Exploring hypotheses of mechanisms behind population dynamics of small pelagic fish: perspectives for comparative and collaborative research

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Graduate School of Agricultural and Life Sciences,
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"Small Pelagic Fish" Symposium
La Paz, Mexico, May 4–8, 2026
Plenary Session, May 6 (Wednesday), 2026

Day-1 General Plenary Talks

Ruben Rodriguez Sanchez

“The Rolling Stocks”: A metapopulation perspective on the multiscale spatiotemporal dynamics of the Pacific sardine (*Sardinops sagax*) in the California Current System

Population structure is dynamic across scales.

Myron A. Peck

International collaboration advancing ecological understanding and sustainable management of small pelagic fish

Comparative and collaborative frameworks are essential.

Ryan R. Rykaczewski

Beyond boundary currents: Toward dynamic understanding of mesopelagic communities

Looking beyond fisheries-dependent systems reveals hidden dynamics.

Context matters: scale, systems, and what we observe — determining which mechanisms dominate.

Exploring hypotheses of mechanisms behind population dynamics of small pelagic fish: perspectives for comparative and collaborative research

1. Perspectives on hypotheses
   - Perspectives on issues and future directions in hypotheses of mechanisms behind population dynamics

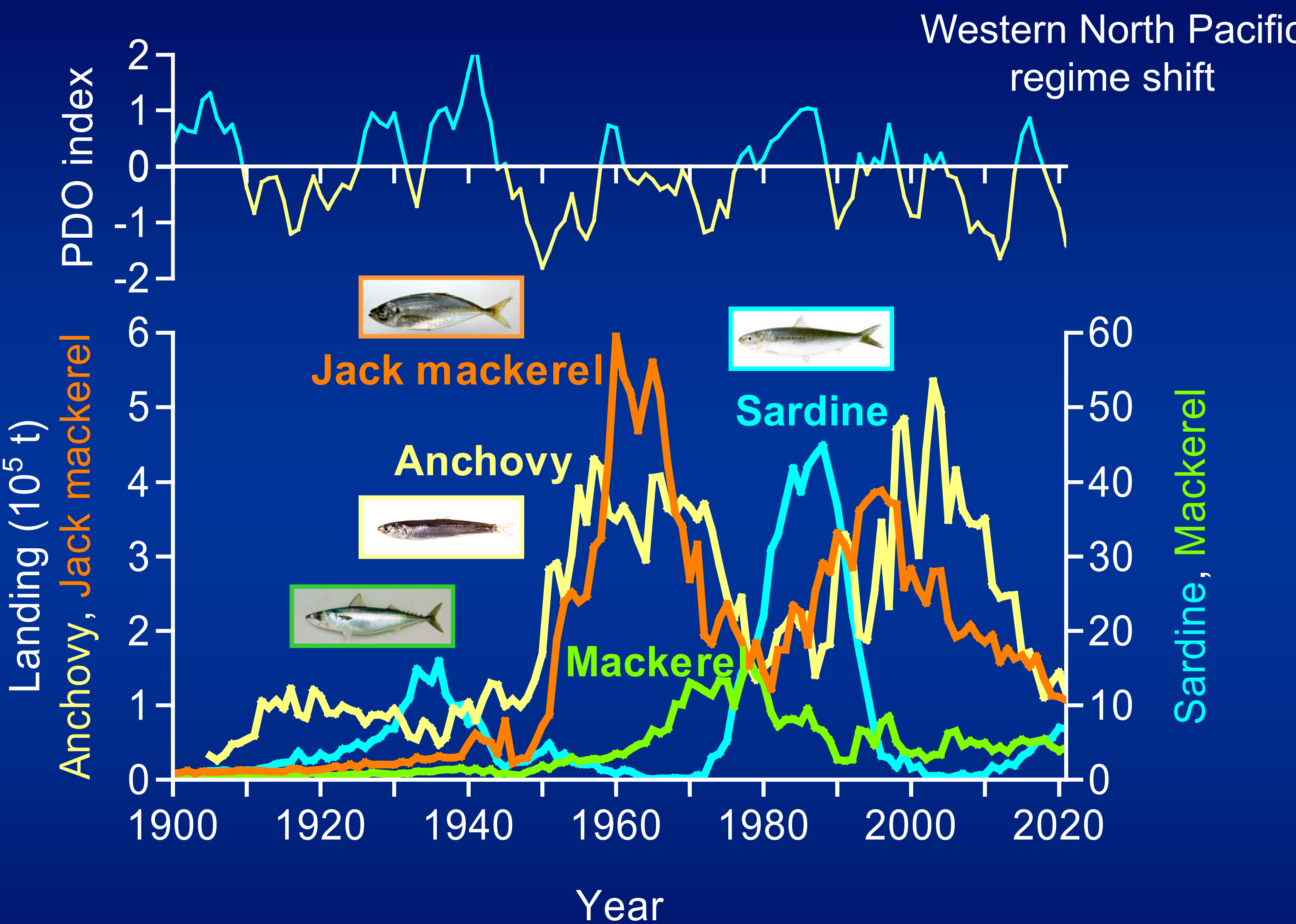
Specific topics relevant to the perspectives

2. Spawning responses to environmental factors
   - Spawning responses of anchovy and sardine across ecosystems: comparative international collaborations

3. Density-dependent egg production
   - Improving current understanding of density-dependent processes in the life history of fish

Takasuka *et al*.

Population dynamics



Long-term landing histories of small pelagic fish in waters around Japan in response to Pacific Decadal Oscillation (PDO).

Hypotheses

WGSPF/WG43 Activity

- Task Force 1: Ecological Process Knowledge (EPK)
- Activity 1: Critical review, evaluation and testing of hypotheses

  Activity leaders: Akinori Takasuka & Myron Peck (co-chairs)

  Activity members: Rebecca Asch, Matthew Baker, Arnaud Bertrand, Ignacio Catalan (co-chair), Fei Chai, Marta Coll, Jana del Favero, Jason Everett, Susana Garrido, Dimitri Gutierrez, Martin Huret, Xabier Irigoien, Sukyung Kang, Toshihide Kitakado, Martin Lindegren, Salvador Lluch-Cota, Andres Ospina, Ryan Rykaczewski (co-chair), Stelios Somarakis, Yongjun Tian, Carl van der Lingen

Objective

- Literature review to evaluate and test hypotheses related to biology, ecology, and management of SPF.

When we focus on hypotheses of

mechanisms behind population dynamics, …

Hypotheses

Major hypotheses

Approximately 50 ideas were extracted from literature and the SPF symposia.

1. Environmental factors

   Food availability, Match/mismatch, Trophic dissimilarity, Optimal temperature,
   Oxygen limitation, Habitat suitability
   Climate periodicity, Ocean triads (e
   Advection and retention, Hydrodyna

2. Population and life-history p

   Critical period, Starvation, Density

   Bigger is better, Stage duration, Gro ity,
   Maternal effects, Reproductive success

3. Trophic interactions

   Top-down control, Bottom-up control, Wasp-waist control, Predation,
   Interspecific competition, Inter- and intra-guild competition, Trophodynamics

4. Spatial dynamics and population structure

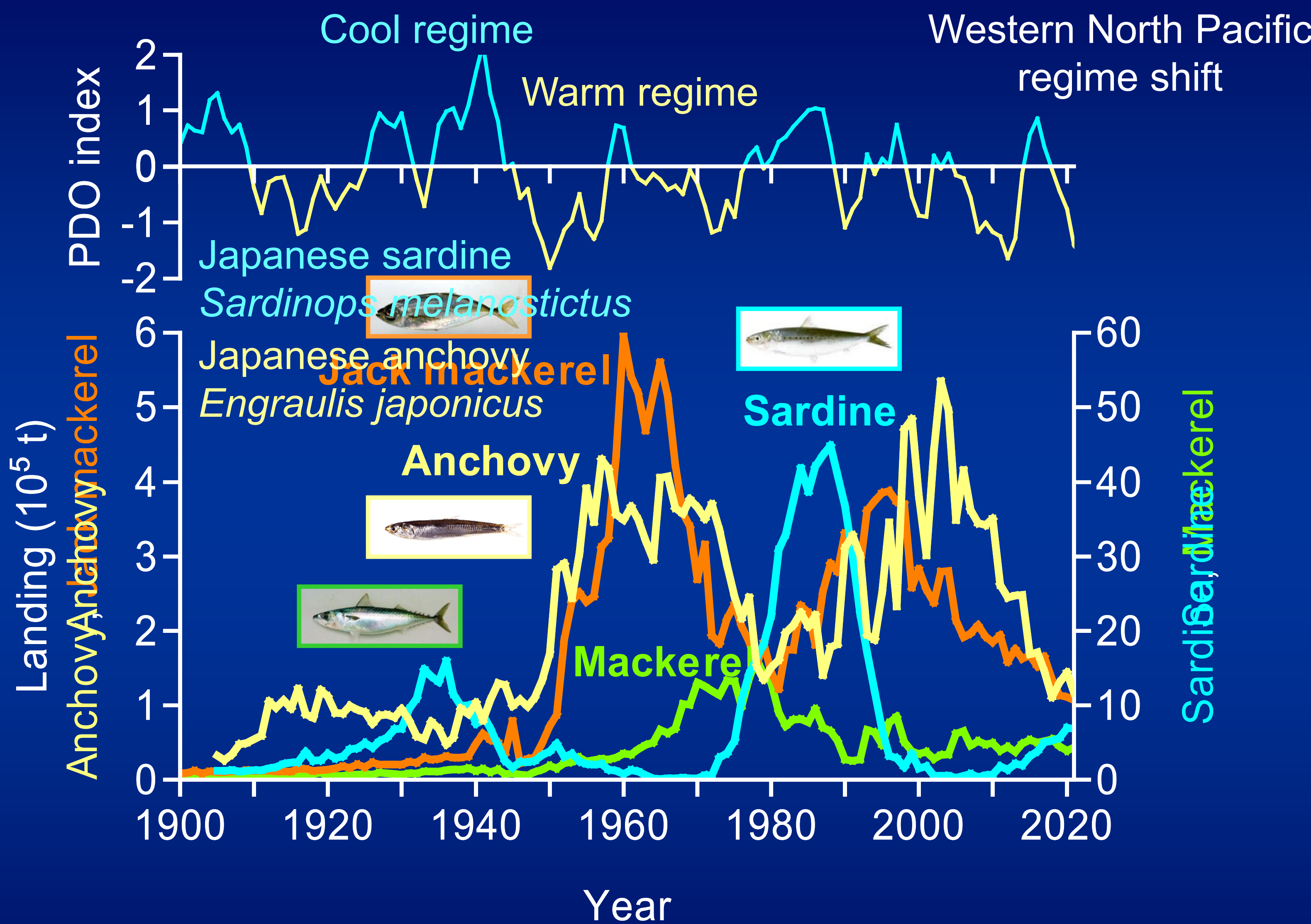
   Spatial dynamics, Movement, Metapopulation, Homing, Member–vagrant,
   Frontal eddy, Spatial partitioning, Diel vertical migration, MacCall's basin model

5. Emergent patterns

   Boom and bust cycles, Regime shifts, Alternating dominance, Global synchrony,
   Winners and losers

As a good pair of contrasting hypotheses of mechanisms behind anchovy–sardine dynamics

Species alternations



Long-term landing histories of small pelagic fish in waters around Japan in response to Pacific Decadal Oscillation (PDO).

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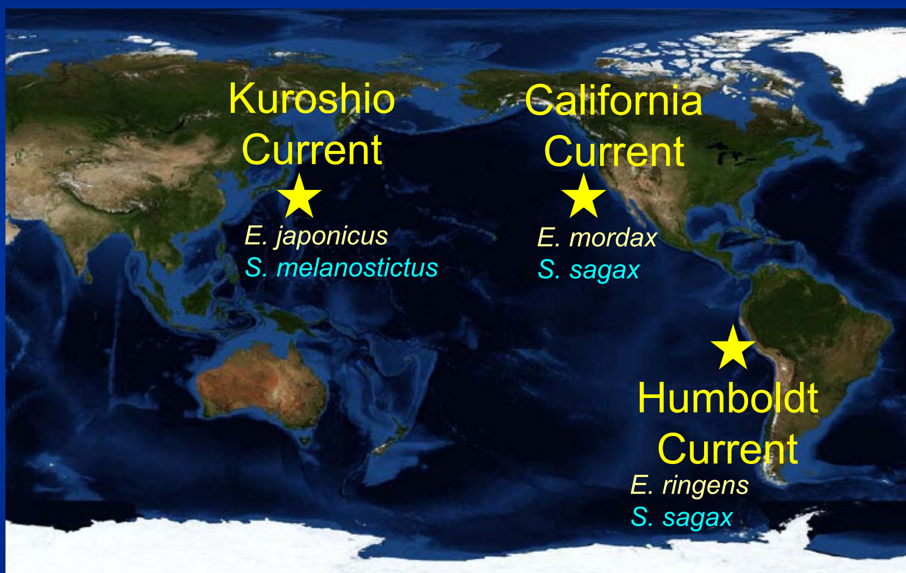
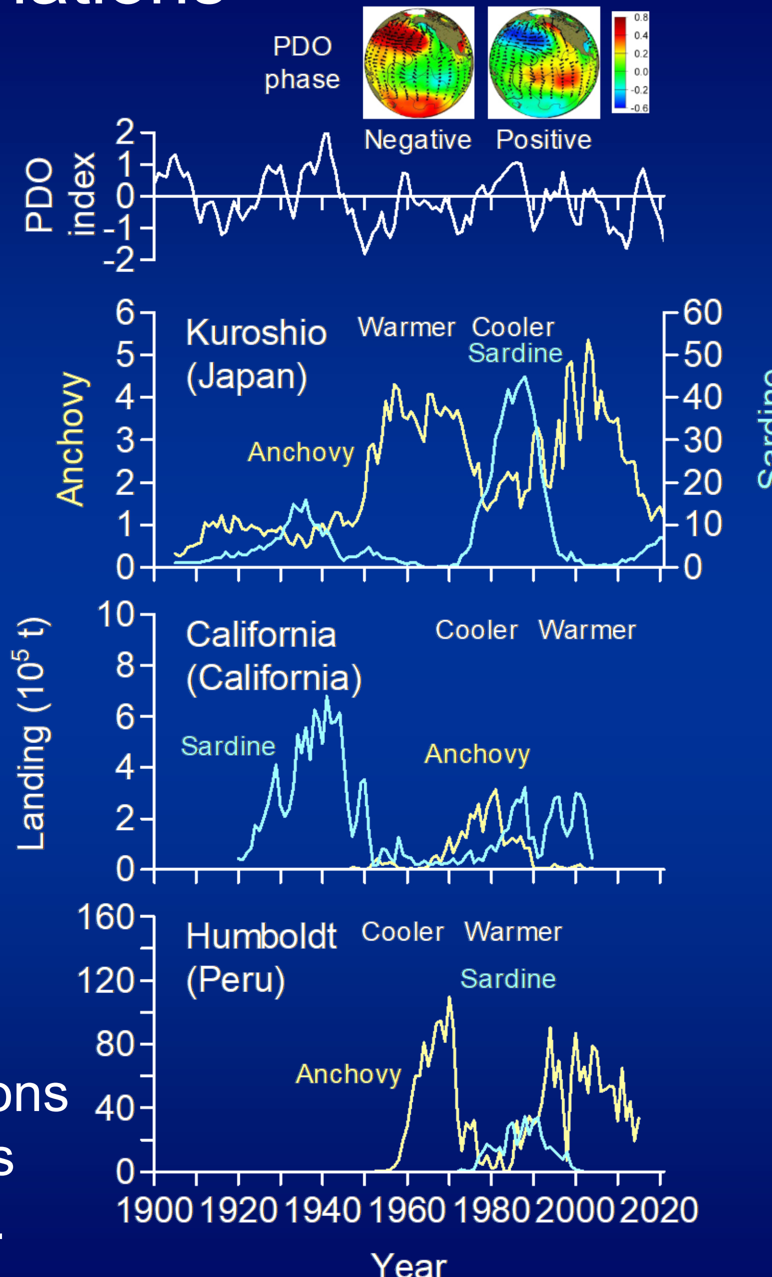
Species alternations

Different current systems

Anchovy *Engraulis* spp.
Sardine *Sardinops* spp.



The species alternations tended to be synchronous among the Pan-Pacific regions despite the reversed temperature regimes between the opposite sides of the Pacific.



Key questions

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

Why can species alternations be synchronous despite the reversed temperature regimes across the Pacific?

Concept:
Differences in biological responses to environmental variability are key to understanding differences in population dynamics.

Trophic dissimilarity

Cool regime		Warm regime
	Physical forcing (wind, etc.)	
Intermittent mixing (upwelling, cool)	Water column (temperature)	Highly stable (warm)
Larger-cell (diatom) High biomass	Phytoplankton community	Smaller cell (flagellate) Low biomass
Larger copepods	Zooplankton community	Smaller copepods
Particulate-feeder favored	Pelagic fish community	Filter-feeder favored

Anchovy ← Differential feeding strategies → Sardine

Conceptual framework of the “trophic dissimilarity” hypothesis from the Benguela Current system (van der Lingen *et al*. 2006 *AJMS*).

Trophic dissimilarity

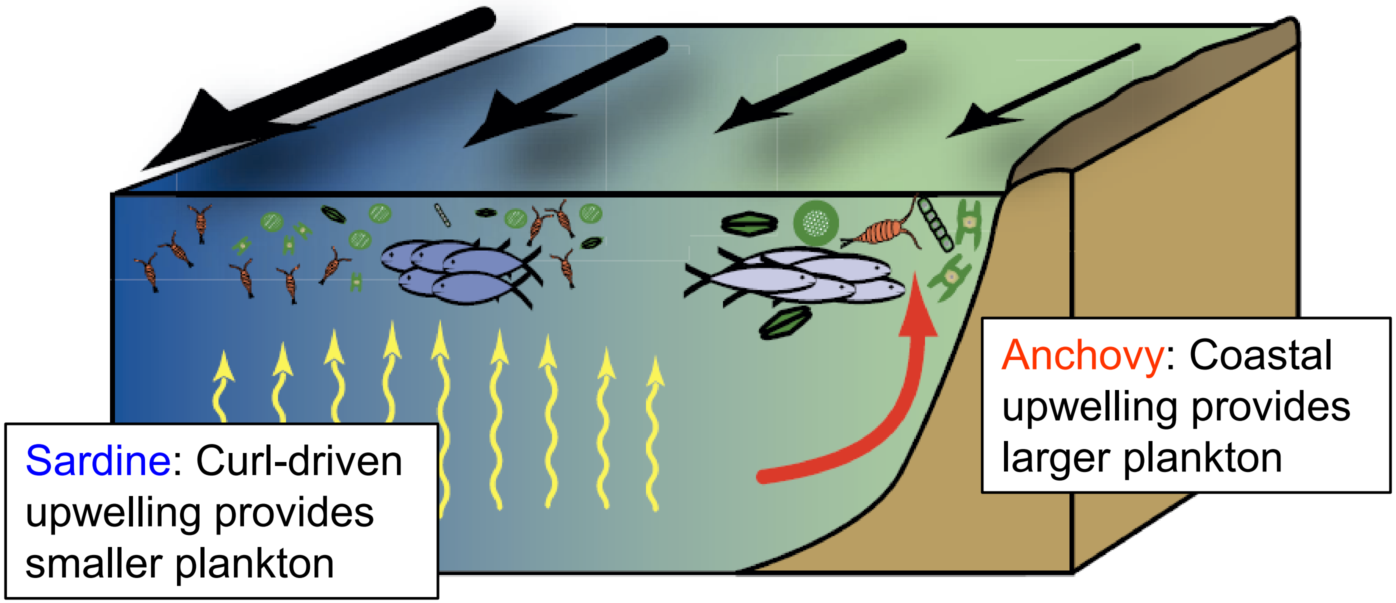


Fig. 1. Conceptual diagram displaying the hypothesized relationship between wind-forced upwelling and the pelagic ecosystem. Alongshore, equatorward wind stress results in coastal upwelling (red arrow), supporting production of large phytoplankters and zooplankters. Between the coast and the wind-stress maximum, cyclonic wind-stress curl results in curl-driven upwelling (yellow arrows) and production of smaller plankters. Anchovy (gray fish symbols) prey on large plankters, whereas sardine (blue fish symbols) specialize on small plankters. Black arrows represent winds at the ocean surface, and their widths are representative of wind magnitude.

Influence of ocean winds on the pelagic ecosystem in the California Current system (Rykaczewski & Checkley 2008 *PNAS*).

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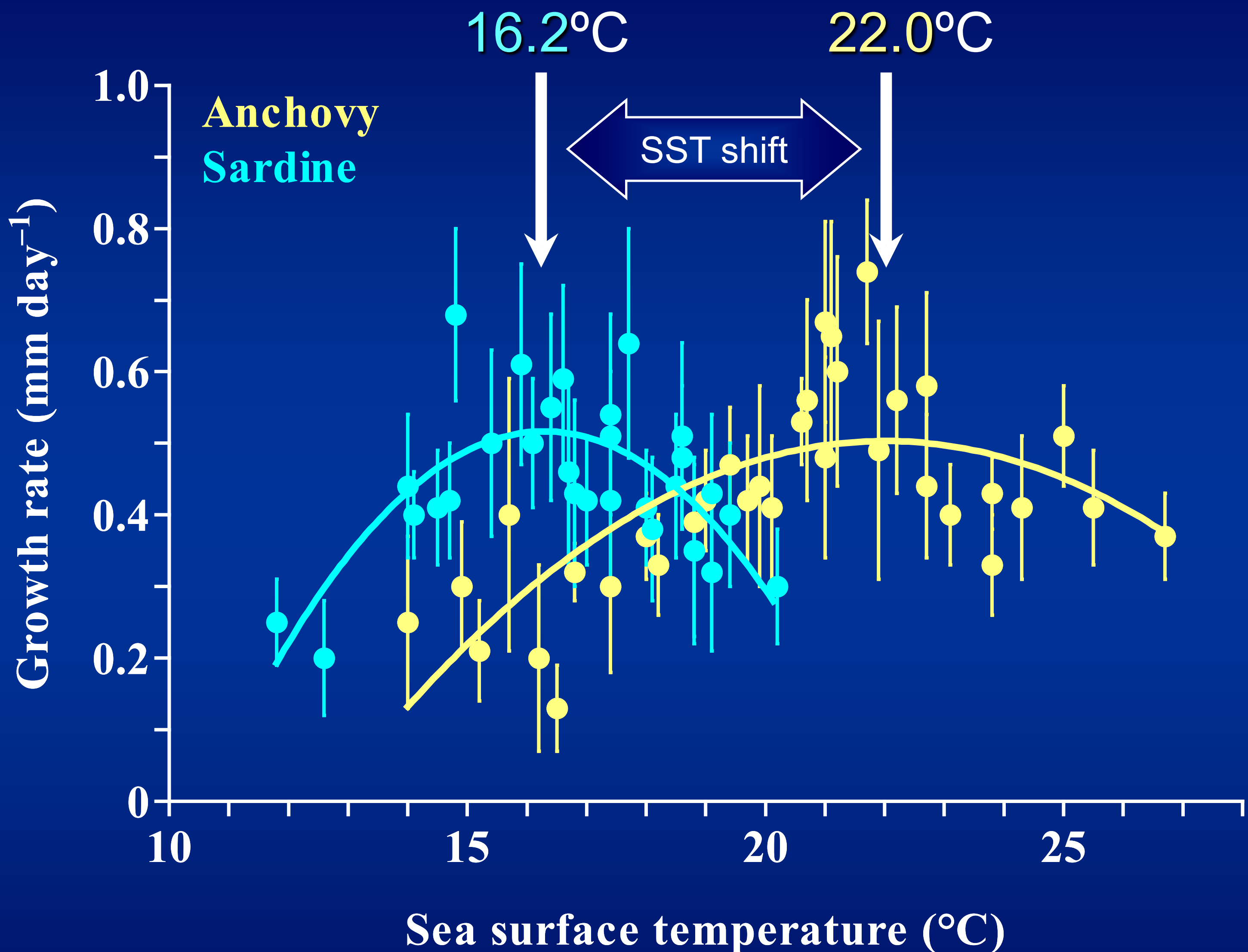
Takasuka *et al*.

Optimal growth temperature



Relationship between recent 3-day mean growth rates and sea surface temperature for anchovy and sardine larvae (Takasuka *et al*. 2007 *CJFAS*).

Dichotomies

Controversies and dichotomies

Environmental drivers

Food availability VS Temperature

Direct mortality sources

Predation VS Starvation

Causes of population collapse

Climate impacts VS Fishing

Ecosystem controls

Bottom-up VS Top-down

Regulation processes

Density-dependent VS Density-independent

These dichotomies are not mutually exclusive
but interact across scales and processes.

Perspectives

Overview and issues

- Each hypothesis is theoretically sound in addressing how its focal factor/process regulates population dynamics within the target system.
- However, controversies remain regarding their applicability to other ecosystems.
- Debates framed as dichotomies have also emerged:
  food availability vs temperature, predation vs starvation,
  climate variability vs fishing, bottom-up vs top-down,
  density-dependent vs density-independent processes, etc.

Future directions

- There is a pressing need to establish integrative frameworks that reconcile such dichotomies through meta-analyses or modelling.
- Such frameworks require interspecific and intersystem comparison in a unified approach within the same study framework.

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2. Spawning responses to environmental factors
   - Spawning responses of anchovy and sardine across ecosystems: comparative international collaborations

3. Density-dependent egg production
   - Improving current understanding of density-dependent processes in the life history of fish

Note:

The slides of the following topic have been removed from the web version, as they included unpublished materials.

2. Spawning responses to environmental factors
   - Spawning responses of anchovy and sardine across ecosystems: comparative international collaborations

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Density-dependent egg production

Improving current understanding of density-dependent processes in the life history of fish

Akinori Takasuka[1], Michio Yoneda[2], Yoshioki Oozeki[2], Haruka Nishikawa[3], Sho Furuichi[2], Ryuji Yukami[2]

[1]*Graduate School of Agricultural and Life Sciences, The University of Tokyo*
[2]*Japan Fisheries Research and Education Agency*
[3]*Japan Agency for Marine-Earth Science and Technology*

Paradigm

A paradigm of fisheries science

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

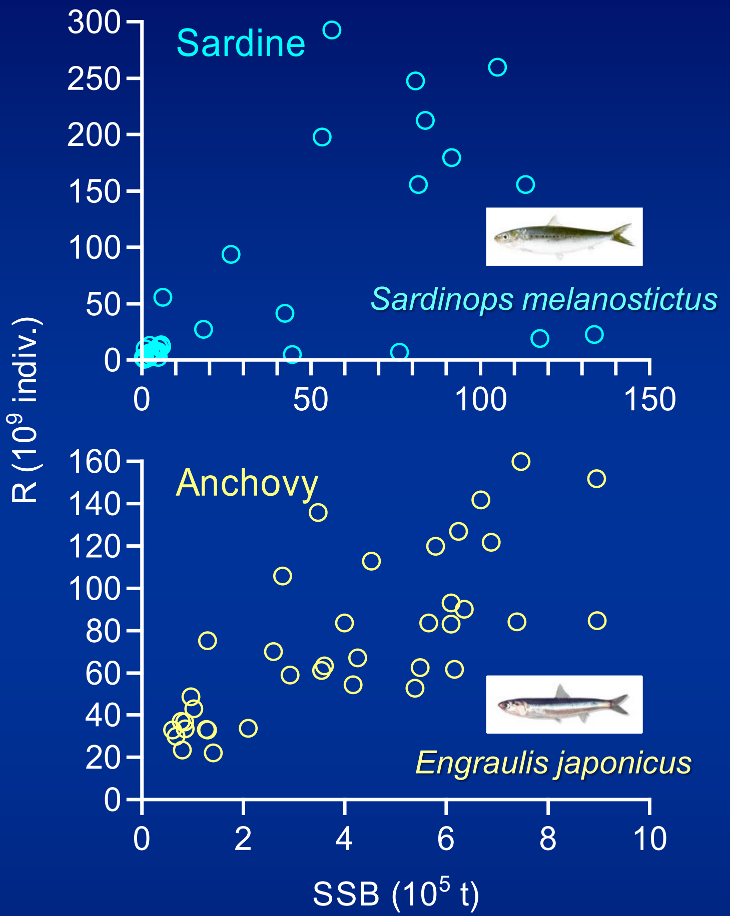
Leggett & Frank (2008) "Paradigms in fisheries oceanography"

A basic premise underlying the spawner–recruitment models for fisheries management and recruitment studies.

- Progress in studies on maternal effects on reproductive potential has led to doubt about the paradigm.
- Nonetheless, a direct test of the paradigm at multidecadal scales has been difficult because it has been difficult to prepare TEP data independent of SSB data.

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 and density-independent mortality from hatching to recruitment.

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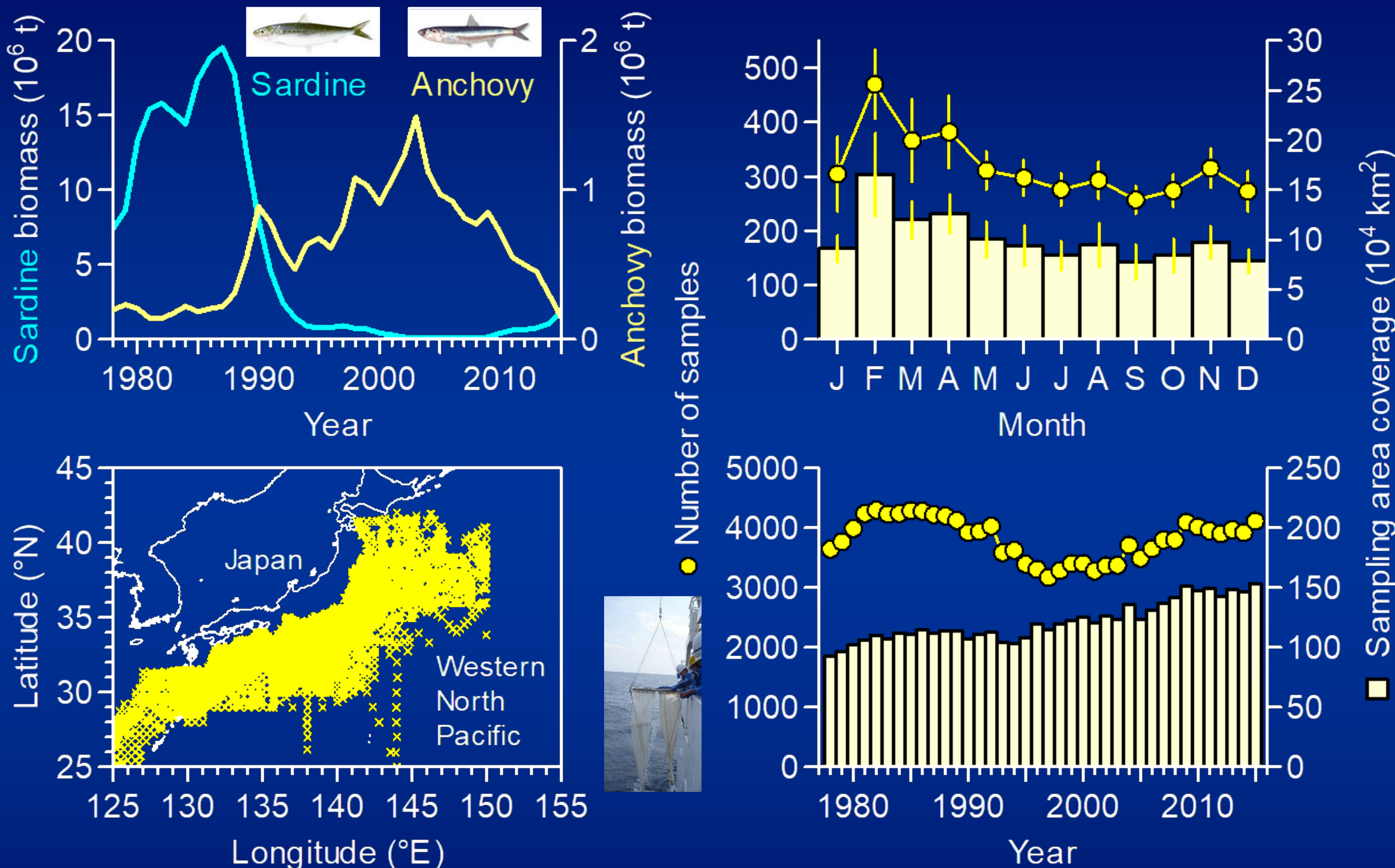
Egg surveys



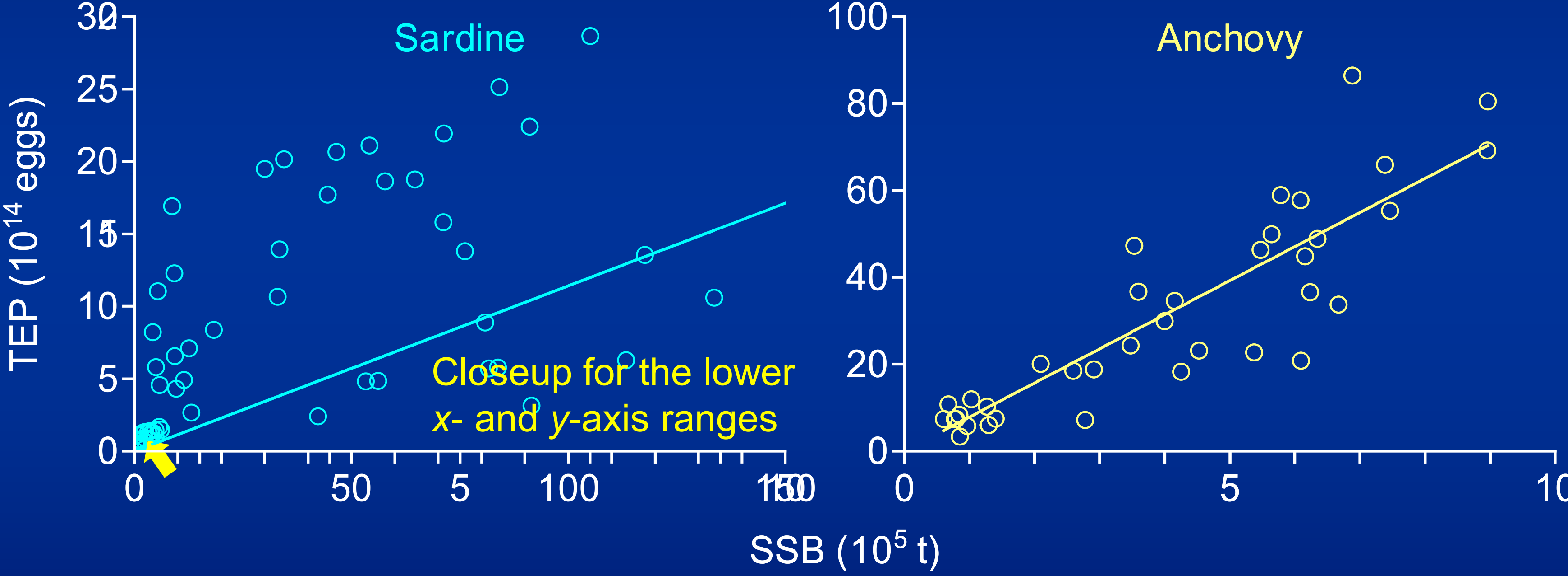
Egg surveys covering the spawning grounds during the high- and low-biomass periods of sardine and anchovy in the western North Pacific from 1978 to 2015 (38 years). The data set includes a total of 145,157 vertical tows of plankton nets.

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



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

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

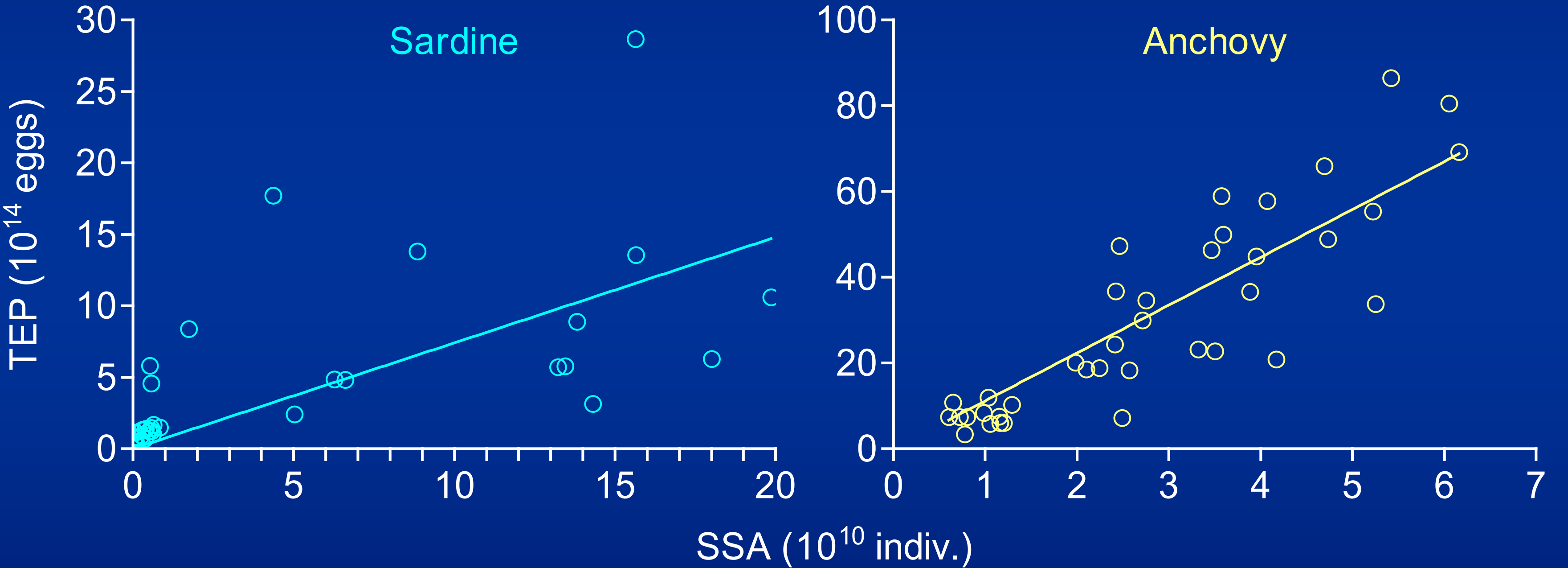
Relationships of annual total egg production (TEP) to spawning stock biomass (SSB) for sardine and anchovy.

Takasuka *et al.*

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



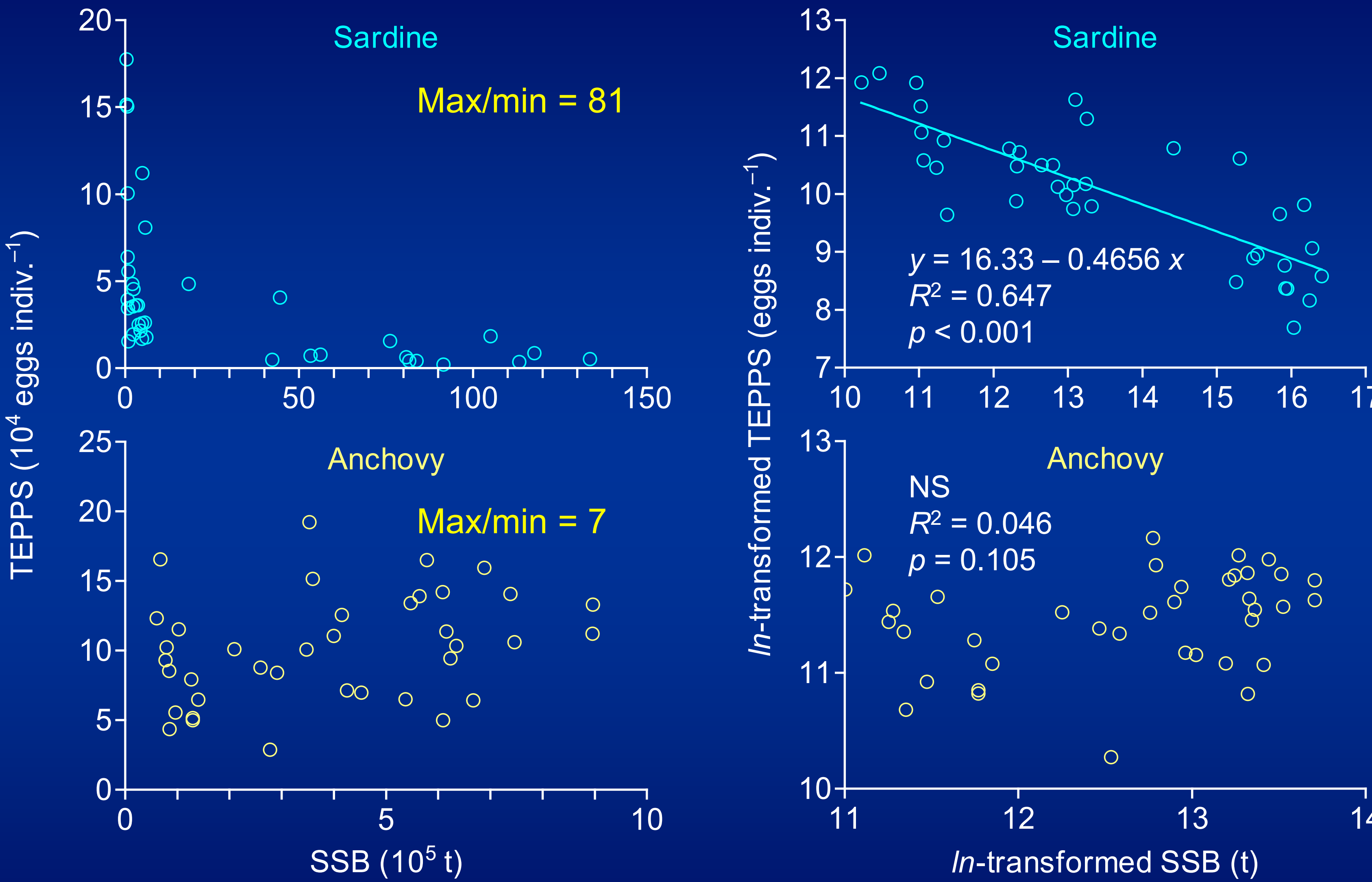
$y = 7{,}400 \times x$
(n = 37, R^2 = 0.353, $p < 0.001$)

$y = 111{,}605 \times x$
(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.

Takasuka *et al.*

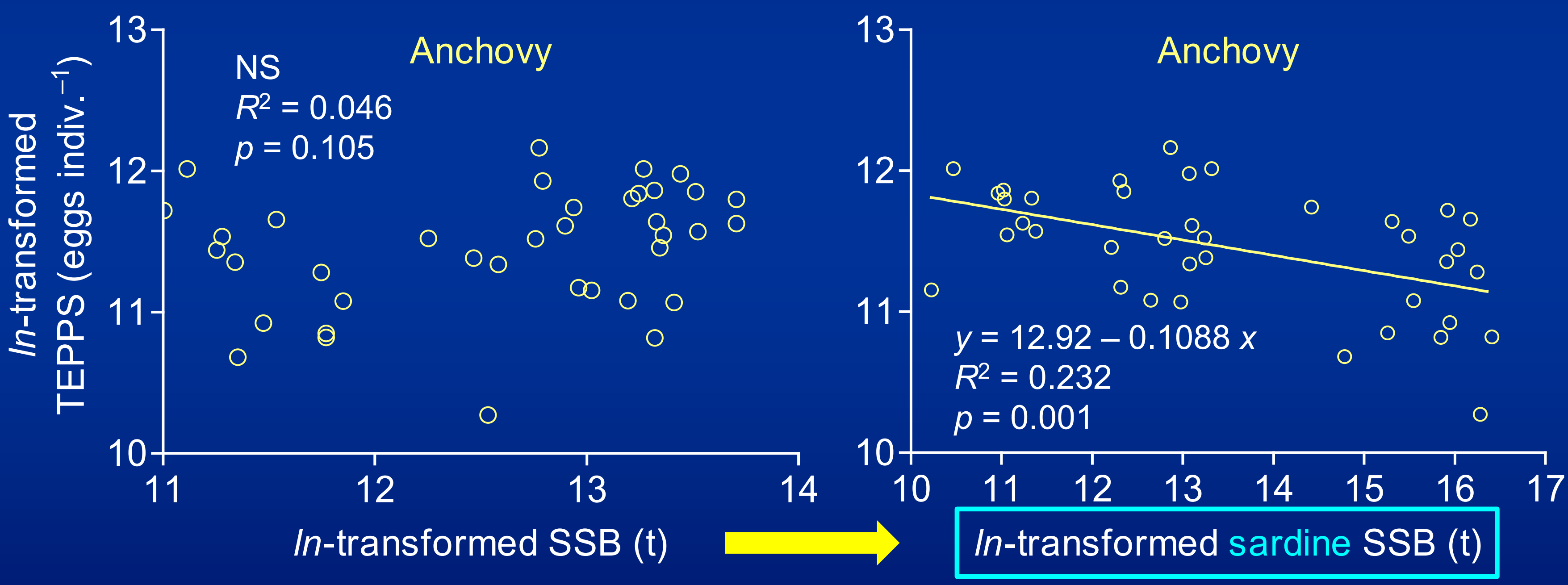
TEPPS vs SSB



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

TEPPS vs SSB

- When anchovy TEPPS was related to sardine SSB, a significantly negative relationship appeared.
- Anchovy TEPPS can be influenced by sardine biomass.



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

Takasuka *et al*.

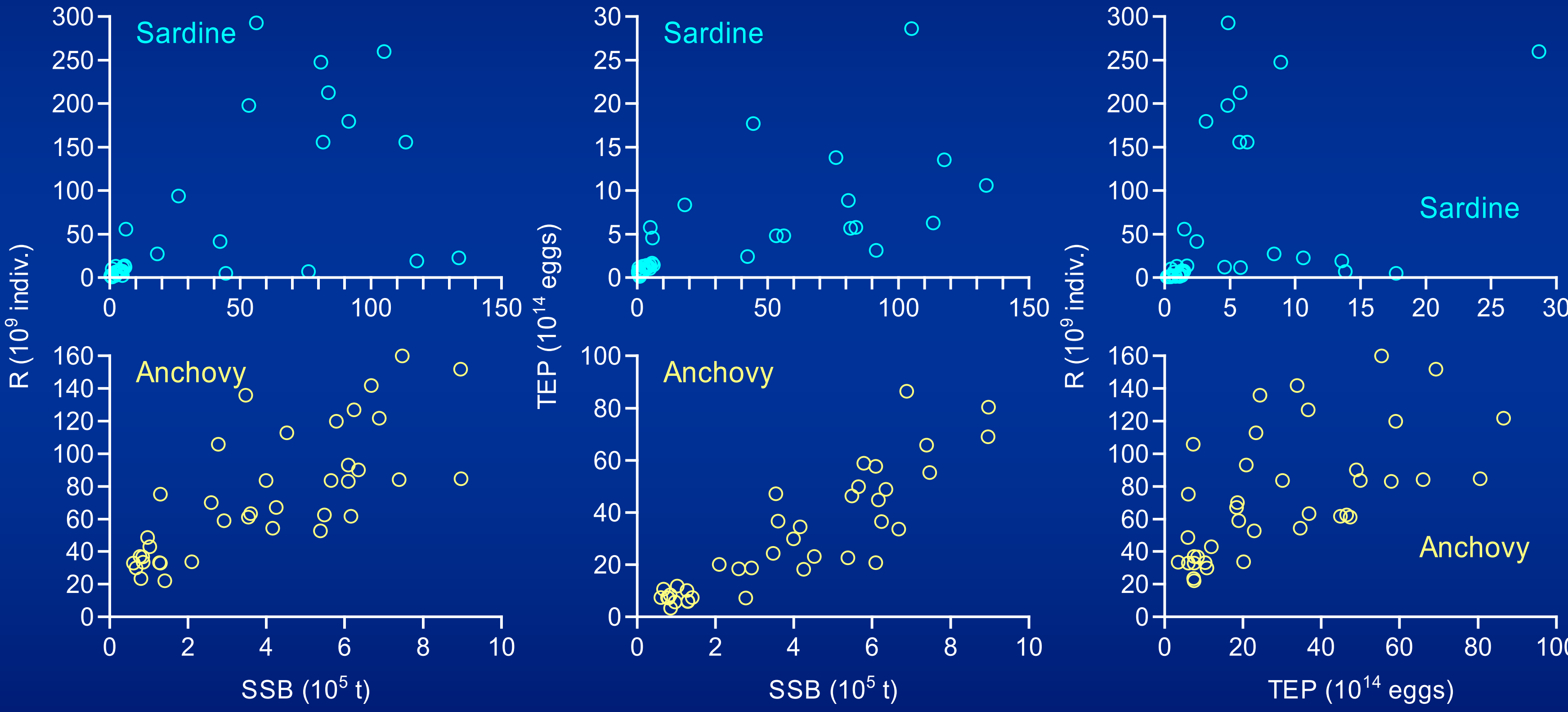
Disentangling

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

Spawner to recruit
SSB–R

Spawener to egg
SSB–TEP

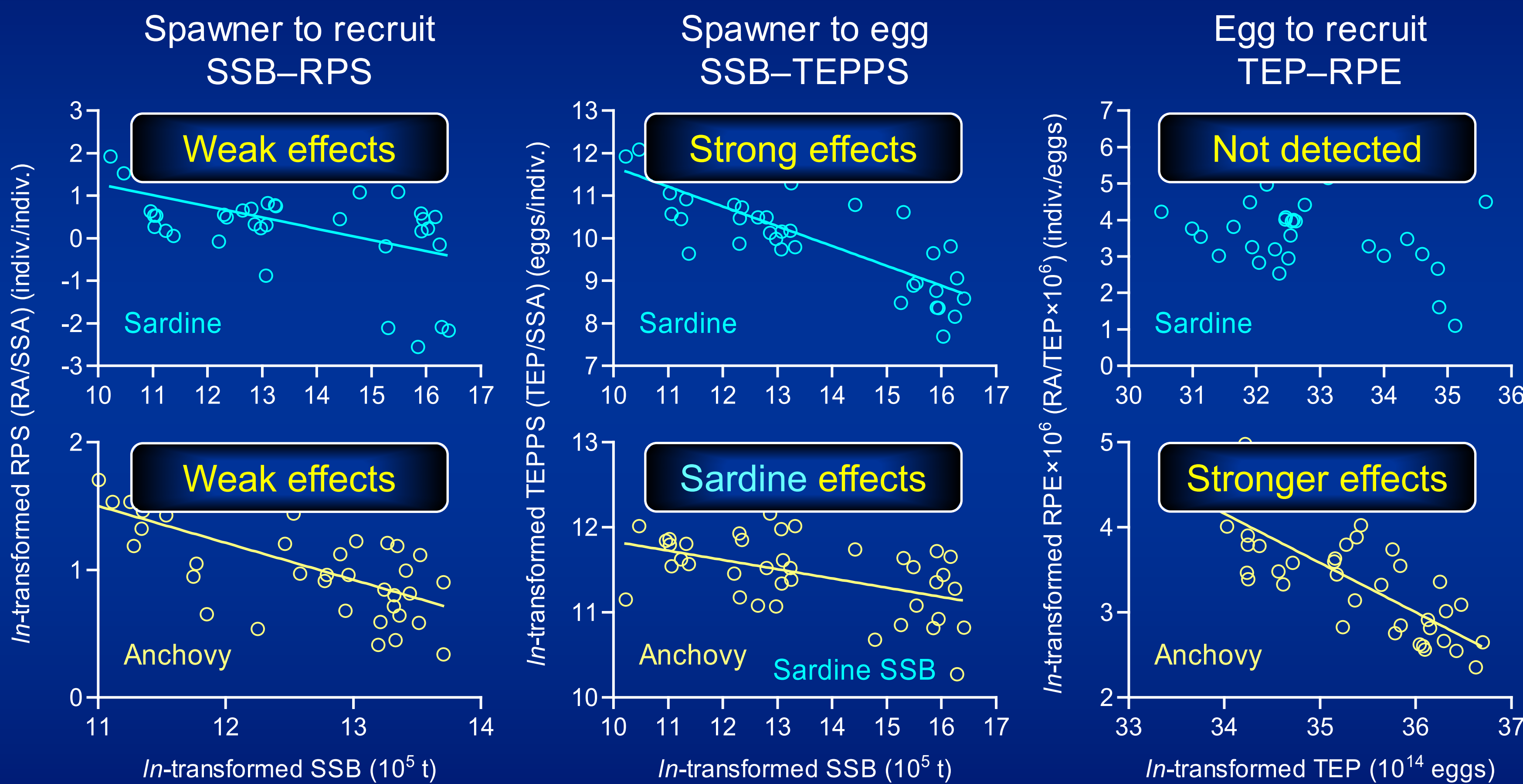
Egg to recruit
TEP–R



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).

Survival indices

- Recognizing density-dependent egg production calls into question the traditional use of recruitment per spawning stock biomass (RPS) as a survival index.

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 for Japanese sardine in the Kuroshio Current system at a multidecadal scale.

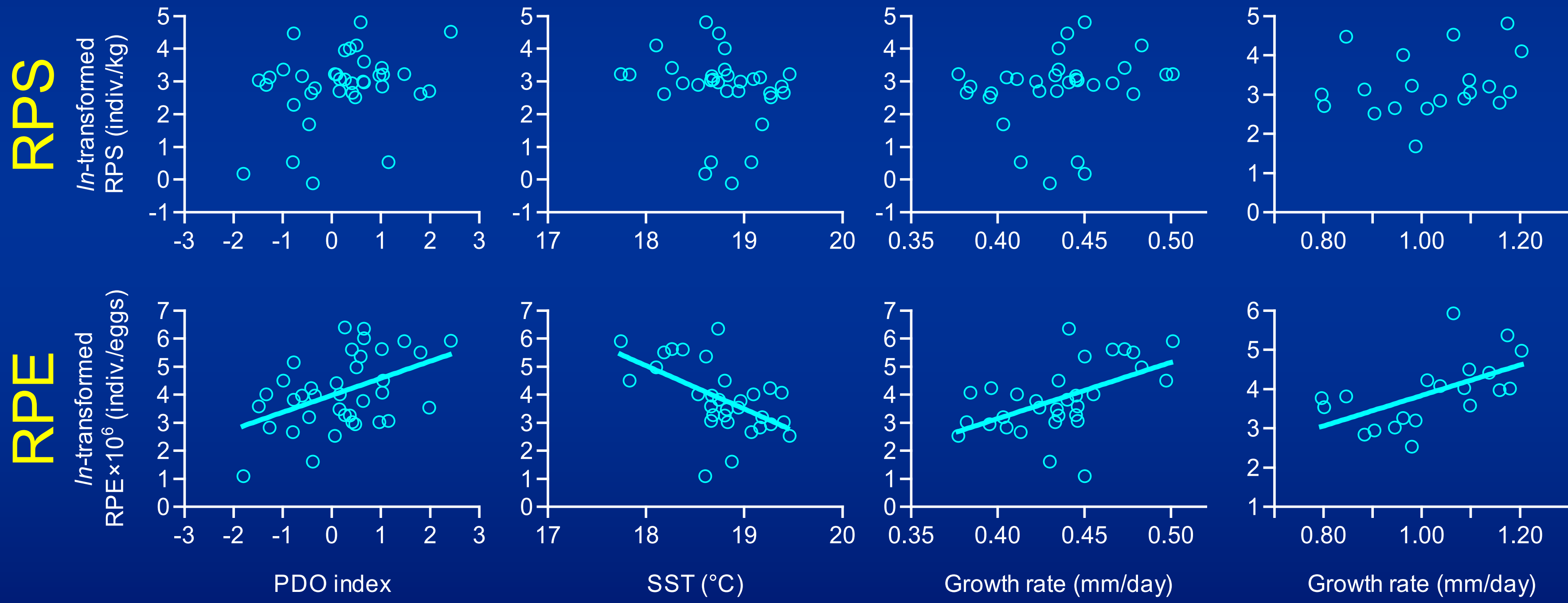
Hypotheses revisited

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

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)



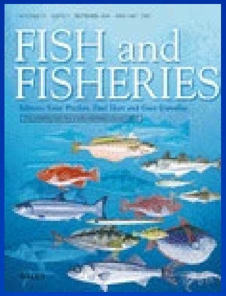
Relationships of survival indices for sardine to climate index (large-scale ocean climate anomaly), ambient temperature (ambient temperature in the nursery grounds), and growth rate (growth rate during the early life stages) at a multidecadal scale.

Publication

Note: this slide has been added only for the web version.

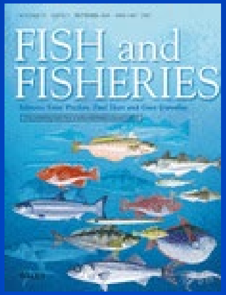
1. Takasuka, A., Yoneda, M., Oozeki, Y. (2019)
Density dependence in total egg production per spawner for marine fish.
Fish and Fisheries, 20: 125–137.

Density dependence
(sardine, anchovy)



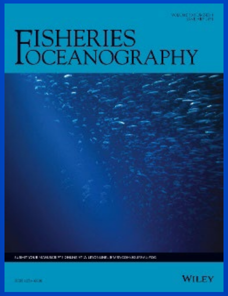
2. Takasuka, A., Yoneda, M., Oozeki, Y. (2019)
Disentangling density-dependent effects on egg production and survival from egg to recruitment in fish.
Fish and Fisheries, 20: 870–887.

Disentangling
(sardine, anchovy)



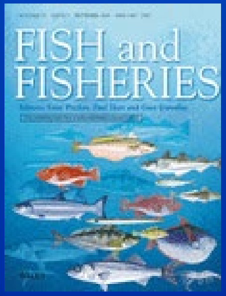
3. Takasuka, A., Yoneda, M., Oozeki, Y. (2021)
Density-dependent egg production in chub mackerel in the Kuroshio Current system.
Fisheries Oceanography, 30: 38–50.

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)



Summary

Direct test of the paradigm

- Direct test of the paradigm revealed the existence of density-dependent egg production.

  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.

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.

Revisiting sardine recruitment hypotheses

- Using the egg-production-based survival index (considering density-dependent egg production) improved understanding of recruitment mechanisms under climate variability.

Dichotomies

Controversies and persistent dichotomies

Environmental drivers

Food availability VS Temperature

Direct mortality sources

By improving our understanding of
"density-dependent processes",
we improved our understanding of
"density-independent processes".

Regulation processes

Density-dependent VS Density-independent

These dichotomies are not mutually exclusive
but interact across scales and processes.

The SPF symposium provides a platform for developing collaborative ideas.

- Comparative international collaborations
- Reconciling controversies and dichotomies

We hope that our examples will serve as possible ideas or references for comparative studies and further international collaboration within our community.