Density dependence at the time of spawning: disentangling density-dependent effects in the life histories of fish

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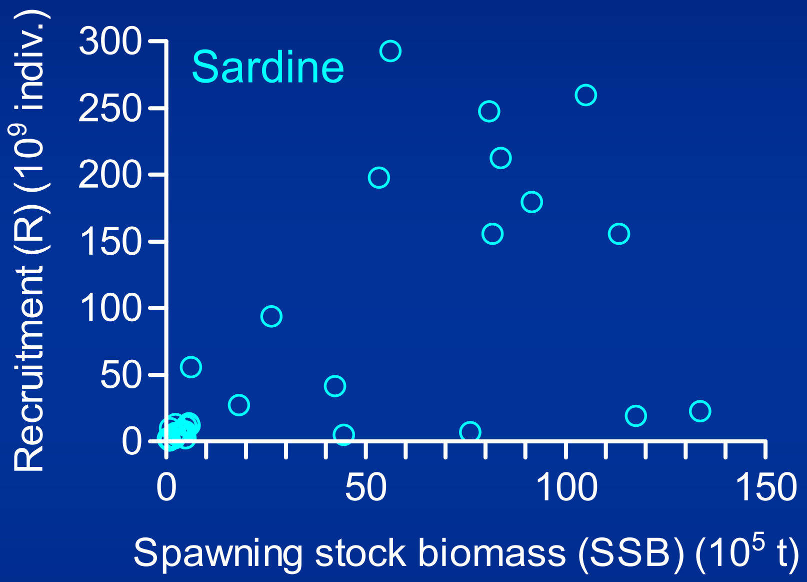
Spawner–recruitment

Spawner–recruitment relationship of
the Pacific stock of Japanese sardine
(Yukami *et al*. 2017 Stock assessment report)



Backgrounds

- 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).
- Evidence of density-dependent effects on juvenile growth and maturation.

Interpretation

- Density-dependent mortality from hatching to recruitment.
- Density-independent mortality due to climate impacts.

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

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"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)

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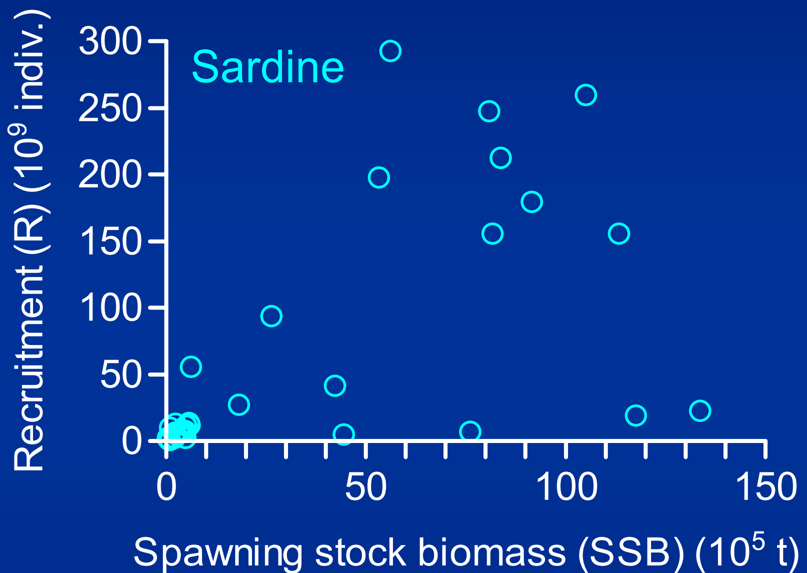

Reproductive potential of a stock

Total egg production (TEP)

Spawning stock biomass (SSB)

Backgrounds

- The asymptotic pattern represents density-dependent effects on recruitment (i.e. self-regulating processes).
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Interpretation

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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 distorted by density dependence in egg production.

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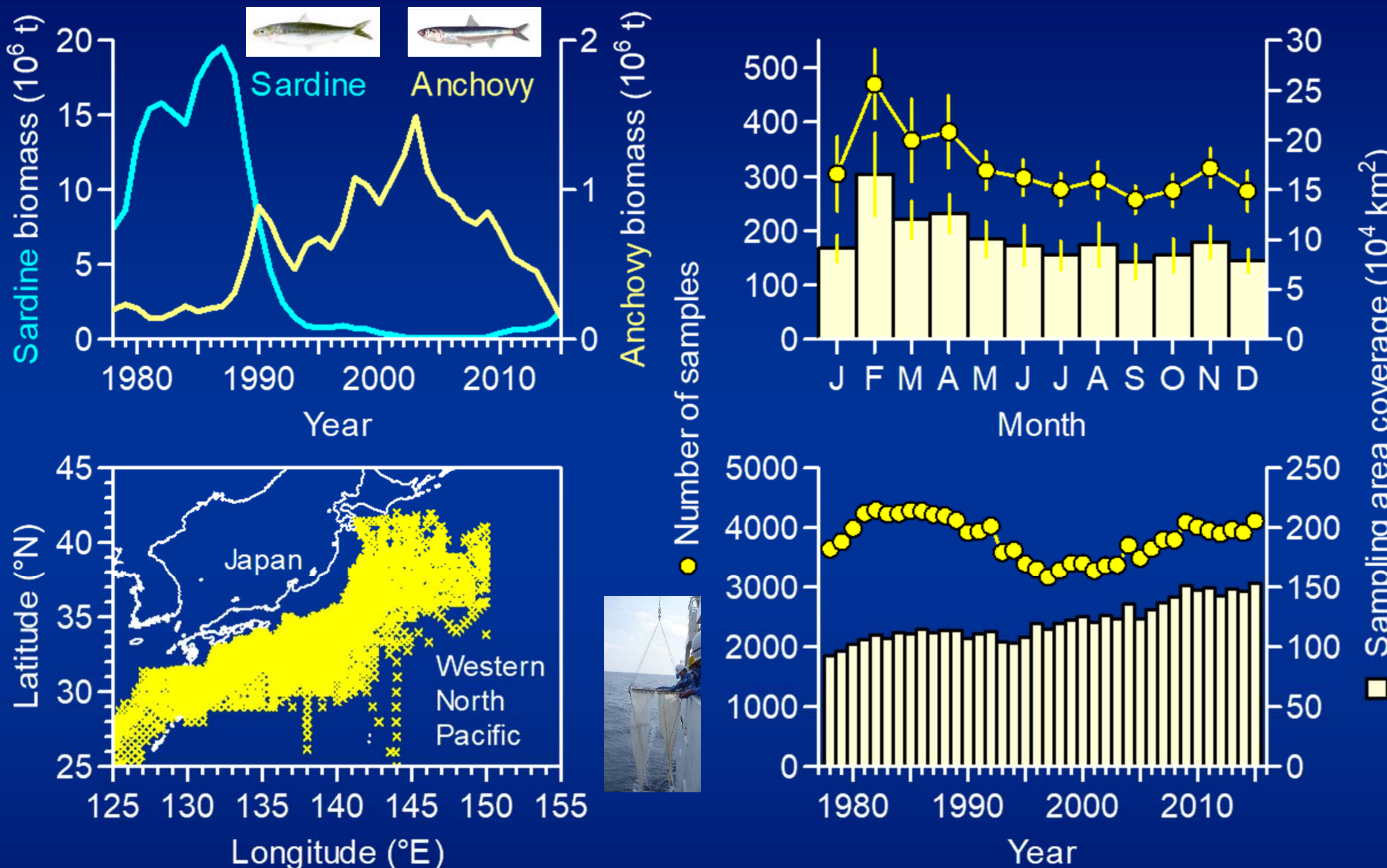
Egg surveys



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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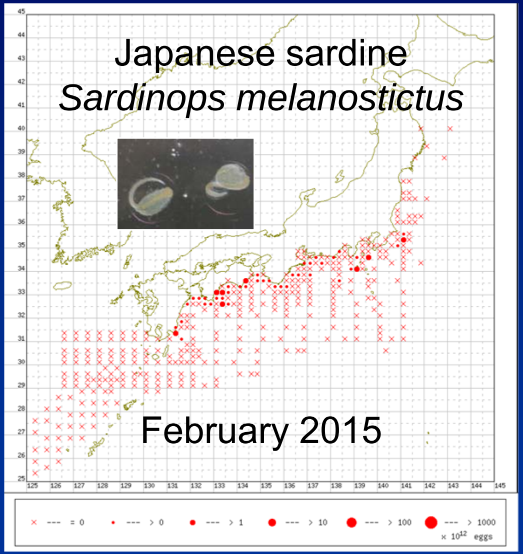
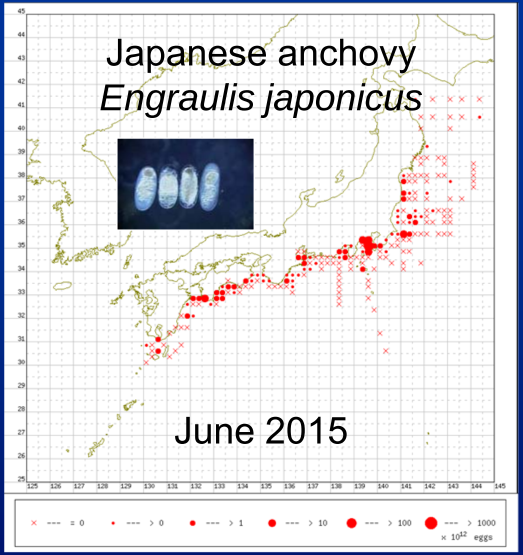
Egg production

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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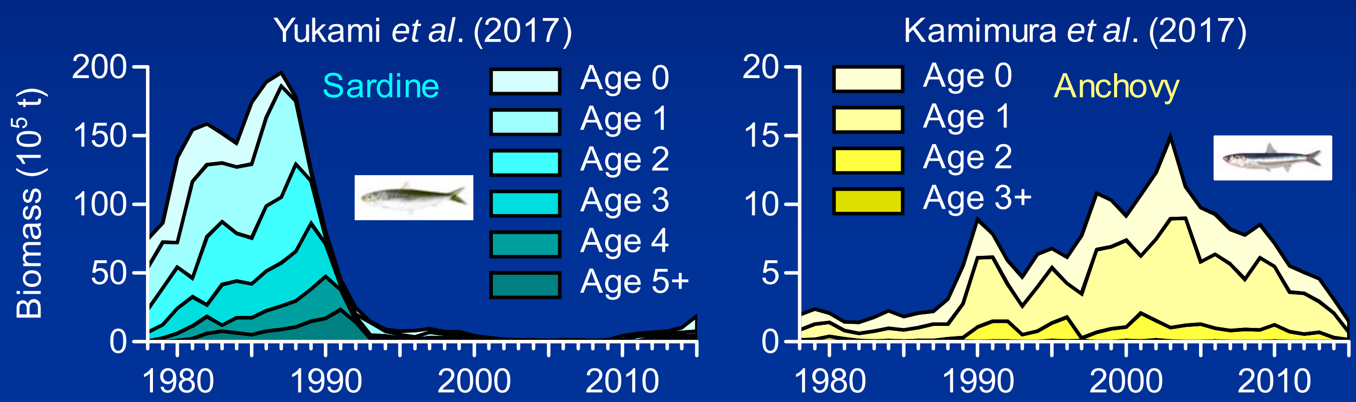
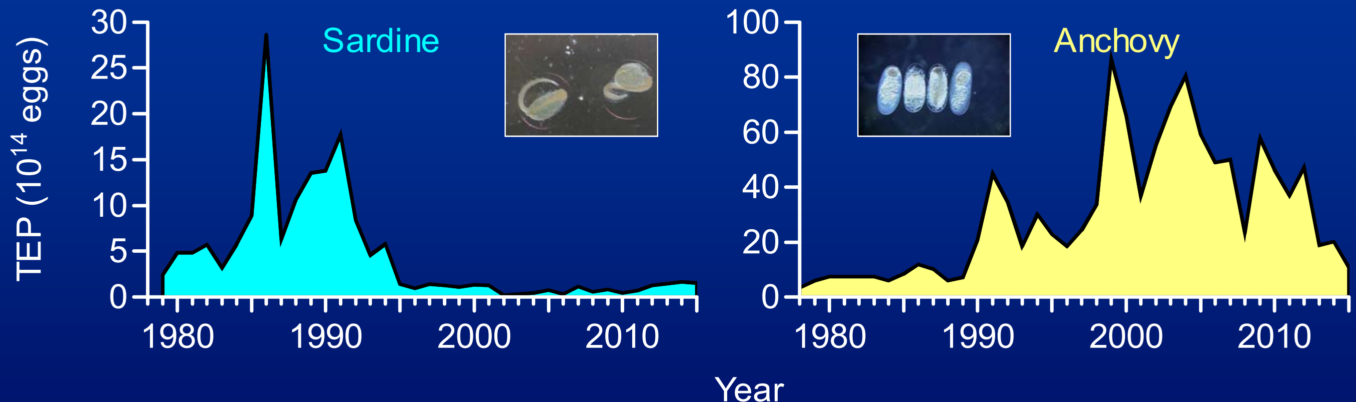
Biomass and TEP

A combination of two independent 38-year time series

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



Fishery-independent egg survey data

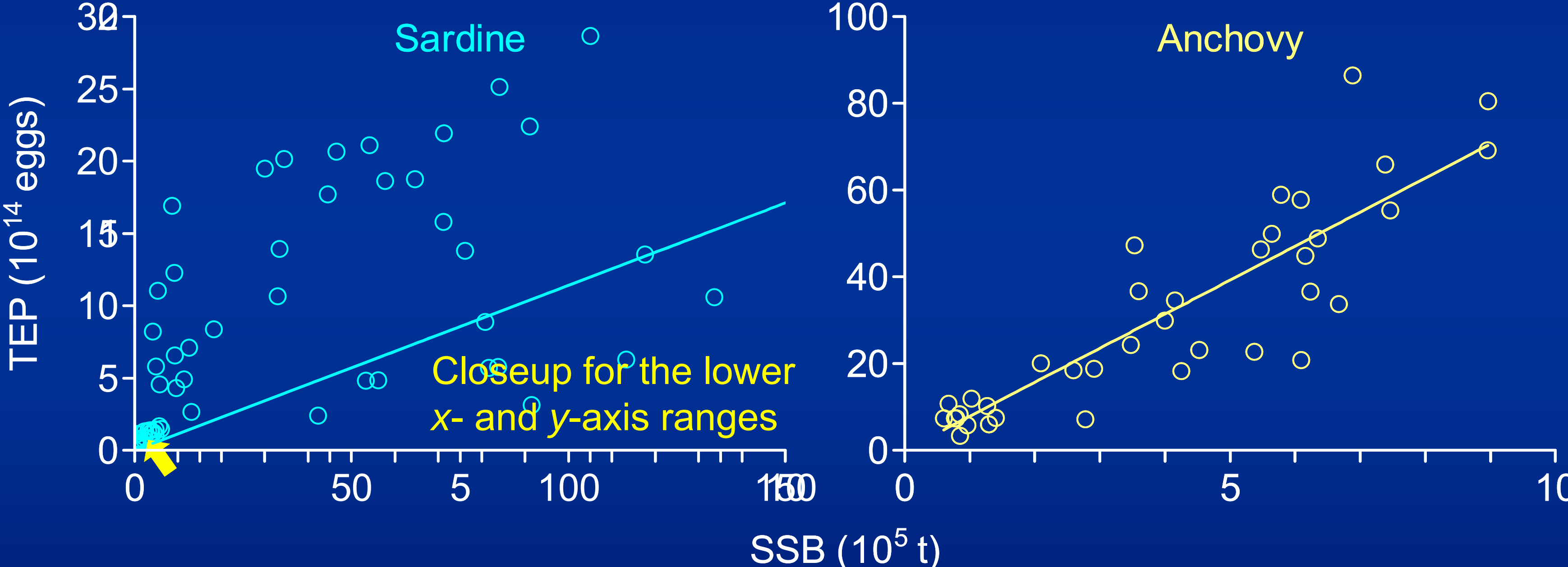


Multidecadal changes in biomass and annual total egg production (TEP) of the Pacific stocks of sardine and anchovy.

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



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

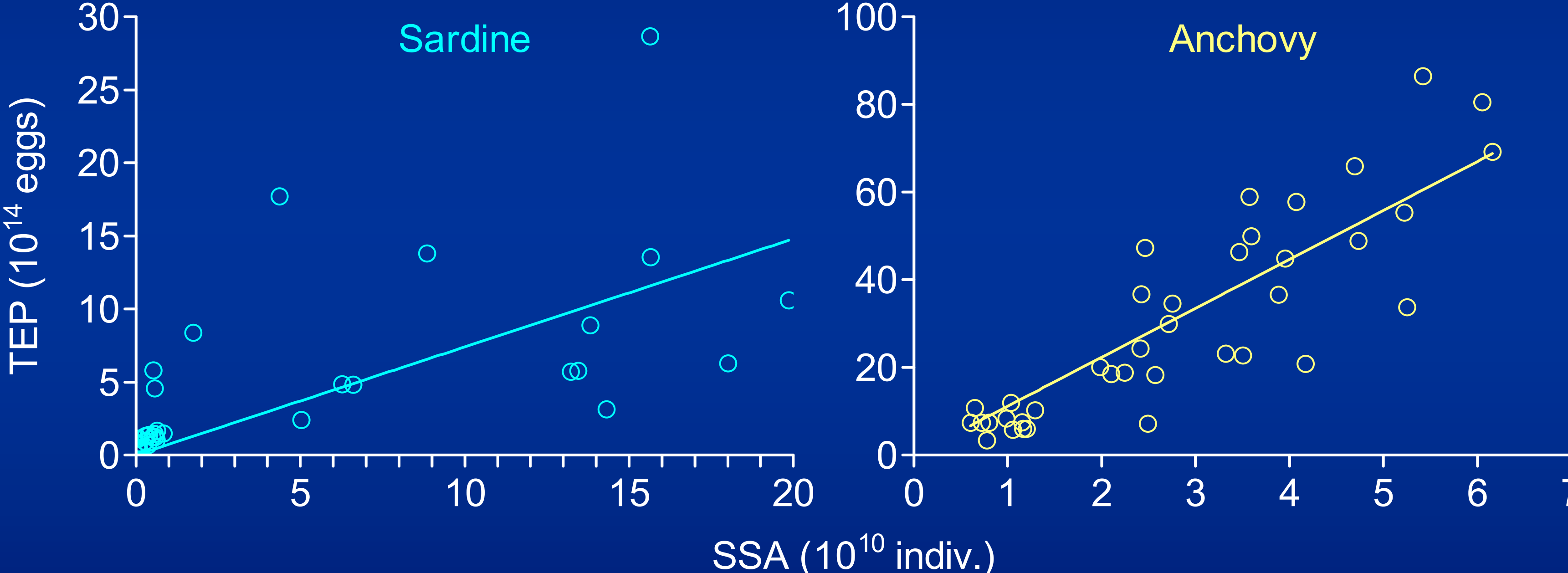
$y = 7792 \times 10^6\, x$
($n = 38$, $R^2 = 0.917$, $p < 0.001$)

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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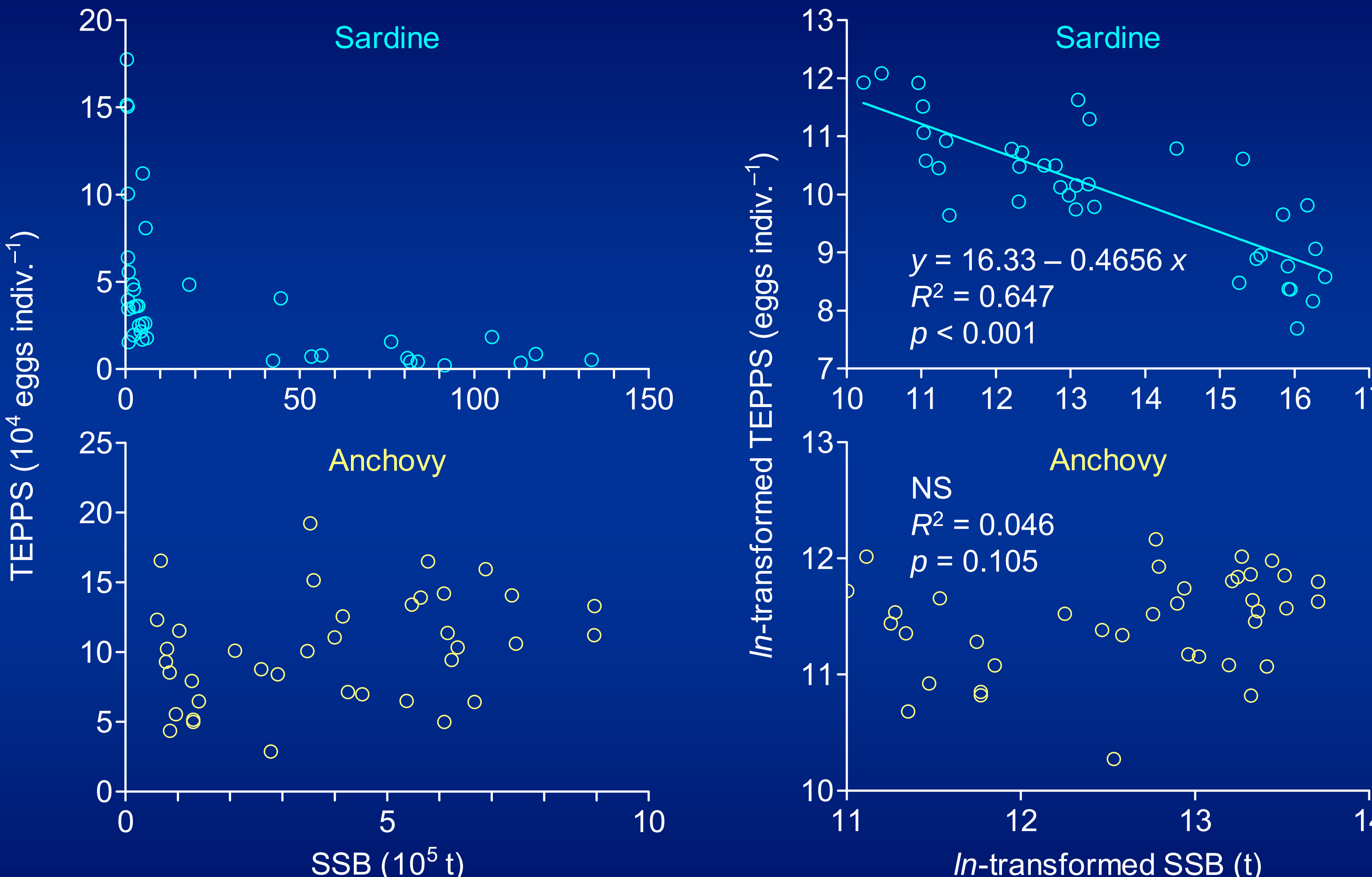
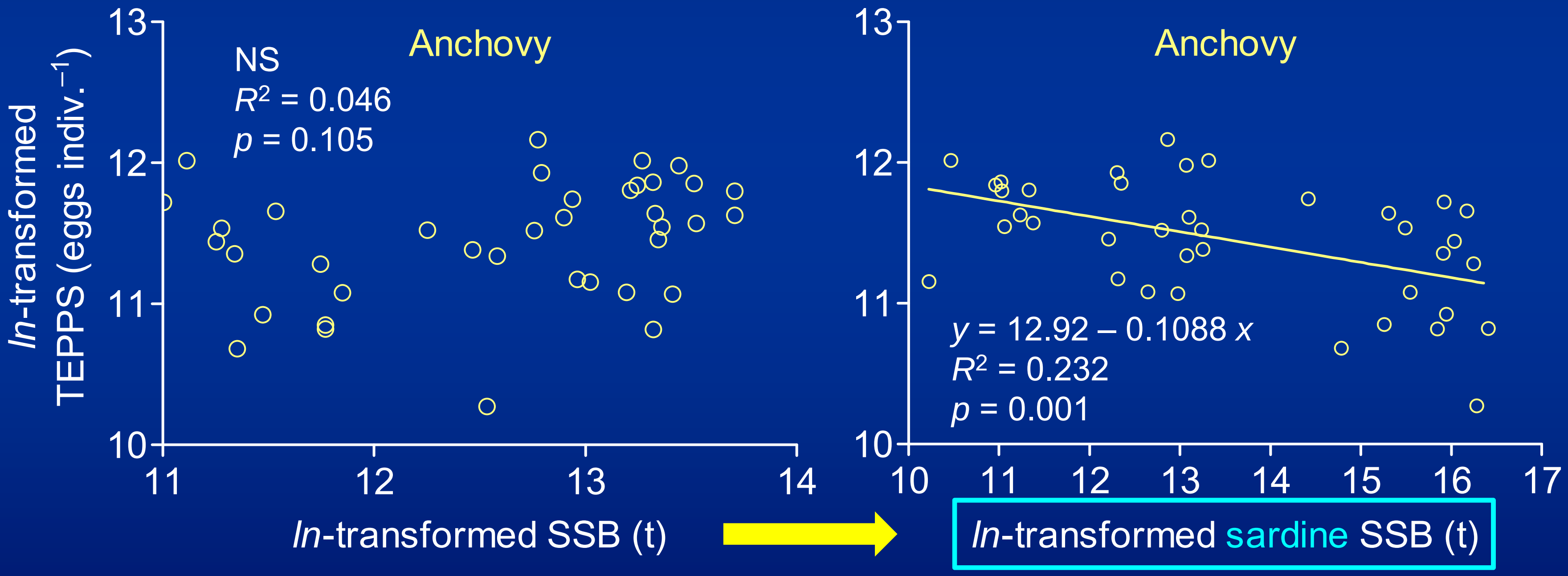
TEPPS vs SSB



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 TEPPS of anchovy was related to SSB of sardine.
- Hypothesis: TEPPS of anchovy is influenced by sardine biomass.
- Analysis: seasonal/regional TEPPS of anchovy versus SSB of sardine.



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

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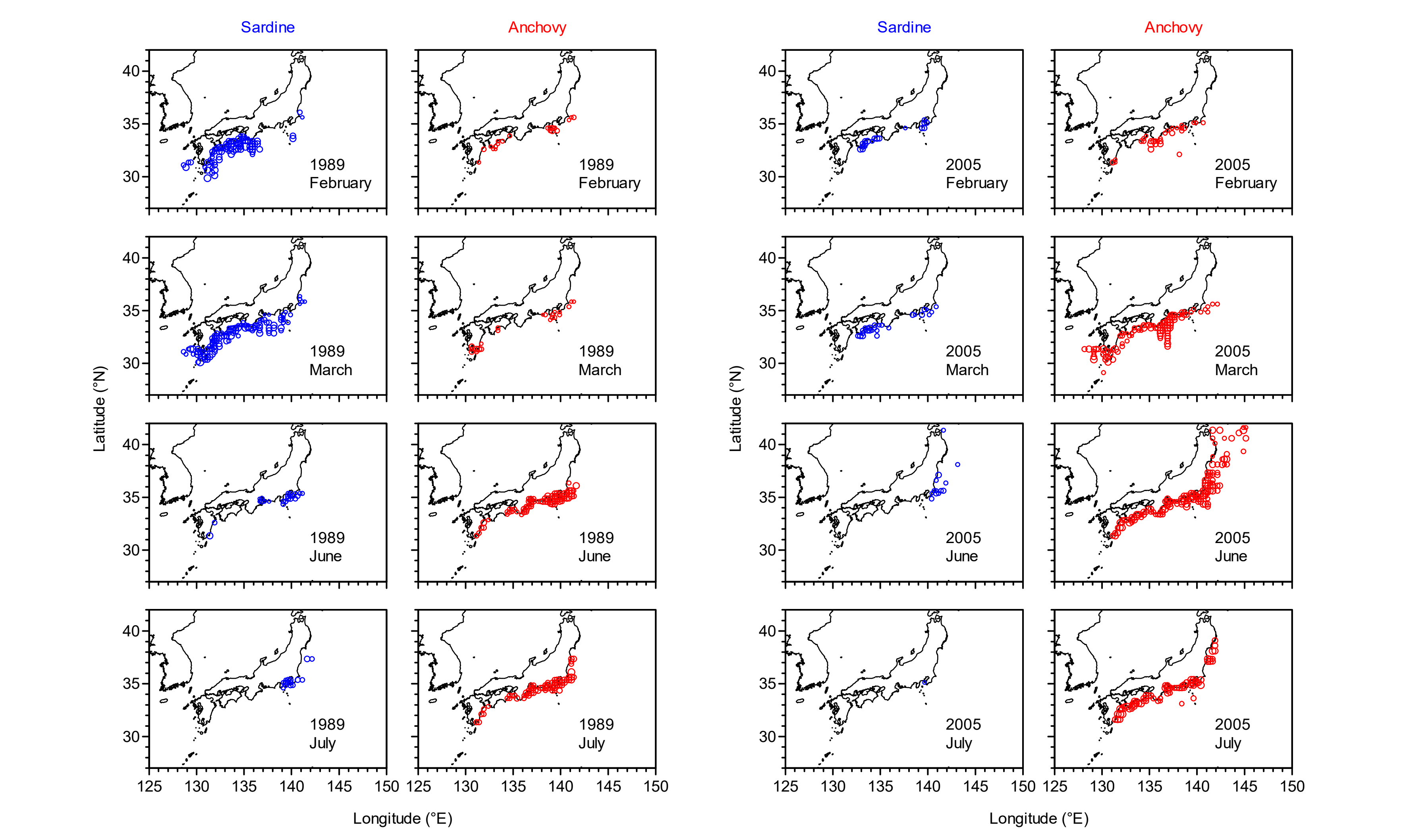
Seasons



Examples of distributions of monthly egg production of sardine and anchovy off the Pacific coast of Japan.

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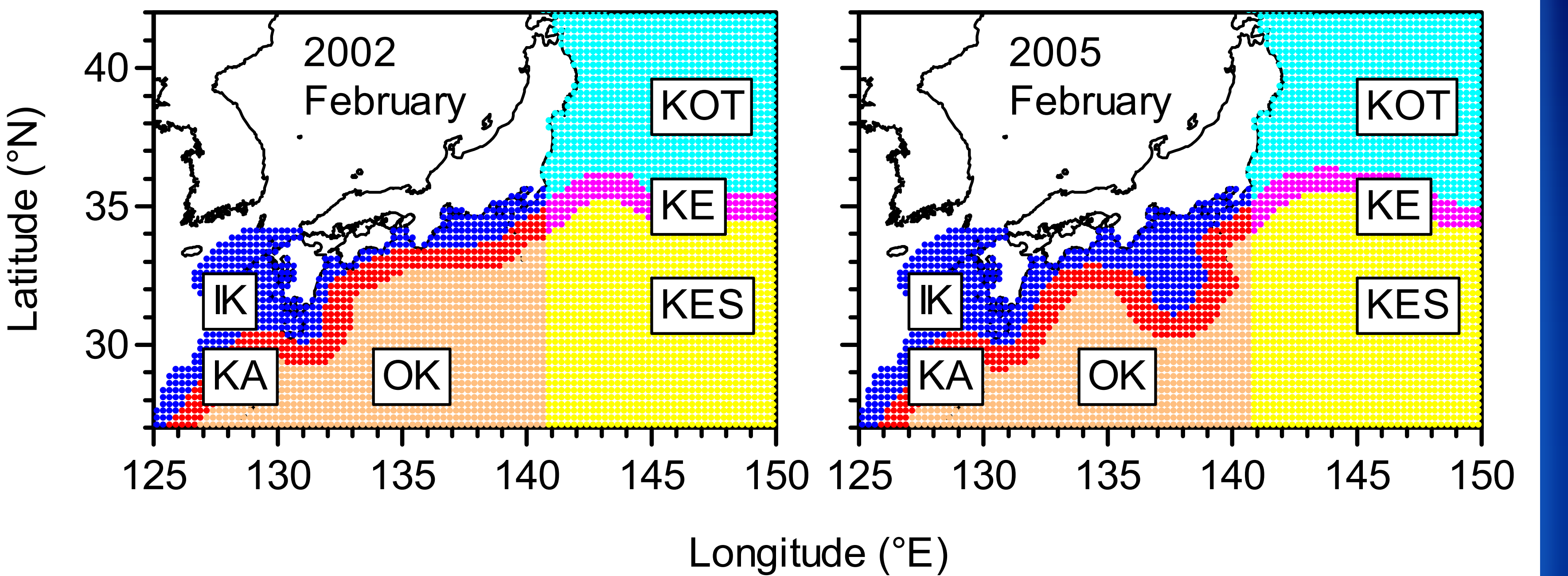
Regions



The six regions were classified by the location of the Kuroshio axis. The regions spatially and temporally change with the spatial (mesoscale) and temporal (daily) variability of the Kuroshio axis.

Definitions

IK: Inshore side of the Kuroshio axis region
KA: The Kuroshio axis region
OK: Offshore side of the Kuroshio axis region
KE: The Kuroshio Extension region
KES: The Kuroshio Extension southern region
KOT: The Kuroshio–Oyashio transition region

Examples of regions classified by the location of the Kuroshio axis.

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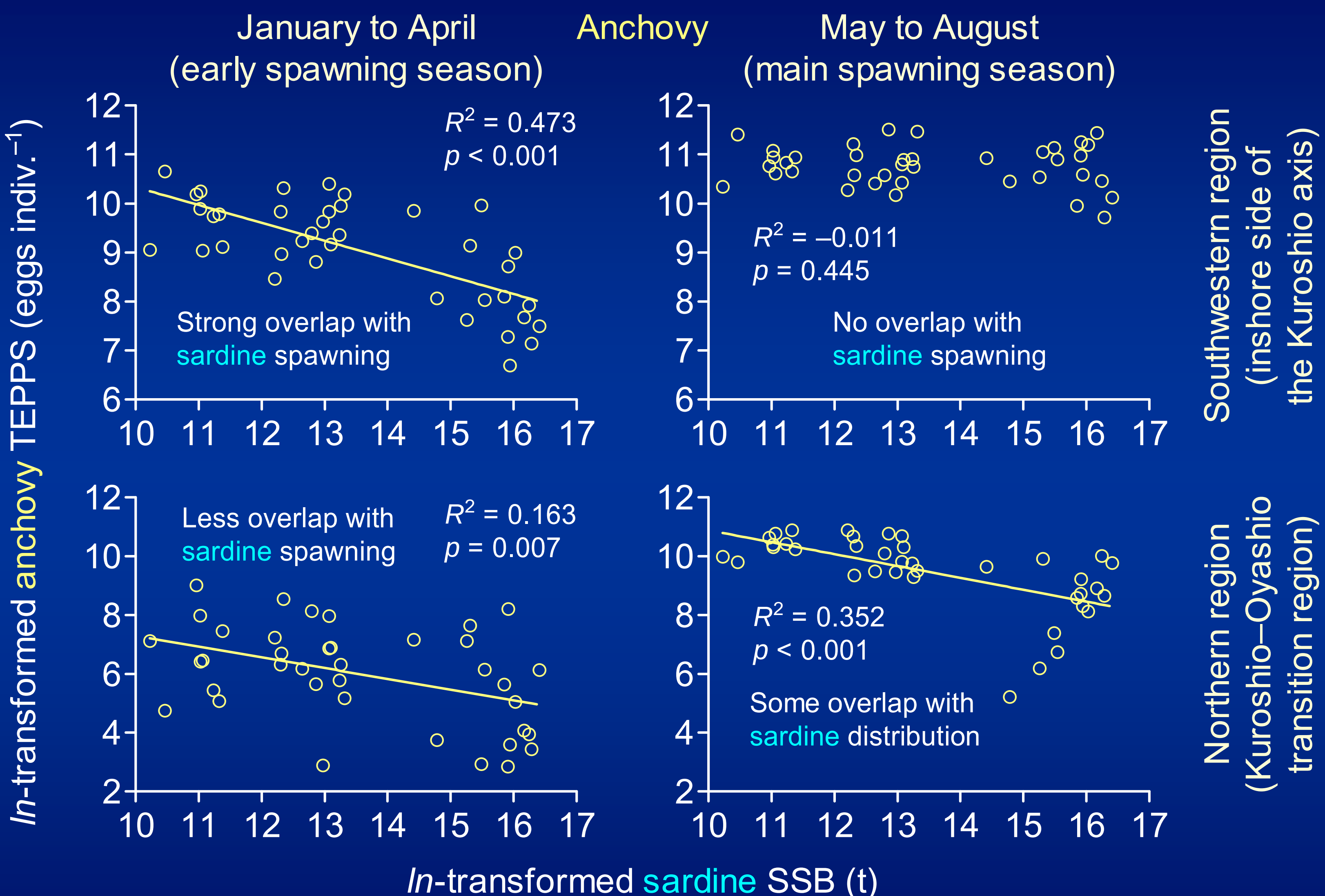
TEPPS vs SSB



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

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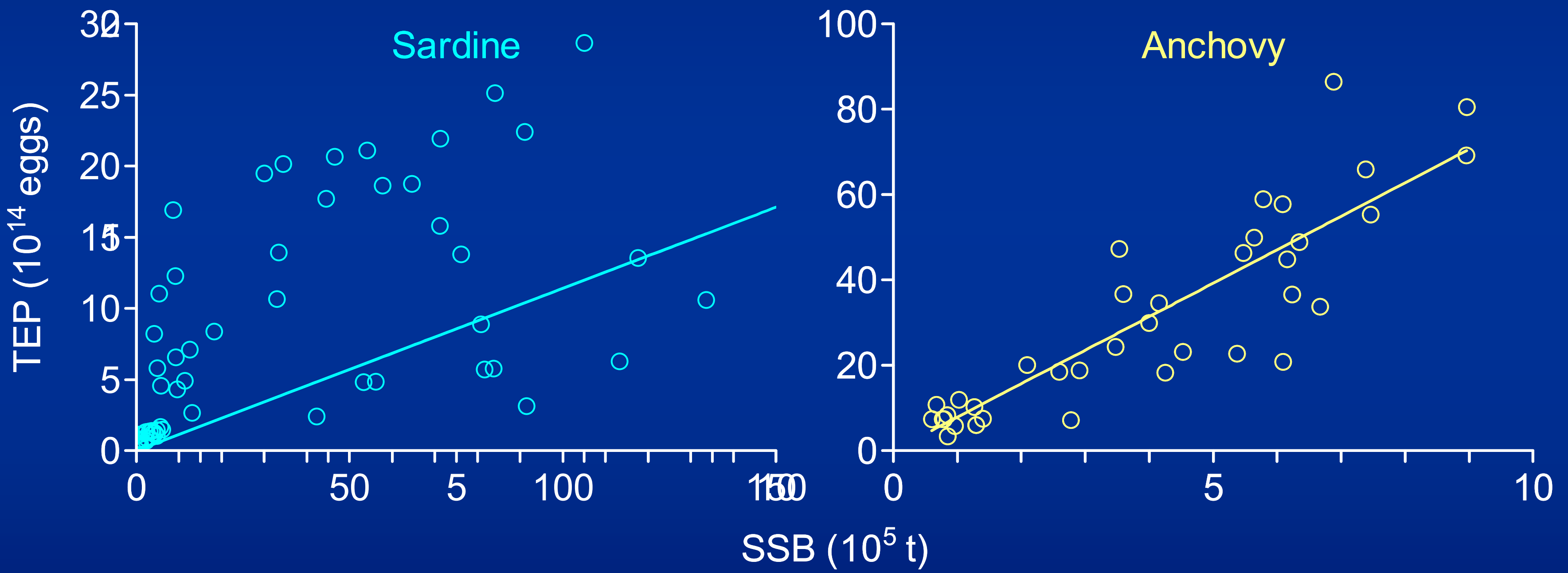
TEPPSW

Annual total egg production per spawner unit weight (TEPPSW)

= Annual total egg production (TEP) / spawning stock biomass (SSB)

= How many eggs are produced from a body mass unit weight of spawner for a year

= Annual relative fecundity (annual realized fecundity relative to body mass of spawner)



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

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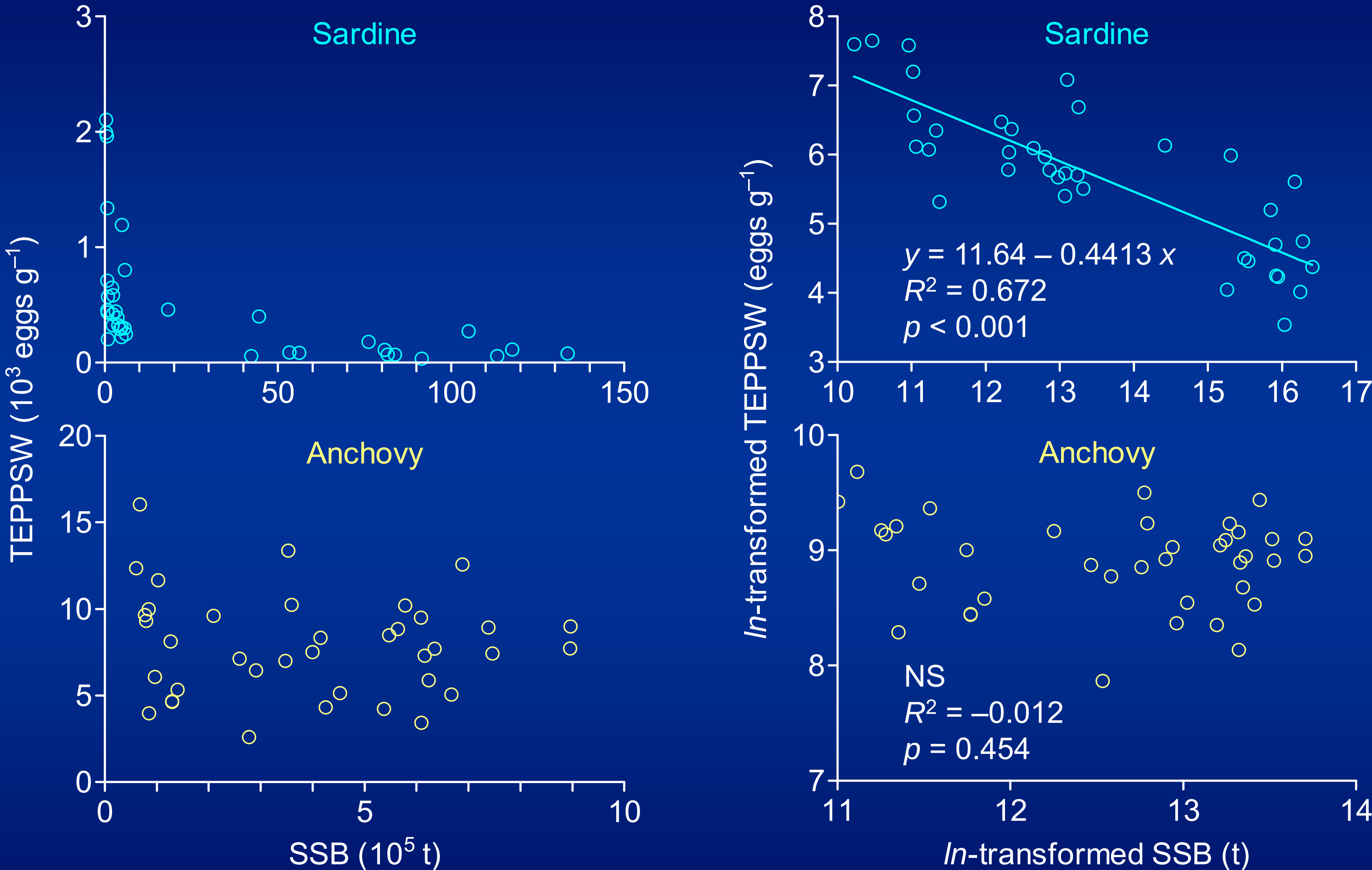
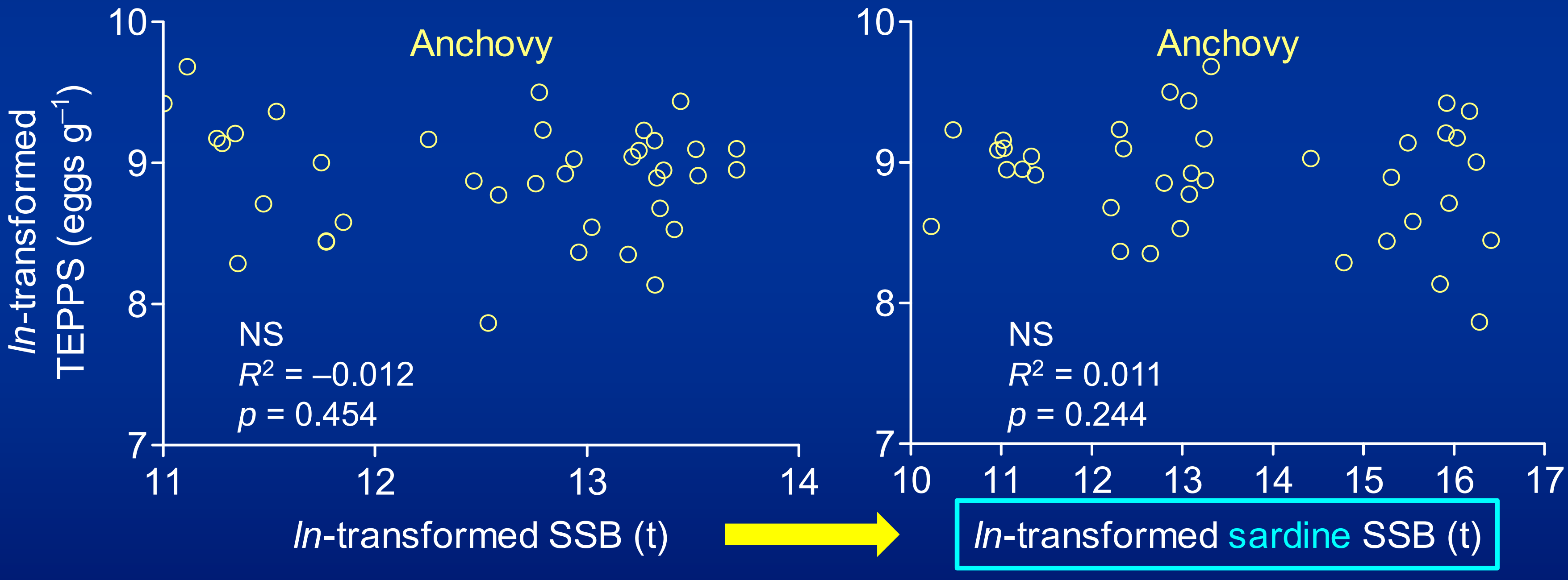
TEPPSW vs SSB



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

TEPPSW vs SSB

- No significant relationship appeared when TEPPS of anchovy was related to SSB of sardine.
- However, negative relationships of TEPPS of anchovy to SSB of sardine were confirmed by an analysis on seasonal/regional TEPPS of anchovy versus SSB of sardine.



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

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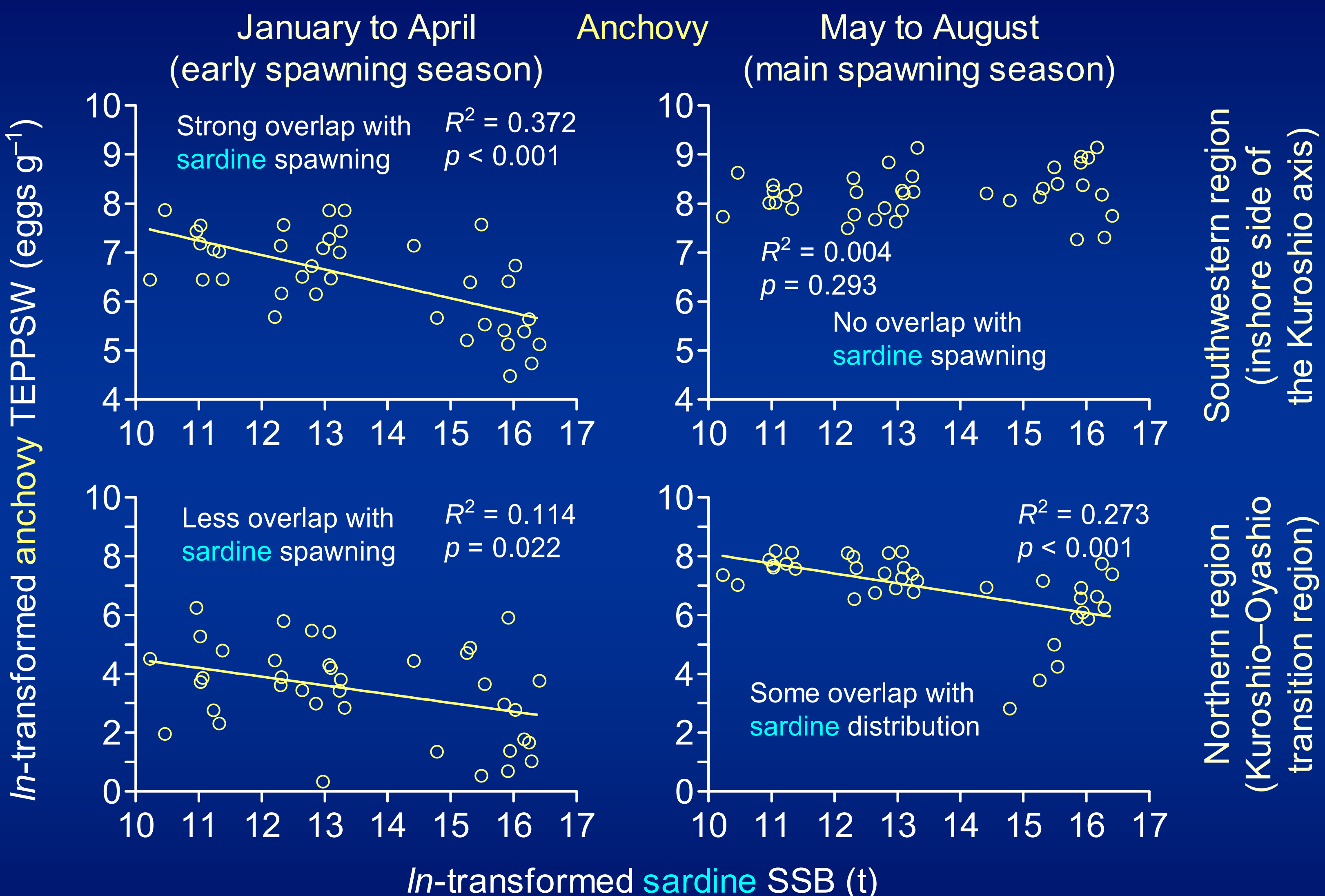
TEPPSW vs SSB



Relationships of <u>seasonal/regional</u> total egg production per spawner unit weight (TEPPSW) of anchovy to spawning stock biomass (SSB) of sardine.

Summary I

Direct test of the paradigm

- We directly tested the “SSB–TEP proportionality” paradigm based on a combination of two independent time series.
- The “SSB–TEP proportionality” is distorted by intraspecific and interspecific density dependence in TEPPS/TEPPSW (egg production).

Density dependence in TEPPS/TEPPSW

- The operation markedly differed 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 dependence in egg production was previously unaccounted for in spawner–recruitment relationships.
- How does the density dependence in egg production change the current understanding of density-dependent processes in the life history of fish?

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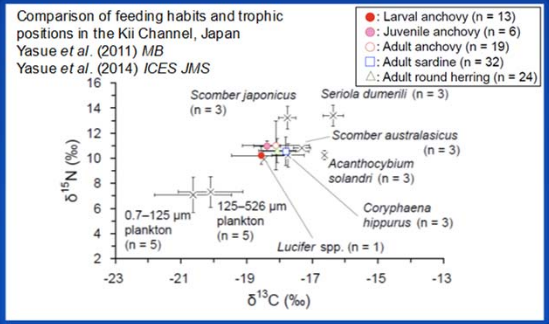
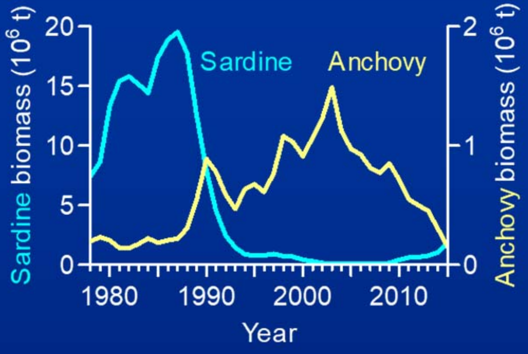
Summary I

➢ The phenomena would be attributable to maternal effects through intraspecific and interspecific competition for food resources required as energy for reproduction.



(1) Trophic overlap
Sardine and anchovy have strong trophic overlaps throughout their life histories.

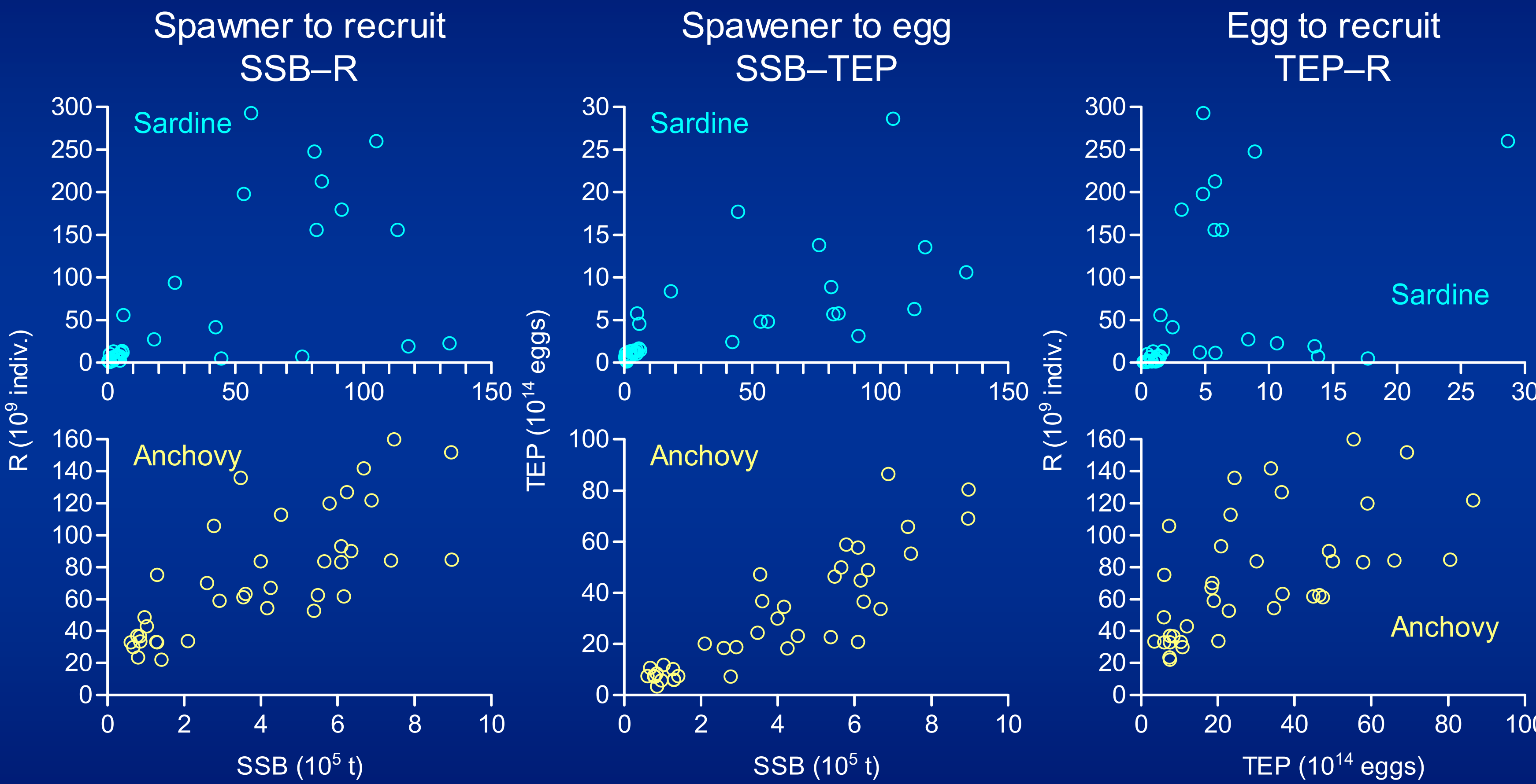
(2) Population fluctuation
The maximum biomass is 13 times greater for sardine (19.5×10^6 t) than for anchovy (1.5×10^6 t); the extent of population fluctuation is 20 times greater for sardine (225) than for anchovy (11).



(3) Energy allocation strategy for reproduction
Sardine: “capital–income” breeder (expending stored energy reserves)
Anchovy: “income” breeder (expending energy recently acquired)

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.

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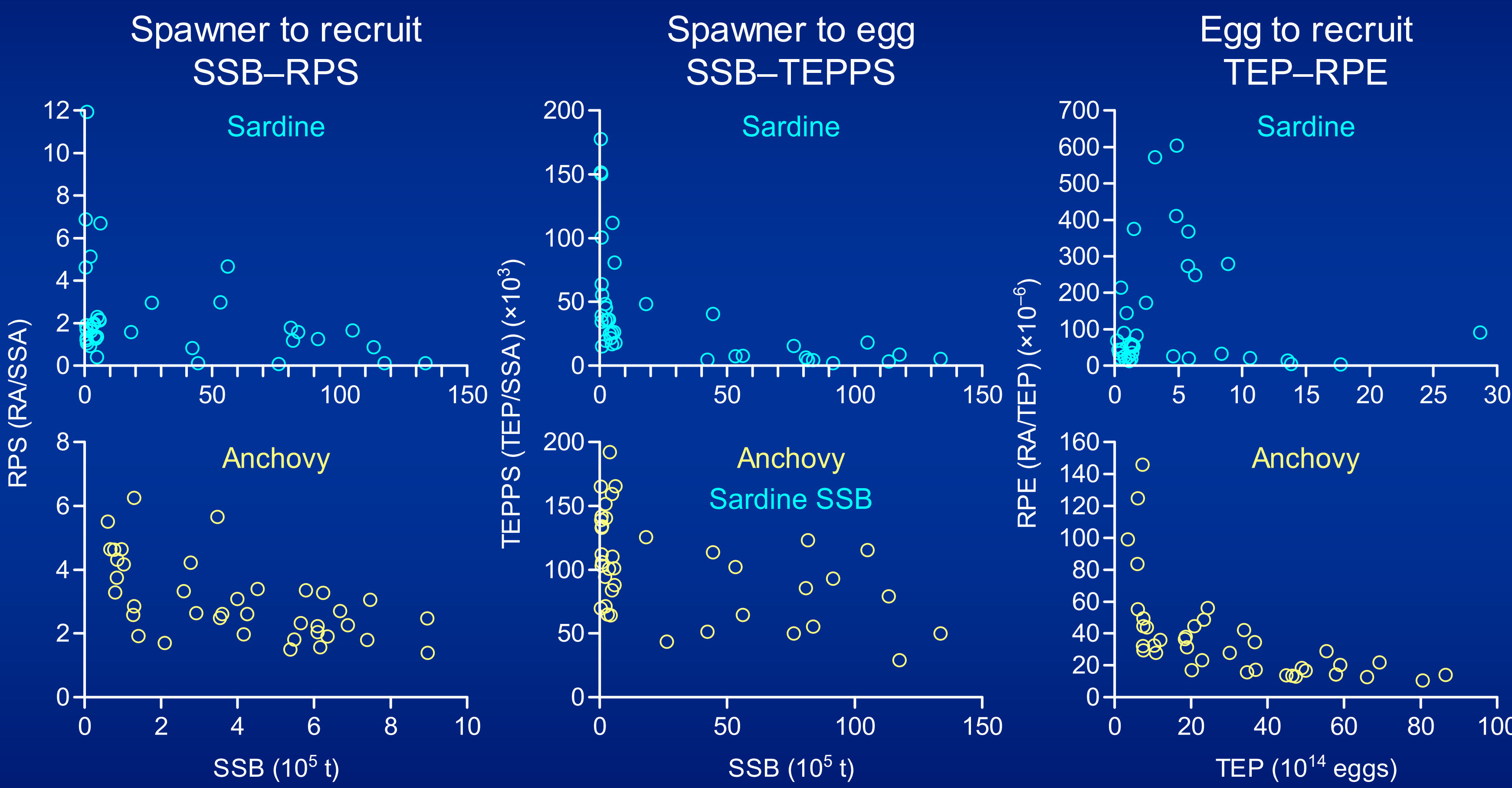
Disentangling

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).

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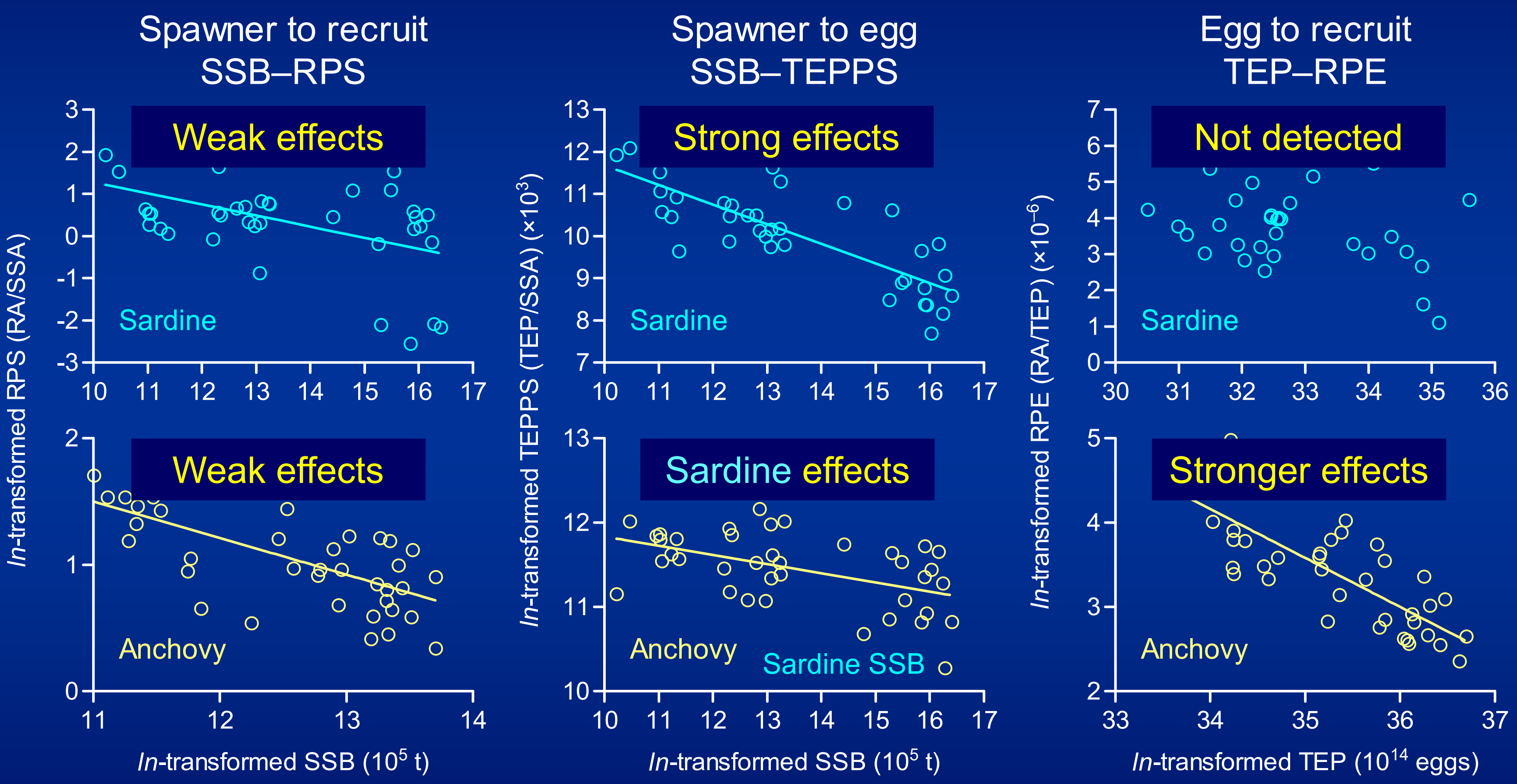
Disentangling

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).

Summary II

Disentangling density-dependent effects

- The existence of density dependence in 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 in fisheries management and recruitment studies.

1. Implications for fisheries management

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

2. Applications to recruitment studies

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

3. Contributions to numerical modelling

- Closing the life cycle by quantifying the SSB–TEP relationships.
- Constructing multispecies or interactive models.

Future perspectives

- Application to other pelagic and demersal species.
- Promoting and implementing fishery-independent egg surveys.

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ORIGINAL ARTICLE

WILEY FISH and FISHERIES

Density dependence in total egg production per spawner for marine fish

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Abstract

A paradigm of fisheries science holds that spawning stock biomass (SSB) is directly proportional to total egg production (TEP) of fish stocks. This "SSB–TEP proportionality" paradigm has been a basic premise underlying the spawner–recruitment models for fisheries management and numerous studies on recruitment mechanisms of fish. Studies on maternal effects on reproductive potential of a stock have progressed during the last few decades, leading to doubt concerning the paradigm. Nonetheless, a direct test of the paradigm at multidecadal scales has been difficult because of data limitations in the stock assessment systems worldwide. Here, we tested the paradigm for marine fish based on a novel combination of two independent 38-year time

Takasuka, A., Yoneda, M., Oozeki, Y. (2018) Density dependence in total egg production per spawner for marine fish. *Fish and Fisheries*.