based index
    - Recruitment per egg production (RPE): TEP-based index
- By adopting RPE, we detected statistically significant relationships of the survival from hatching to recruitment to the following factors.

  (1) "Climate index": large-scale ocean climate anomaly
  (2) "Ambient temperature": ambient temperature in the nursery grounds
  (3) "Growth rate": growth rate during the early life stages
- None of these relationships were detected by RPS.

Proposals

- We propose the adoption of TEP-based survival indices rather than SSB-based ones in future studies on recruitment mechanisms of fish.
- Developing egg-production-based survival indices has the potential to improve understanding of recruitment mechanisms of fish under climate variability.

Paradigms

Leggett & Frank (2008)

"Paradigms in fisheries oceanography"

1. Spawning stock biomass (SSB) is a suitable proxy for the reproductive potential of a stock.
2. Marine fish eggs and larvae are generally designed for dispersion and potential colonization (panmixia).
3. In marine temperate systems, fish spawn in springtime so that peak larval abundance coincides with maximum prey availability (Cushing's match/mismatch hypothesis).
4. Environmentally based recruitment models, when updated with new data, invariably fail; recruitment prediction is an intractable problem, particularly when it is based on processes associated with the growth and mortality of the early life-history stages.
5. Populations cannot irreversibly collapse/collapsed populations will recover in the absence of fishing.
6. Fish stocks can be managed in isolation from their total environment/habitat.
7. Population recovery is synonymous with rebuilding.

Paradigms

Leggett & Frank (2008)

"Paradigms in fisheries oceanography"

1. Spawning stock biomass (SSB) is a suitable proxy for the reproductive potential of a stock.

4. Environmentally based recruitment models, when updated with new data, invariably fail; recruitment prediction is an intractable problem, particularly when it is based on processes associated with the growth and mortality of the early life-history stages.

- We suppose a possible reason for the 4th paradigm is that previous studies failed to evaluate the survival success/failure during the early life stages based on the 1st paradigm.
- Previous findings or hypotheses need to be re-evaluated by an appropriate survival index.
- The assumed relationships may be strengthened, or new relationships may be unveiled.

Hypotheses revisited

Hypothesis	Original source	Data	Problem
"Climate index" Large-scale ocean climate anomaly	Mantua & Hare (2002)	Wintertime Pacific Decadal Oscillation (PDO) index	Inconsistency between the timings of regime shifts and population dynamics
"Ambient temperature" Ambient temperature in the nursery grounds	Nishikawa (2019)	Sea surface temperature (SST) in the vicinity of the Kuroshio axis during the winter to early spring seasons (Kuroshio SST)	**Solved by RPE.** The timings were actually consistent.
"Growth rate" Growth rate during the early life stages	Takasuka *et al*. (2007)	Growth rate during the larval stage estimated from the Kuroshio SST based on the dome-shaped relationship of larval growth rate to temperature	Lack of significant relationships for periods extending over the high-biomass and low-biomass phases **Solved by RPE.** Significant relationships were detected for the extended periods.
	Furuichi *et al*. (2020)	Growth rate during the early juvenile stage estimated through otolith microstructure analysis (samples collected in the Kuroshio–Oyashio transition region during May to June)	

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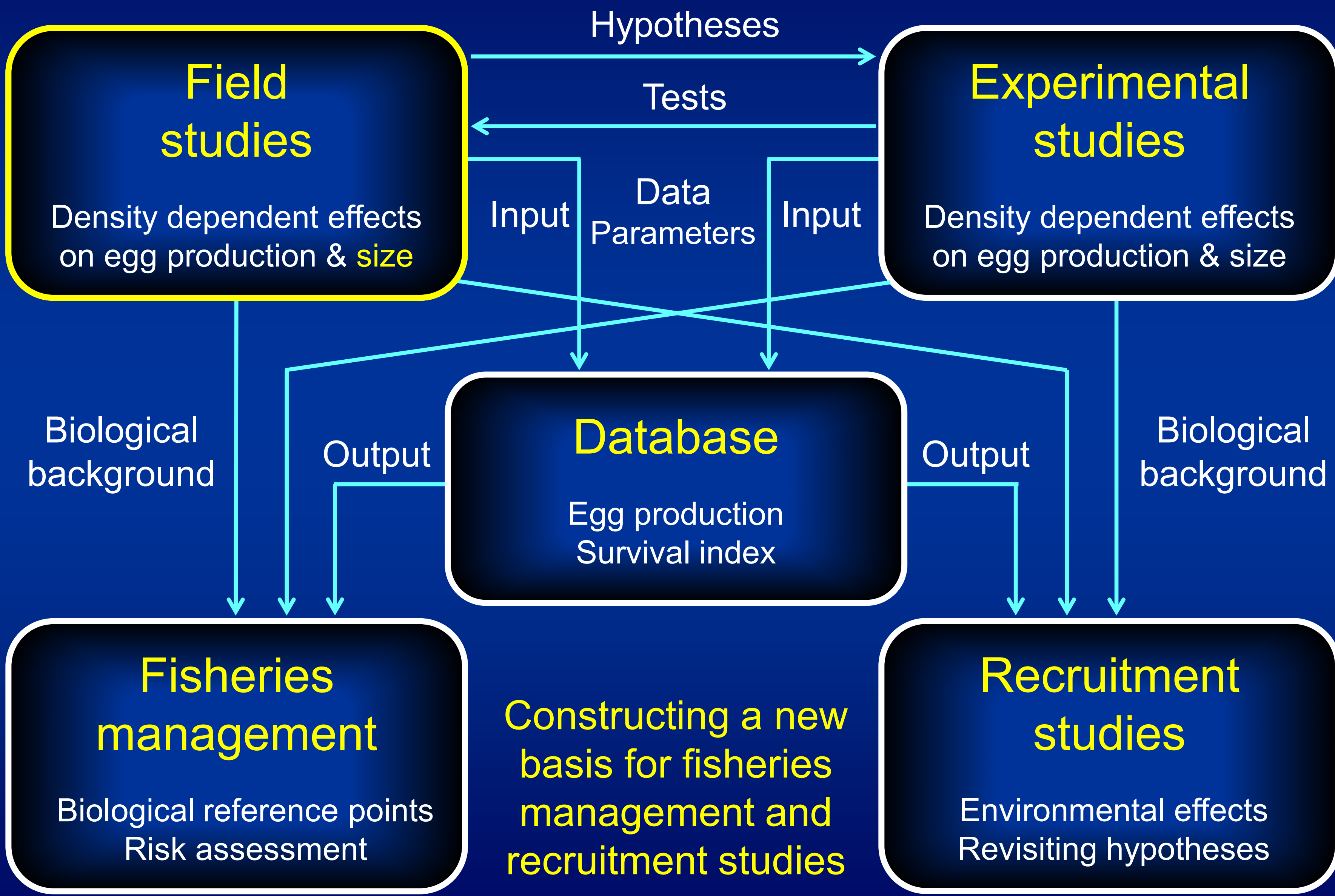
Takasuka *et al*.

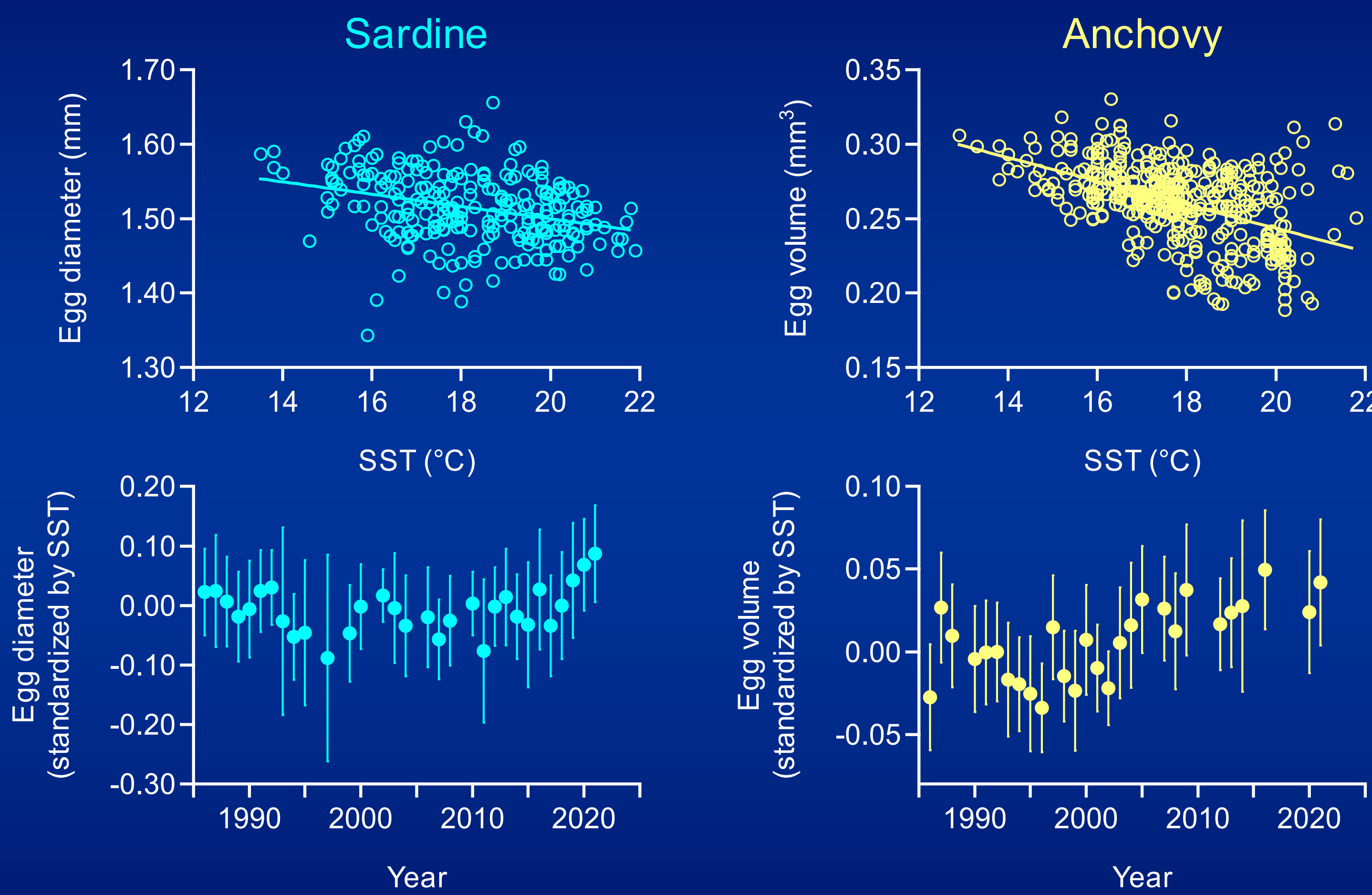
Project structure

How about size?



Egg size variability

Egg size variability at large spatial and temporal scales



Rikuto Utsugi *et al*.

Tomohiro Hirasawa *et al*.

Session 2: Life Cycle Closure: Advances in Process Understanding

Density-dependent egg production in small pelagic fish: a key to life cycle closure

1. Density-dependent egg production
   - Evidence of density-dependent egg production through a direct test of the paradigm of fisheries science

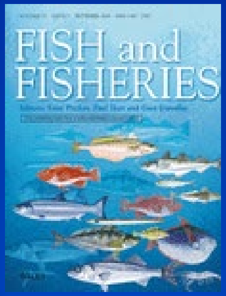
2. Disentangling density-dependent effects
   - Disentangling density-dependent effects on egg production and survival from egg to recruitment

3. Application to recruitment studies
   - Revisiting sardine recruitment hypotheses by an egg-production-based survival index

Publication

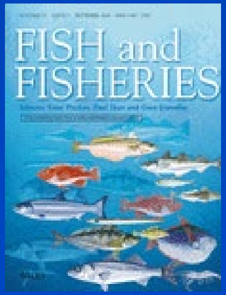
1. Takasuka, A., Yoneda, M., Oozeki, Y. (2019)
Density dependence in total egg production per spawner for marine fish.
Fish and Fisheries, 20: 125–137.

Density dependence
(sardine, anchovy)



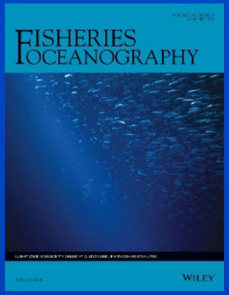
2. Takasuka, A., Yoneda, M., Oozeki, Y. (2019)
Disentangling density-dependent effects on egg production and survival from egg to recruitment in fish.
Fish and Fisheries, 20: 870–887.

Disentangling
(sardine, anchovy)



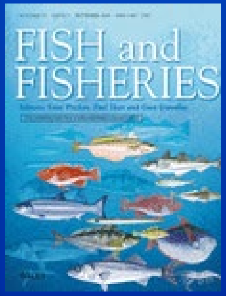
3. Takasuka, A., Yoneda, M., Oozeki, Y. (2021)
Density-dependent egg production in chub mackerel in the Kuroshio Current system.
Fisheries Oceanography, 30: 38–50.

Extension
(mackerel)



4. Takasuka, A., Nishikawa, H., Furuichi, S., Yukami, R. (2021)
Revisiting sardine recruitment hypotheses: Egg-production-based survival index improves understanding of recruitment mechanisms of fish under climate variability.
Fish and Fisheries, 22: 974–986.

Revisiting hypotheses
(sardine)

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Thank you for your attention.