

Reaching consensus on the growth–survival paradigm in early life stages of fish

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(31 co-authors from Japan, Canada, Norway, Germany, Spain, USA, Chile, and Perú)

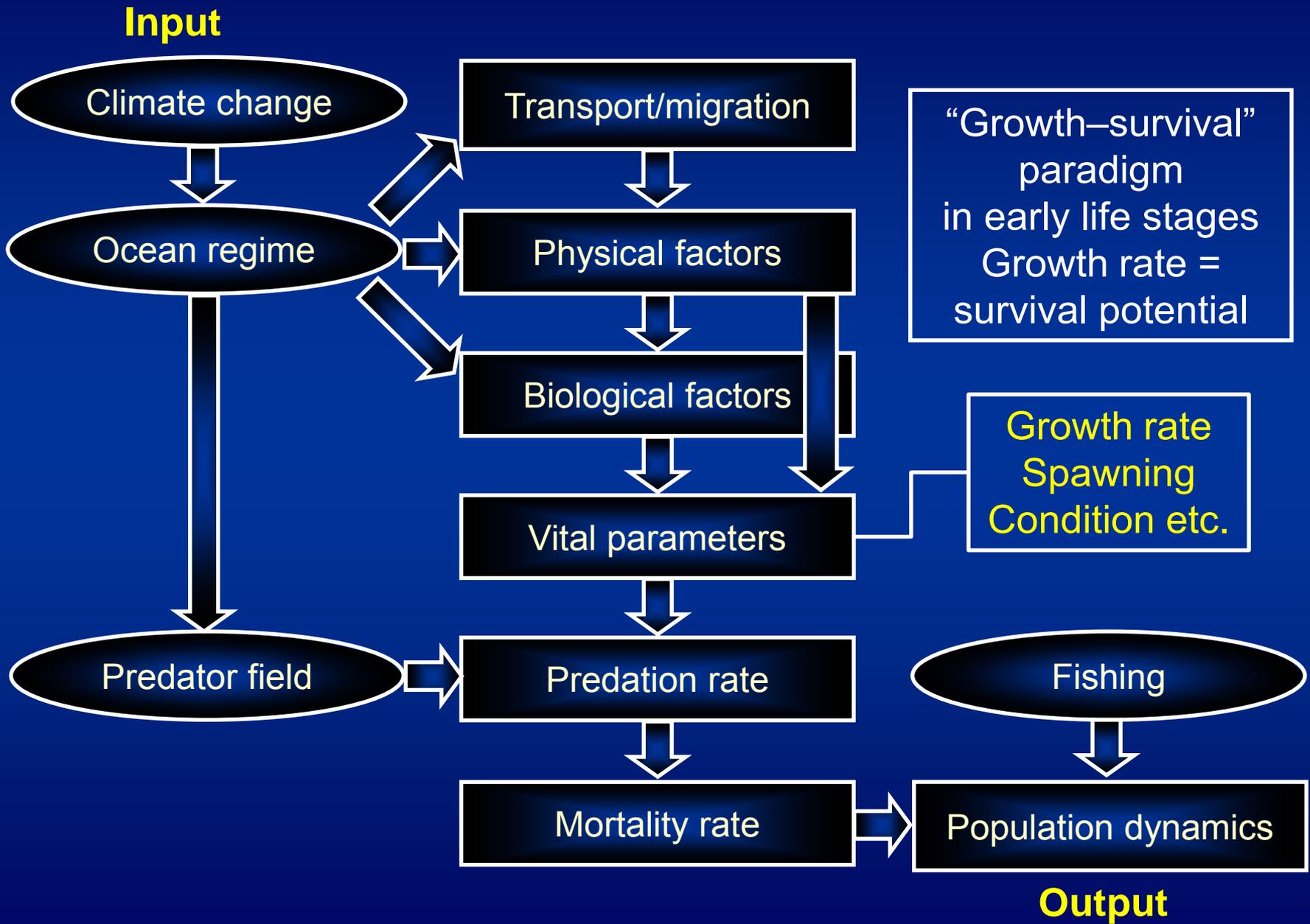
Symposium on “Drivers of dynamics of small pelagic fish resources”

Victoria Conference Centre, Victoria, BC, Canada

W4 “*Modeling migratory fish behavior and distribution*”

Invited talk, March 11, 2017

Cascade



Background

Growth–survival paradigm (GSP) in early life stages of fish

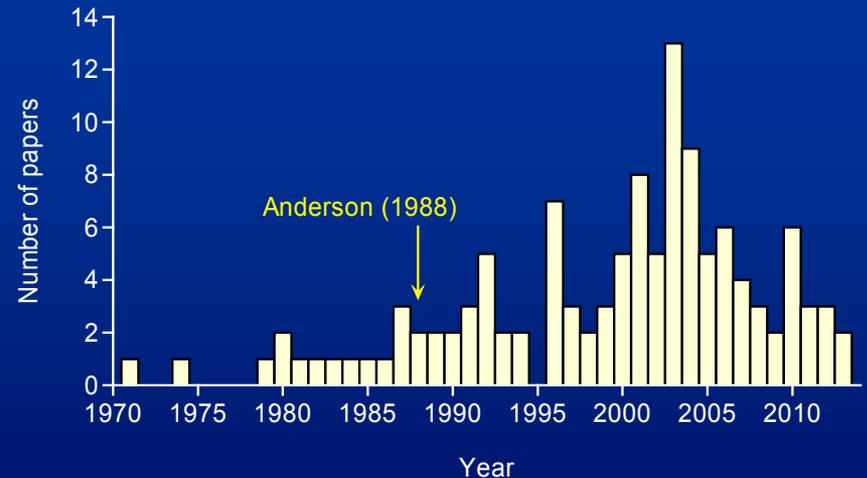
“Larger and/or faster growing individuals are more likely to survive than smaller and/or slower growing conspecifics”

History

- “Growth–mortality” hypothesis (Anderson 1988 *JNAFS*)

Progresses

- Numerous field, laboratory, and modeling studies have tested the paradigm.
- Contributing to early life biology and recruitment studies.



Number of published studies which include GSP tests.

Background

Quick review

1. Previous field studies tended to support the paradigm/mechanisms.
2. Some laboratory studies provided evidence contrary to the paradigm/mechanisms.
3. Recent studies showed a variability of direction of selective survival and dynamics of the mechanisms.

Current status

- The actual growth–survival relationships seem to be much more variable and dynamic than previously recognized.
- Predicting recruitment dynamics from early growth dynamics has revealed difficult.

It is time to review studies on GSP after Anderson (1988).

GSP workshop in 2011



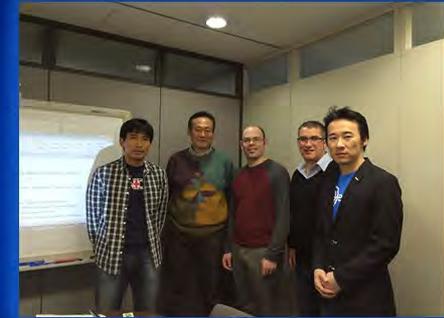
Japan–Québec collaboration workshop on
“Growth–survival paradigm in early life stages of fish:
theory, advance, synthesis, and future”

Yokohama, Japan

October 26 – November 1, 2011



Follow-up workshop in 2013



Japan–Canada collaboration workshop on
“Growth–survival paradigm in early life stages of fish:
theory, advance, synthesis, and future” Part III

Yokohama, Japan

November 8–15, 2013



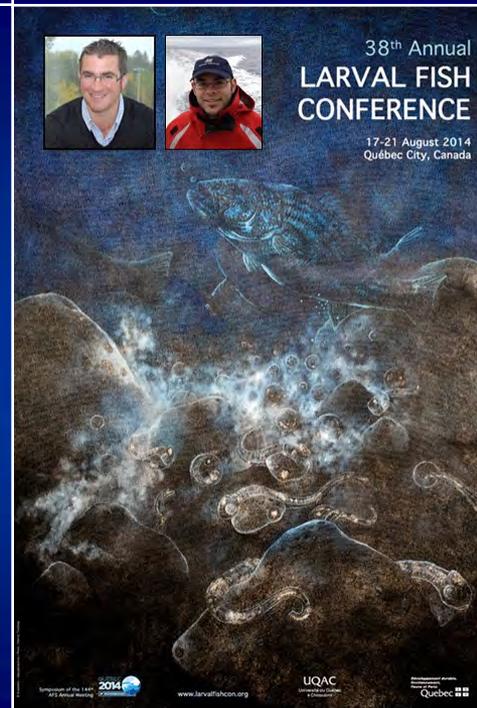
Follow-up workshop in 2012



Japan–Québec collaboration workshop on
“Growth–survival paradigm in early life stages of fish:
theory, advance, synthesis, and future” Part II

Vancouver, Canada

May 23–26, 2012



Growth–survival paradigm in early life stages of fish

I. Theory

Summarizing a theoretical framework of the current paradigm and its functional mechanisms

II. Advance

Reviewing recent advances in studies on the paradigm

III. Synthesis

Proposing a conceptual framework which reconciles contradictory evidence from field, laboratory, and modeling studies across systems and taxa

IV. Future

Presenting recommendations for future study directions

Theory

Growth–survival paradigm (GSP) in early life stages of fish

“Larger and/or faster growing individuals
are more likely to survive than
smaller and/or slower growing conspecifics”

Survival advantages of faster-growing individuals
Why do they survive better?

Functional mechanisms

1. “Bigger is better” (Miller *et al.* 1988 *CJFAS*)
2. “Stage duration” (Chambers & Leggett 1987 *CJFAS*, Houde 1987 *AFSS*)
3. “Growth-selective predation” (Takasuka *et al.* 2003, 2007 *MEPS*)

Theory

“Bigger is better” mechanism

(Miller *et al.* 1988 *CJFAS*)

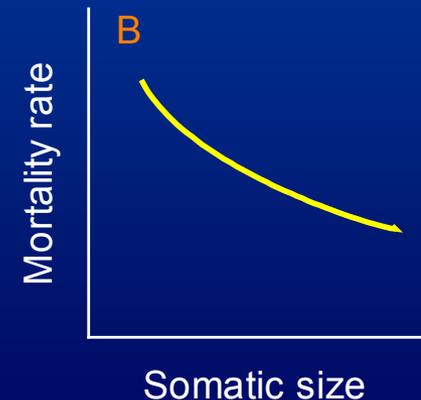
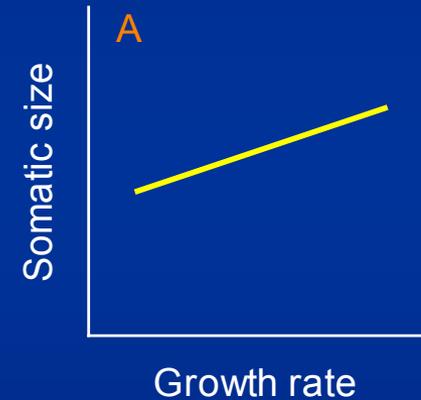
Faster-growing individuals will have a larger somatic size at a given age, which leads to various survival advantages.

Factor

- Somatic size
- Effect of growth rate: indirect

Operation conditions

1. Positive relationship between growth rate and somatic size at the population level (A)
2. Negative size-selective mortality (B)



Theory

“Stage duration” mechanism

(Chambers & Leggett 1987 *CJFAS*, Houde 1987 *AFSS*)

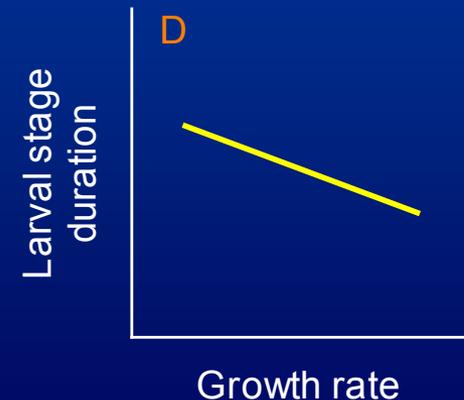
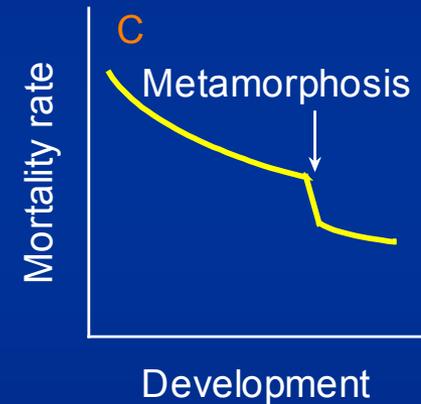
Faster-growing individuals will experience a much lower cumulative mortality rate during the larval stage.

Factor

- Time (stage duration)
- Effect of growth rate: indirect

Operation conditions

1. Larval stage characterized by higher mortality rate (C)
2. Negative relationship between growth rate and larval stage duration (D)



Theory

“Growth-selective predation” mechanism

(Takasuka *et al.* 2003, 2007 *MEPS*)

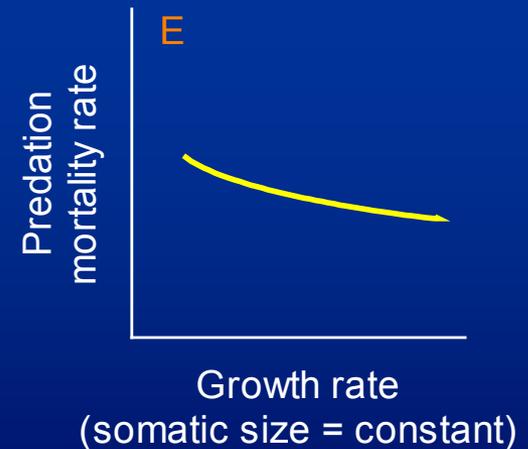
Faster-growing individuals will be less vulnerable to predation mortality than slower-growing conspecifics, even if they are the same size, at a given moment.

Factor

- Growth rate (*per se*)
- Effect of growth rate: direct

Operation conditions

1. Predation mortality
2. Negative growth-selective mortality at a given somatic size (E)



Growth–survival paradigm in early life stages of fish

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II. Advance

Reviewing recent advances in studies on the paradigm

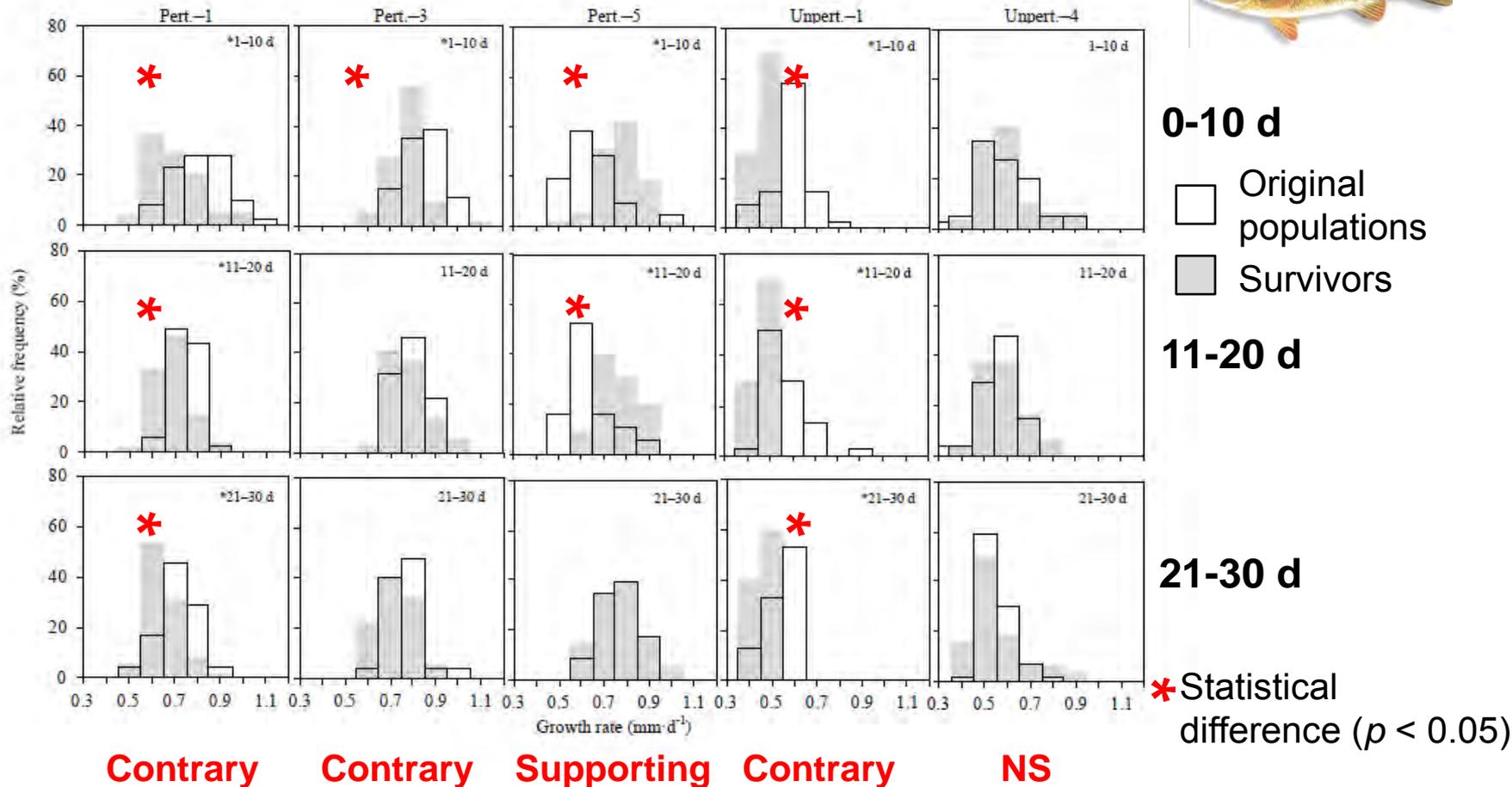
III. Synthesis

Proposing a conceptual framework which reconciles contradictory evidence from field, laboratory, and modeling studies across systems and taxa

IV. Future

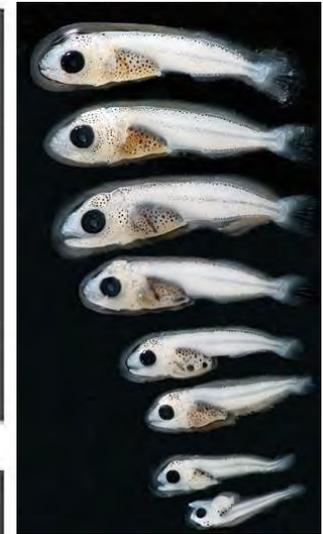
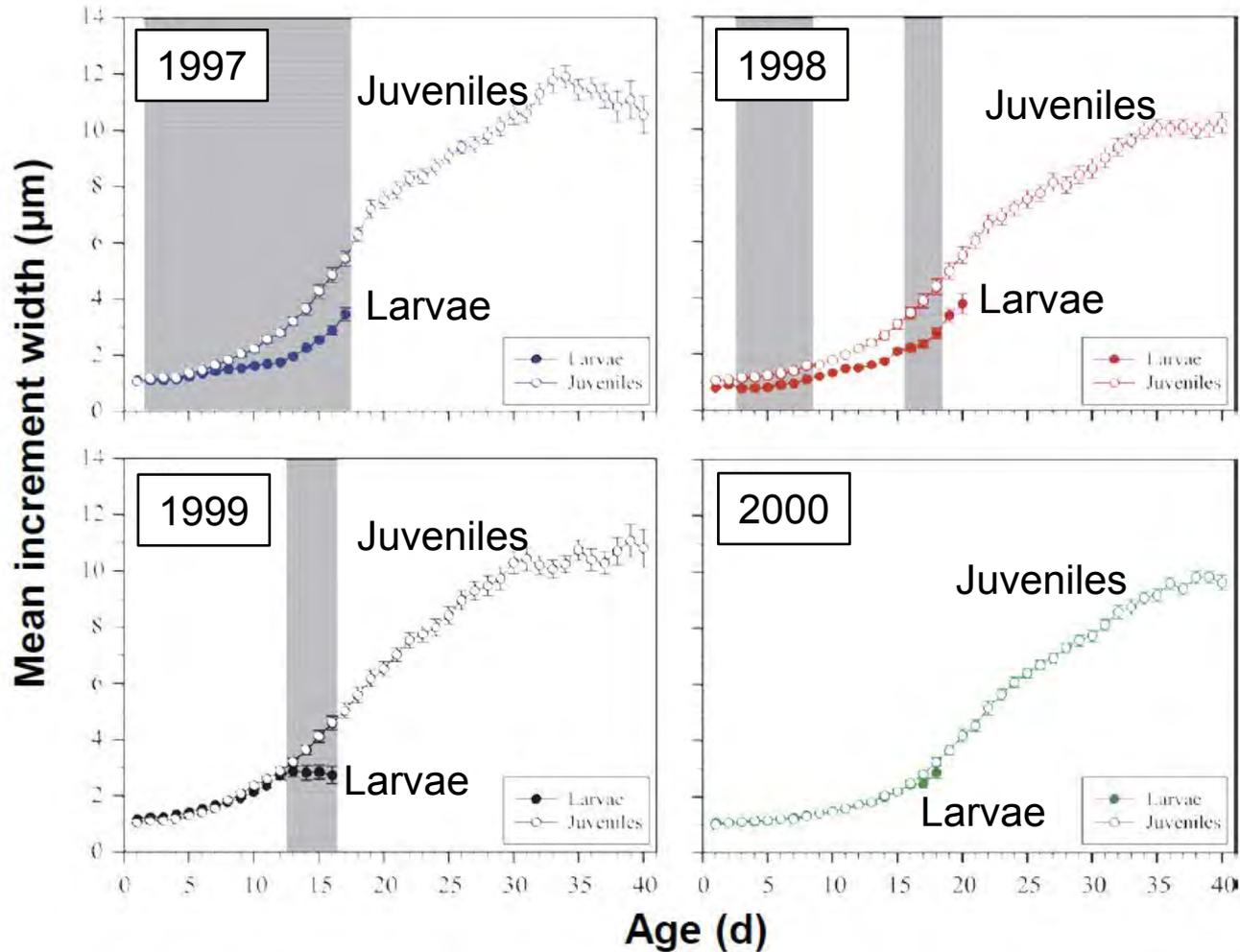
Presenting recommendations for future study directions

Spatial variability of selective mortality



Spatial variability of the direction of selective mortality of yellow perch *Perca flavescens* larvae in perturbed and unperturbed boreal lakes.

Temporal variability of selective mortality



Early growth and recruitment in Atlantic mackerel *Scomber scombrus*: discriminating the effects of fast growth and selection for fast growth.

Advance

Takasuka *et al.* (2003, 2004a,b, 2007) *MEPS*
Robert *et al.* (2010) *FS*

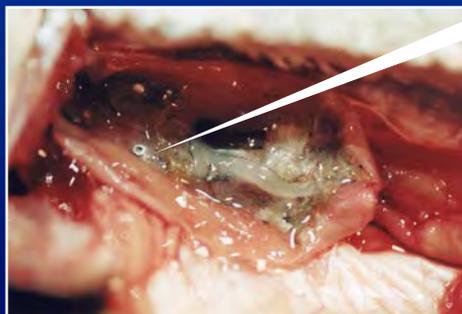
Field sampling

- Japanese anchovy larvae and their predatory fish were captured simultaneously by the same tows of a trawler in a coastal fishing ground and offshore waters.



Growth comparison

Ingested larvae



The larvae actually ingested by the predators



Otolith microstructure analysis

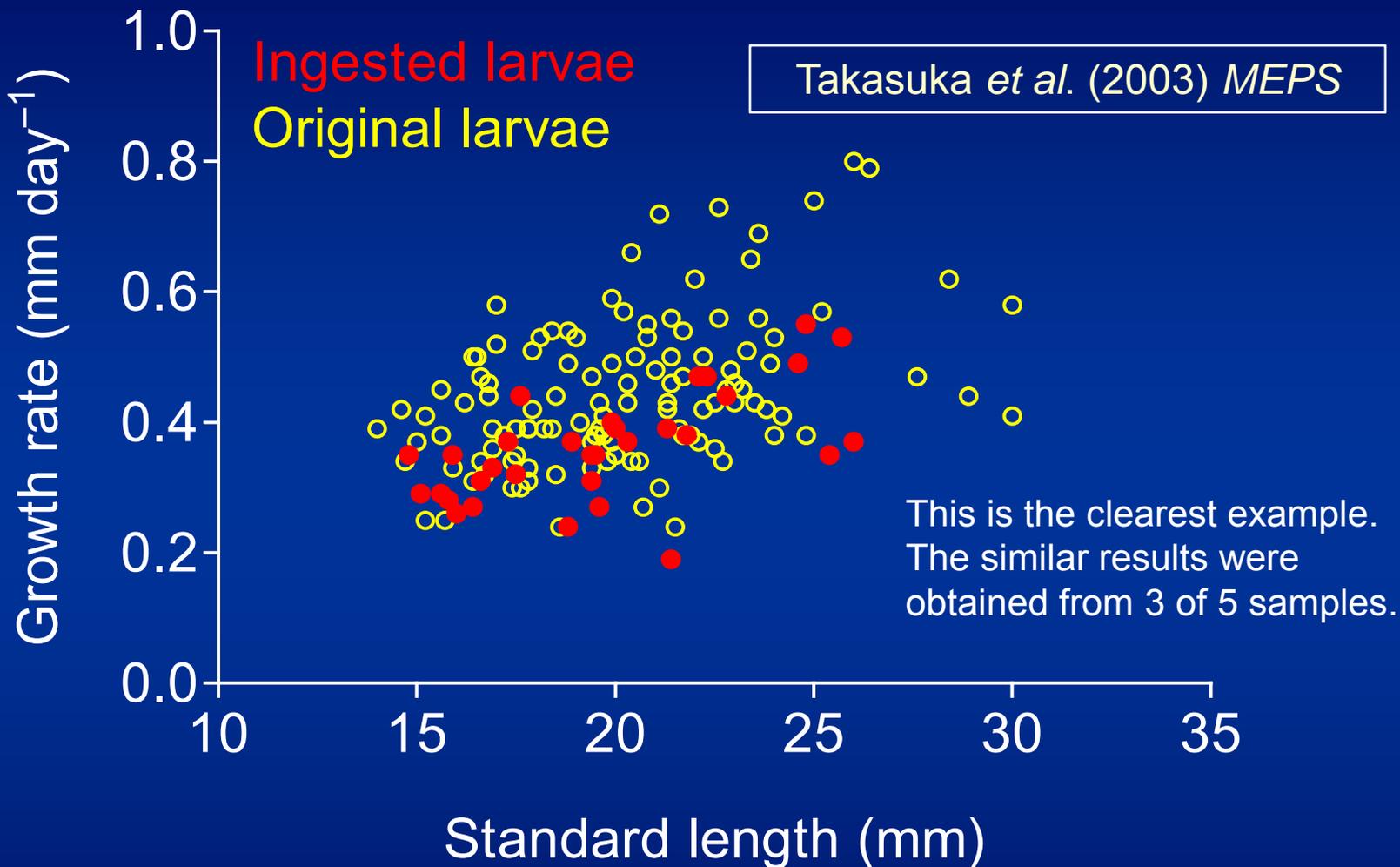
Original larvae



The surviving larvae from the original populations

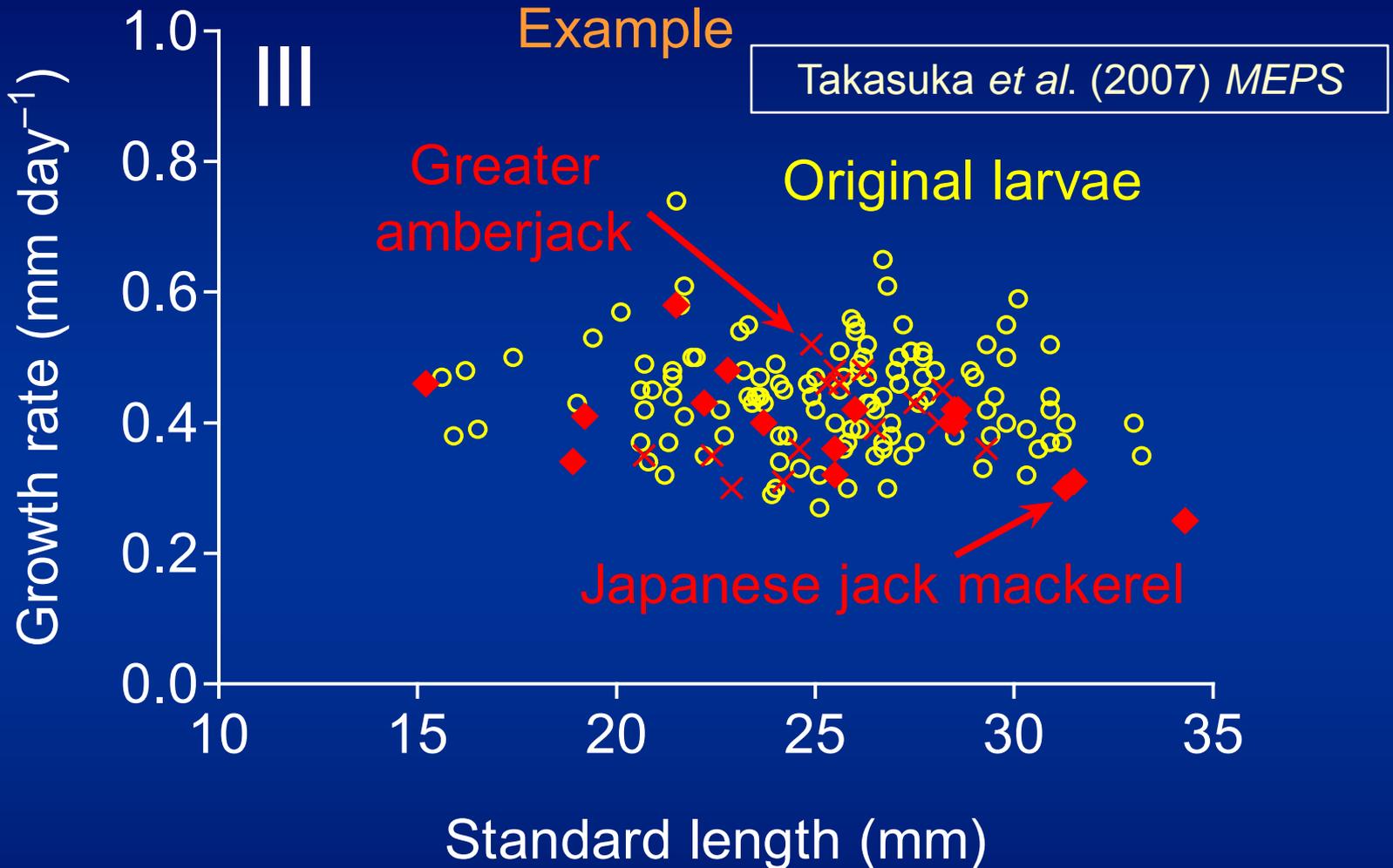
Demonstration of growth-selective predation on anchovy larvae.

Advance



Example of comparison of growth rate on standard length between **ingested larvae** and **original larvae**.

Advance



Example of comparison of growth rate on standard length between **ingested larvae** and **original larvae** for each predatory species.

Advance

Takasuka et al. (2007) MEPS
Robert et al. (2010) FS

Growth-selective predator



Japanese anchovy
Engraulis japonicus



Pacific round herring
Etrumeus teres



Japanese jack mackerel
Trachurus japonicus



White croaker
Pennahia argentatus

Non-growth-selective predator



Japanese sea bass
Lateolabrax japonicus



Greater amberjack
Seriola dumerili



Skipjack tuna
Katsuwonus pelamis



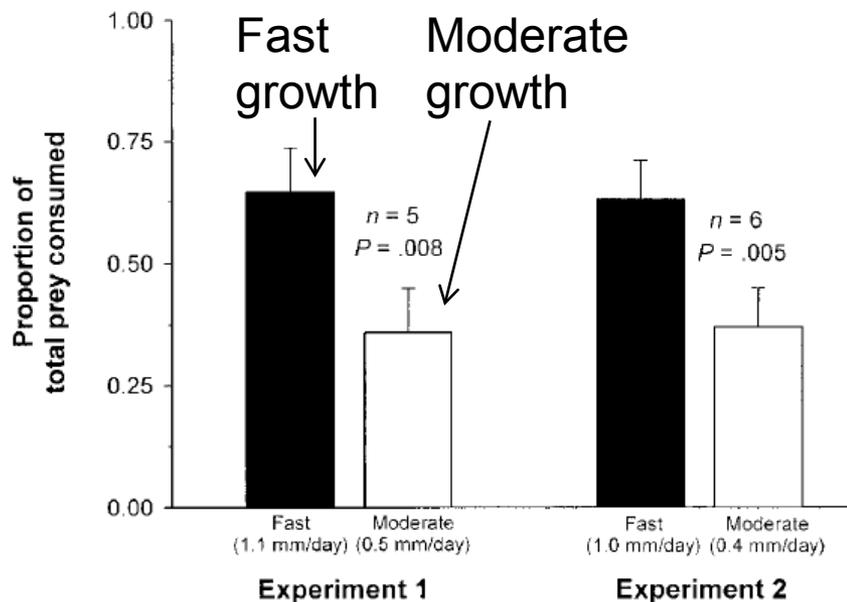
Chub mackerel & Spotted mackerel
Scomber japonicus & *S. australasicus*

Predator-specific growth-selective predation on anchovy larvae.

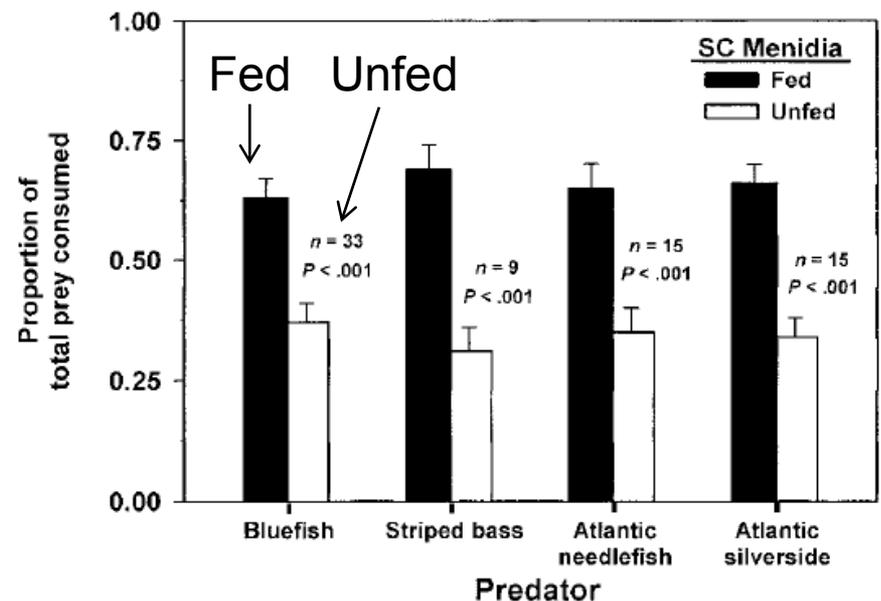
Advance

Evidence contrary to GSP from laboratory experiments

Lankford, T. E., Billerbeck, J. M., and Conover, D. O. (2001) Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution*, 55: 1873–1881.



Fast-growth group was more vulnerable to predation mortality.



Fed group was more vulnerable to predation mortality.

Example of energy trade-off between growth and physiological performance (Lankford *et al.* 2001 *Evolution*)

Growth–survival paradigm in early life stages of fish

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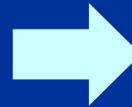
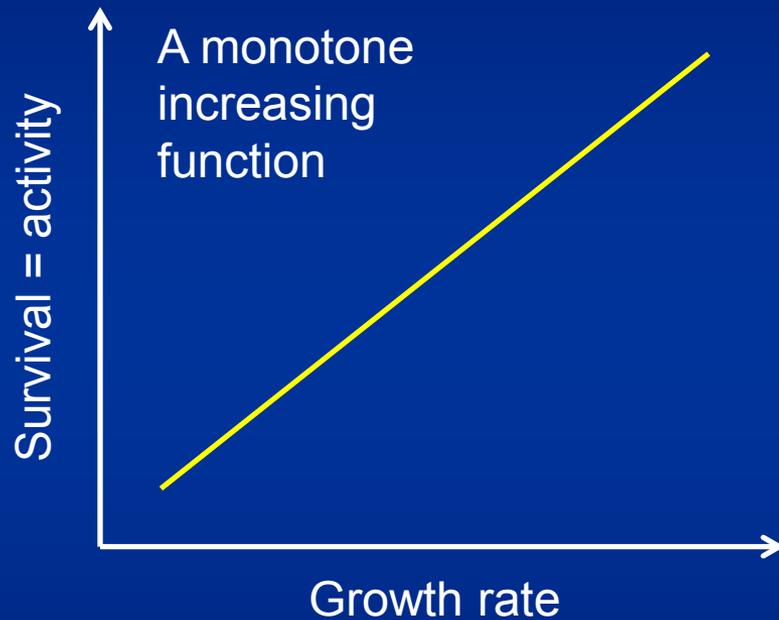
IV. Future

Presenting recommendations for future study directions

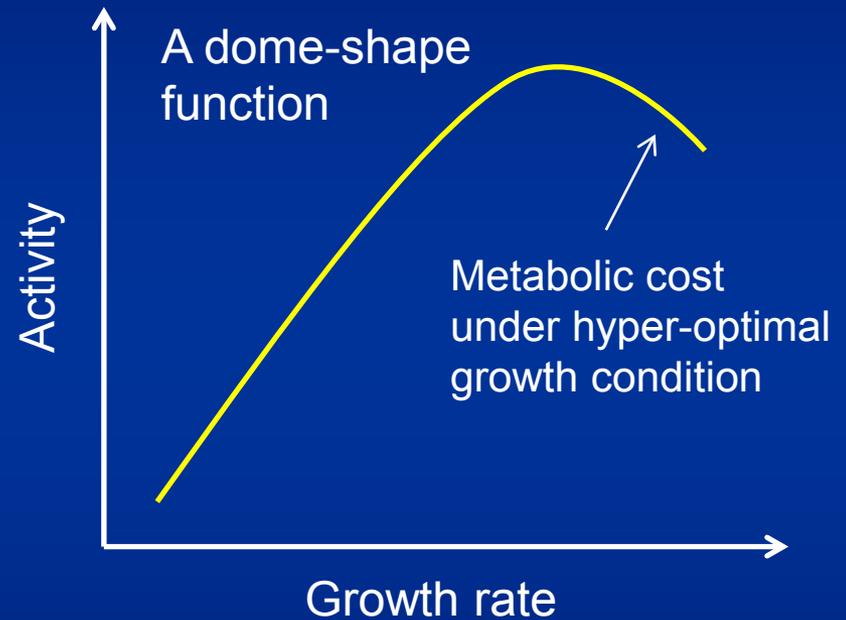
Synthesis

Start point of the conceptual framework

Growth–survival paradigm



Start point of reconstruction



- Energy trade-off between growth and physiological performance (Lankford *et al.* 2001, Munch & Conover 2003 *Evolution*)

Synthesis

Definition of predator type

Predator type	Definition	Example
Filter/ particulate	Fish and invertebrate predators that prey upon zooplankton, ichthyoplankton, or both by filter feeding , particulate feeding , or switching between filter and particulate feeding strategies	Anchovy Sardine Herring Jack mackerel
Raptorial	Fish and invertebrate predators that are strongly piscivorous and exclusively prey upon fish larvae and juveniles by active raptorial feeding strategy	Tuna Mackerel Cod Sea bass
Ambush	Fish and invertebrate predators that prey upon fish larvae and juveniles by ambush raptorial or entangling feeding strategy	Jellyfish Euphausiid Shrimp Ctenophore Hydra

* Predator type: terms for convenience of categorization

Synthesis

Predator type and driving factor for predation

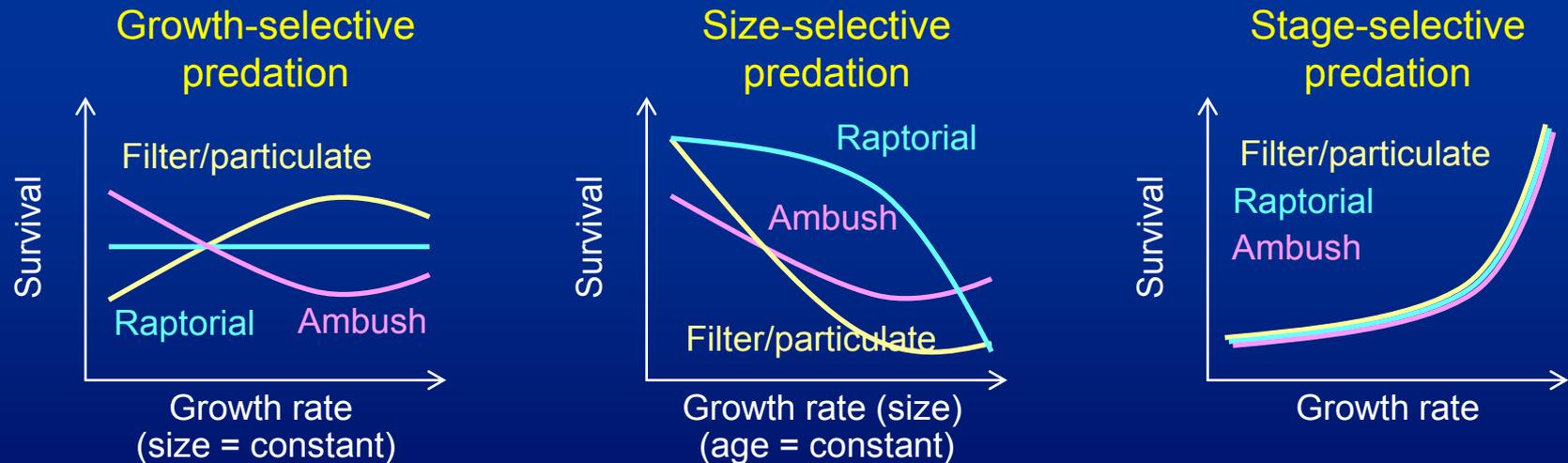
Predator type	Anti-predator behavior (activity)	Energy gain/cost for predator	Encounter rate (activity)
Filter/ particulate	Key	Potential	Potential
Raptorial	Negligible	Key	Negligible
Ambush	Potential	Negligible	Key

Key	Key factor which is considered in the conceptual framework
Potential	Potentially effective factor which is additionally considered
Negligible	Negligible or less effective factor which is not considered

Synthesis

Conceptual curves of growth–survival relationships were constructed for the 3 predator types for the 3 growth–survival mechanisms, respectively.

Predator type	Anti-predator behavior (activity)	Energy gain/cost for predator	Encounter rate (activity)
Filter/particulate	Key	Potential	Potential
Raptorial	Negligible	Key	Negligible
Ambush	Potential	Negligible	Key



Key and potential drivers are considered with optimal foraging theory (energy trade-off) on the side of predators.

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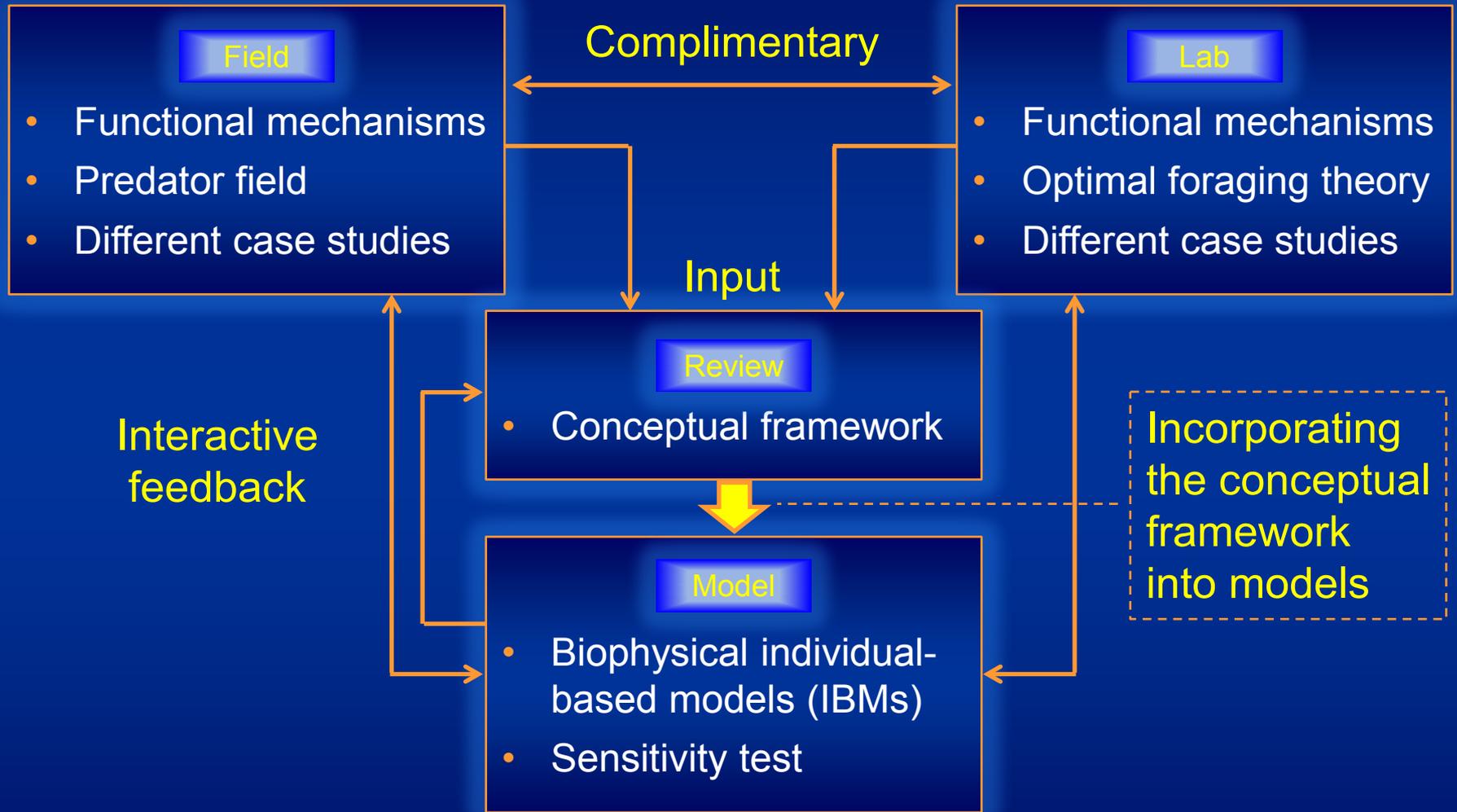
Proposing a conceptual framework which reconciles contradictory evidence from field, laboratory, and modeling studies across systems and taxa

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Presenting recommendations for future study directions

Future

Multidisciplinary approach



How much “**realistic**”?

Maybe a far-reaching goal, but we wish to start discussion.

Next stage

Next stage

Stage-I (Background)

Japan–Canada
collaboration team

Common expertise
Common perspectives

Proposal

“This is what we think.”



Stage-II (Symposium)

Scientists from
around the world

Different expertise
Different perspectives

Discussion

“What do you think?”

Symposium on
**Growth–survival paradigm
in early life stages of fish:**

controversy, synthesis, and
multidisciplinary approach

November 9–11, 2015

*National Research Institute of Fisheries Science,
Fisheries Research Agency, Yokohama, Japan*

Objectives

1. “Controversy”

Extracting controversial issues on the paradigm.

2. “Synthesis”

Proposing ideas for reconciling and synthesizing contradictory results based on different perspectives from different study groups.

3. “Multidisciplinary approach”

Promoting a collaborative framework for field, laboratory, and modeling studies.

- Proposing recommendations for future studies through discussion.

Objectives

Overall goal

To improve our understanding of growth–survival relationships (“comprehensive”, “synthetic”, and “realistic”) in order to facilitate the prediction of recruitment dynamics through numerical modeling.

Organizers

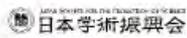
	Akinori Takasuka (Japan)	National Research Institute of Fisheries Science, Fisheries Research Agency E-mail: takasuka@affrc.go.jp
	Dominique Robert (Canada)	Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute, Memorial University of Newfoundland E-mail: dominique.robert@mi.mun.ca
	Jun Shoji (Japan)	Field Science Education and Research Center, Hiroshima University E-mail: jshoji@hiroshima-u.ac.jp
	Pascal Sirois (Canada)	Research Chair on Exploited Aquatic Species, Department of Fundamental Sciences, University of Quebec at Chicoutimi E-mail: pascal_sirois@uqac.ca

Advisers

The organizers asked two scientists to review progresses of the activities as advisers.

	Louis Fortier (Canada)	Québec-Océan, Département de Biologie, Université Laval E-mail: Louis.Fortier@bio.ulaval.ca
	Yoshioki Oozeki (Japan)	Headquarters, Fisheries Research Agency E-mail: oozeki@affrc.go.jp

Funding Agencies

	Japan Society for the Promotion of Science (JSPS) (http://www.jsps.go.jp/english/index.html)
	Fisheries Research Agency (FRA) (http://www.fra.affrc.go.jp/english/eindex.html)

Research projects

	Grant-in-Aid for Scientific Research (A) Takasuka, A. (PI), Oozeki, Y., Kuroda, H., Okunishi, T. KAKENHI No. 26252031 (April 2014 to March 2019) (http://kaken.nii.ac.jp/d/p/26252031.en.html)
	Grant-in-Aid for Scientific Research (B) Shoji, J. (PI), Mitamura, H., Takasuka, A. KAKENHI No. 24380107 (April 2012 to March 2016) (http://kaken.nii.ac.jp/d/p/24380107.en.html)
	Grant-in-Aid for Scientific Research (C) Oozeki, Y. (PI), Okamura, H., Takasuka, A. KAKENHI No. 26450275 (April 2014 to March 2017) (http://kaken.nii.ac.jp/d/p/26450275.en.html)

Unique points

- Independency
- Topic focus
- Invited speakers

Keynote speakers

	Pierre Pepin (Canada)	Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada E-mail: pierre.pepin@dfo-mpo.gc.ca
	Arild Folkvord (Norway)	Department of Biology, University of Bergen and the Hjort Centre for Marine Ecosystem Dynamics E-mail: arild.folkvord@uib.no
	Myron A. Peck (Germany)	Institute of Hydrobiology and Fisheries Science, University of Hamburg E-mail: myron.peck@uni-hamburg.de



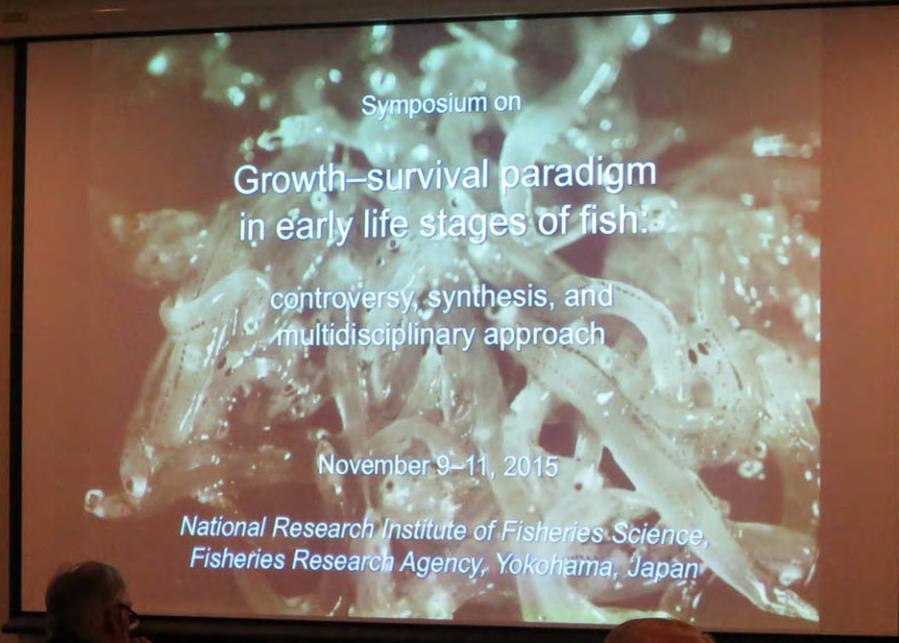
Invited speakers

	Ignacio A. Catalán (Spain)	Instituto Mediterráneo de Estudios Avanzados (IMEDEA)- Consejo Superior de Investigaciones Científicas / Universitat de les Illes Balears E-mail: ignacio@imedea.uib-csic.es
	Alberto G. García (Spain)	Coordinator of the Mediterranean Fisheries Program of the Spanish Institute of Oceanography (IEO) E-mail: agarcia@ma.ieo.es
	Marc Hufnagl (Germany)	Institute of Hydrobiology and Fisheries Science, University of Hamburg E-mail: marc.hufnagl@uni-hamburg.de
	Klaus B. Huebert (Germany / USA)	Institute of Hydrobiology and Fisheries Science, University of Hamburg E-mail: klaus.huebert@uni-hamburg.de
	Louis Fortier (Canada)	Québec-Océan, Département de Biologie, Université Laval E-mail: Louis.Fortier@bio.ulaval.ca
	John F. Dower (Canada)	Department of Biology and School of Earth & Ocean Sciences, University of Victoria E-mail: dower@uvic.ca
	Su Sponaugle (USA)	Department of Integrative Biology, Oregon State University E-mail: Su.sponaugle@oregonstate.edu

PROGRAM

	<p>Shin-ichi Ito (Japan)</p>	<p>Atmosphere and Ocean Research Institute, The University of Tokyo E-mail: goito@aori.u-tokyo.ac.jp</p>
	<p>Mikimasa Joh (Japan)</p>	<p>Mariculture Fisheries Research Institute, Hokkaido Research Organization E-mail: joh-mikimasa@hro.or.jp</p>
	<p>Yosuke Tanaka (Japan)</p>	<p>Seikai National Fisheries Research Institute, Fisheries Research Agency E-mail: yosuket@affrc.go.jp</p>
	<p>Motomitsu Takahashi (Japan)</p>	<p>Seikai National Fisheries Research Institute, Fisheries Research Agency E-mail: takahamt@fra.affrc.go.jp</p>





Symposium on

Growth–survival paradigm in early life stages of fish:

controversy, synthesis, and
multidisciplinary approach

November 9–11, 2015

*National Research Institute of Fisheries Science,
Fisheries Research Agency, Yokohama, Japan*





Spatio-temporal variability and measurement bias in selection for fast growth during the larval stage of fish



Dominique Robert
Akinori Takasuka
Jun Shoji
Pascal Sirois
Ichiro Aoki
Louis Fortier
Yoshioki Oozeki

GSP Symposium Yokohama
9 November 2015

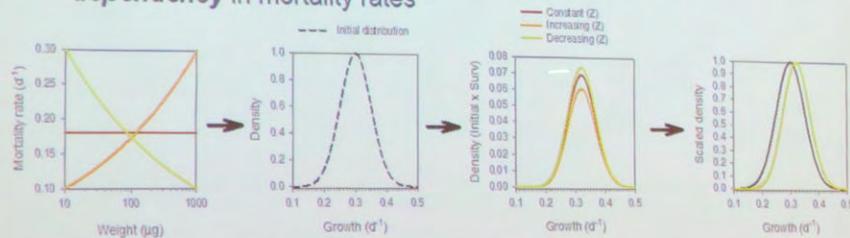


Centre for Fisheries Ecosystems Research
Fisheries & Marine Institute of Memorial University of Newfoundland



Basics of the growth-survival paradigm

- If the patterns of growth and mortality are *invariant* in time and space (i.e. all larvae are subject to the same mortality scenario) the pattern of growth selection will remain constant *irrespective* of any *size-dependency* in mortality rates



- Intensity of selection will increase as average mortality increases or stage duration increases, and vice versa
- Faster growing individuals will *always* have a higher likelihood of survival (high-growth selection) if the pattern of mortality is *invariant*



Predation cycle



modified from Bailey and Houde 1989

Search

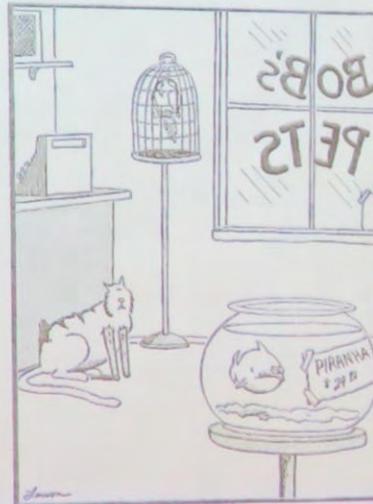


Encounter & Detect

Pursue & Attack

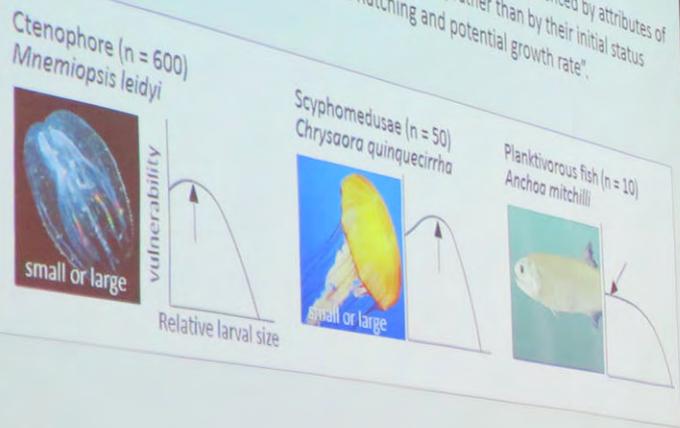


Capture & Ingest

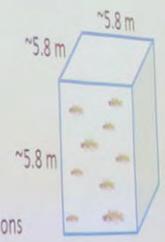


Predation is not a trivial process!

J.H. Cowan et al. 1996:
"We propose that characteristics of larval survivors may be more influenced by attributes of the predators to which they were exposed in early life, rather than by their initial status within a cohort with respect to length at hatching and potential growth rate".



5000 larvae
200m³ virtual habitat
20-d simulations
Prey were goby (*Gobiosoma boscii*) larvae
Predators and prey randomly distributed (no patches)
Mean and variance of larval growth differed among simulations



Spatially-explicit biophysical models of the growth and survival of early life stages of fish: A synthesis with recommendations



Myron A. Peck, Marc Hufnagl, Klaus Huebert, Marta Moyano



Ute Daewel
Uni Bergen



Marc Hufnagl



Markus Kreis



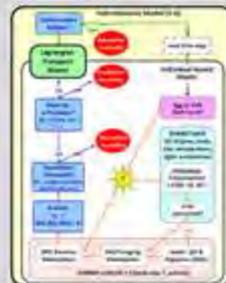
Klaus Hubert



Anna Akimova
Thünen Institute



Marta Moyano



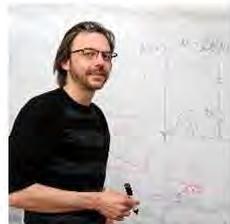
When and how do growth paradigms evolve from IBMs and size-structured models?



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marc.hufnagl@uni-hamburg.de



Myron A. Peck
Uni. Hamburg



Ken Haste Andersen
DTU, Denmark

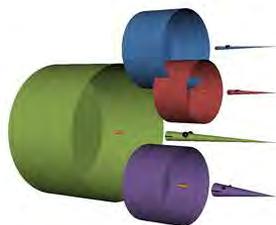
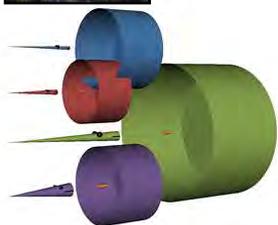


Modeling larval fish growth using Quirks



Klaus B. Huebert^{1,2}, Johannes Pätsch¹, Marc Hufnagl¹, Markus Kreuz¹, and Myron A. Peck¹

¹University of Hamburg, Germany
²Chesapeake Biological Laboratory, USA



Growth-survival problems in a coupled model between fish-growth and environments

Shin-ichi Ito (Univ. Tokyo)

Takeshi Okunishi (TNFRI, FRA)

Michio Yoneda (NRIFEIS, FRA)

Kosei Komatsu (Univ. Tokyo)

Tatsuya Sakamoto (Univ. Tokyo)

Akinori Takasuka (NRIFS, FRA)

Sachihiko Itoh (Univ. Tokyo)



Today's contents

1. backgrounds
2. model developments
3. hindcast simulation on larval growth
4. hindcast simulation on survival rate
5. future perspectives



“Are management goals impeding or fostering the scientific progress of the growth-survival paradigm?”

Ignacio A. Catalán

IMEDEA (Instituto Mediterráneo de Estudios Avanzados: Spanish National Research Council (CSIC)-University of the Balearic Islands (UIB))





Symposium on
Growth-survival paradigm
in early life stages of fish

University synthesis and
collaboration

禁煙

禁煙



Workshop

A post-symposium workshop

(November 12–13)

A total of 30 invited participants

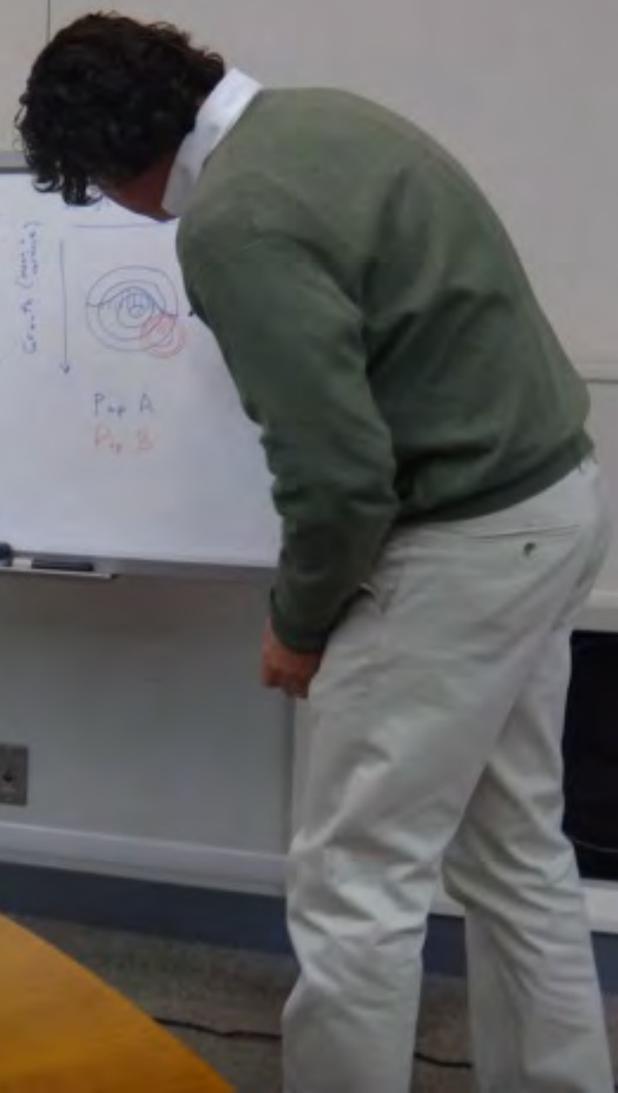
Objectives

1. Providing a networking environment for future collaborations among the participants to resolve some important issues identified during the symposium/workshop.
2. Publishing a “perspective” paper co-authored by all workshop participants to identify what is needed for breakthroughs. The paper will provide concrete study designs to improve our understanding of the growth–survival relationships during early life stages of fish.





樂 融
NO BAKING



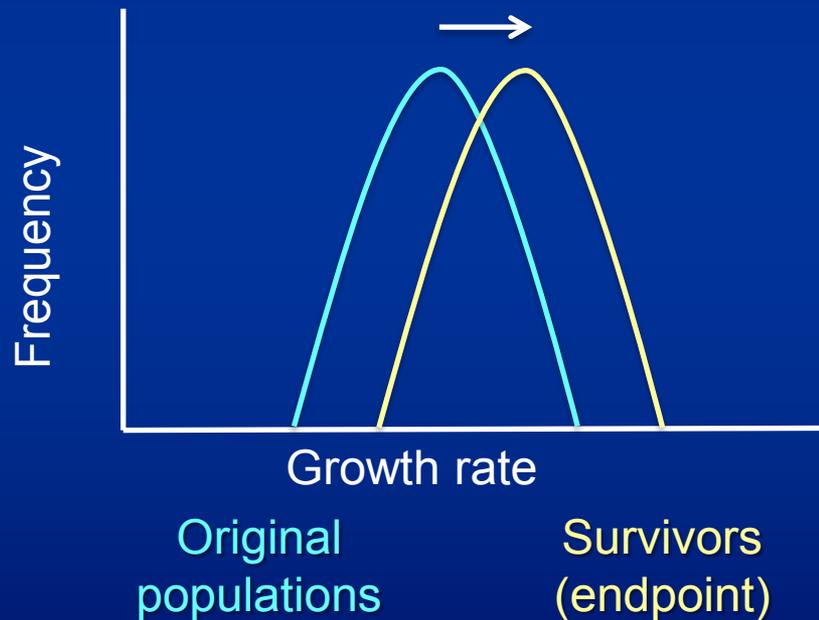
Synthesis

Conceptual framework based on growth rate distribution shift

Random survival

Effect of stage duration

Shift to positive direction
(automatically)



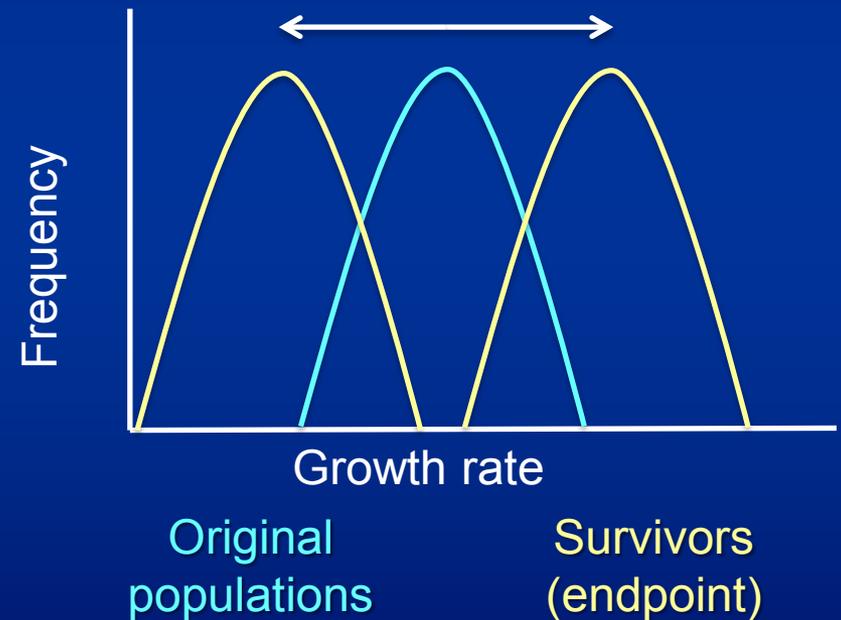
Growth/size-selective survival

Effect of stage duration

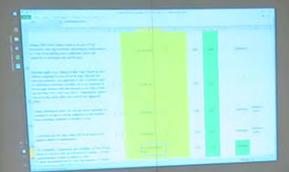
Shift to positive direction

Effect of growth/size selection

Shift to positive or negative direction



- Dealing with the 3 growth–survival mechanisms in the same framework.
- Quantifying direction and intensity of selection by mean and variance.



List of issues

A total of 83 original issues were summarized into 19 issues under 5 topic categories.

1. Predation mortality

- Identification of predator field
- Quantification of predator field
- Size structure and prey selectivity of predators
- Refuge availability
- Predation risk behavior
- Predation mechanisms

2. Endpoint

- Size- and/or age-based endpoint
- Carry-over effects

3. Spatial/temporal scales

- Representativeness of sampling
- Spatial and temporal replication

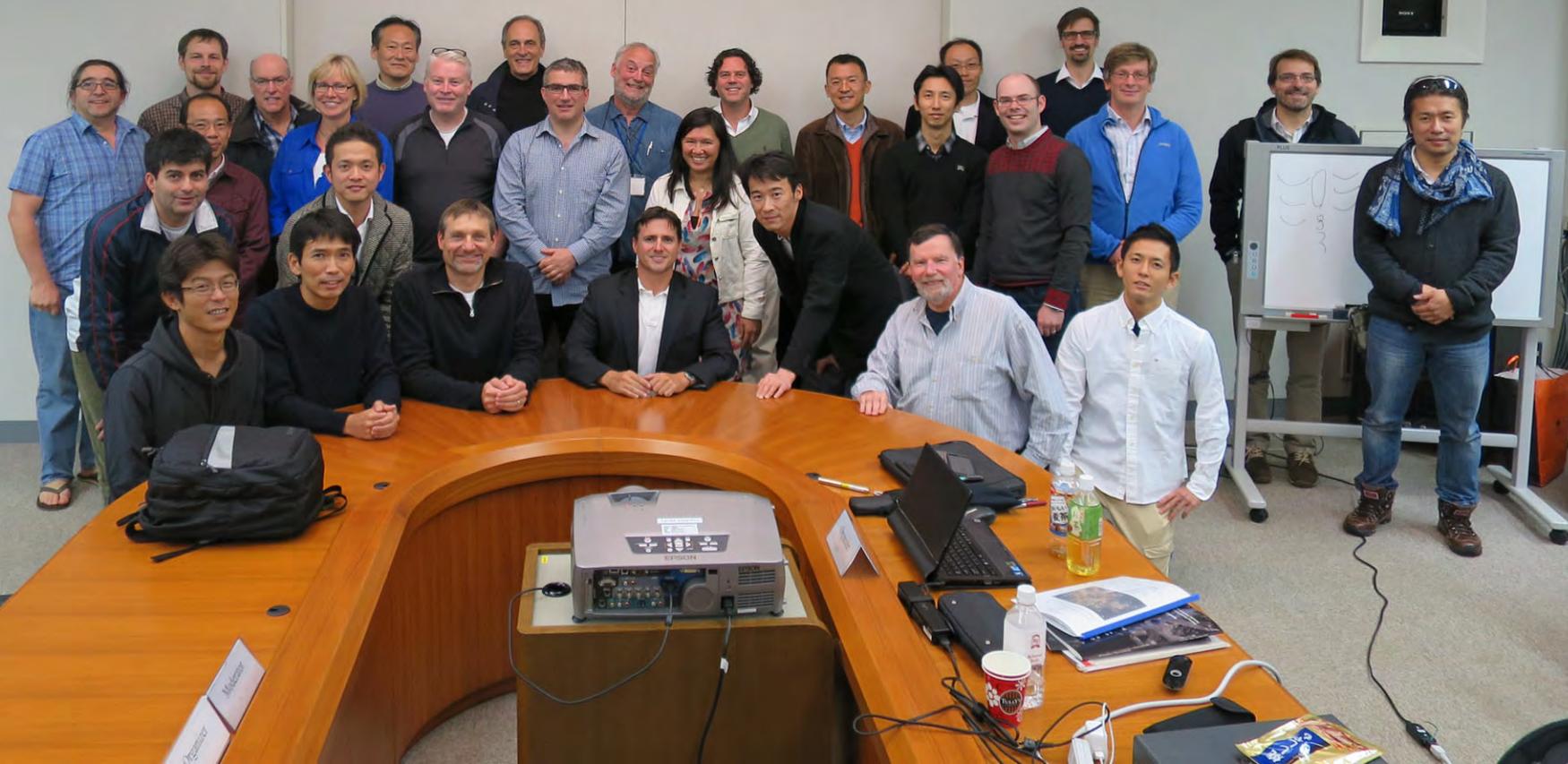
4. Intrinsic factors

- Maternal effects
- Genetic selection
- Behavior repertoire
- Growth and physiology
- Stage development

5. Miscellaneous

- Environmental effects on growth
- Mortality estimation
- Reconciling and synthesizing contradictory results from paradigm tests

Concrete study designs (“recipes”) are being prepared for each issue by the group.



Manuscripts in preparation



Symposium on
Growth-survival paradigm
in early life stages of fish:
controversy, synthesis, and
multidisciplinary approach

November 9-11, 2015
Yokohama, Japan

Organizers:
Akinori Takasuka, Dominique Robert, Jun Shoji, Pascal Sirota

Symposium on "Growth-survival paradigm in early life stages of fish: controversy, synthesis, and multidisciplinary approach" was held in Yokohama, Japan, during November 9-11, 2015.

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[Invited Speakers](#) [Venue & Access](#) [Accommodations](#) [Social Events](#) [Miscellaneous](#)

Dear GBP Symposium participants,

Thank you for your important contribution to the symposium. We, organizers, feel privileged to have had the opportunity to share ideas with you about the growth-survival paradigm and general early life biology. The symposium has allowed this group to review research progresses since Anderson (1988) and identify some key needs for the improvement of the current framework. We deeply appreciate your participation, discussion, and cooperation. We hope that you share the same feeling, and we look forward to seeing you again to work on growth-survival issues in the future.

Best wishes,

Akinori, Dominique, Pascal, Jun

Symposium group photo



November 11, 2015 (the last day of the symposium)

Workshop group photo



November 13, 2015 (the last day of the workshop)

Update
May 1, 2015 Registration and abstract submission open.
April 1, 2015 Website launched.
November 16, 2014 Announced at the Annual Meeting of the Japanese Society of Fisheries Oceanography 2014 in Yokohama, Japan.
August 18, 2014 Announced at the 38th Annual Larval Fish Conference in Quebec City, Canada.

1. "Report"
Report of symposium/workshop
2. "Concept" paper
Proposing a new conceptual framework based on growth rate distribution shift
3. "Recipe" paper
Providing concrete study designs for the issues identified for future breakthroughs



GSP symposium 2015

<http://cse.fra.affrc.go.jp/takasuka/gsp/>

Requested issues

- Examples of prey–predator interactions related to behaviors of larvae and predators.
- What is a consequence of growth variability of larvae in the shoals?
 - What can happen when larval shoals encounter predators.
 - Examples from our previous studies on Japanese anchovy larvae.

Advance

Takasuka et al. (2007) MEPS
Robert et al. (2010) FS

Growth-selective predator



Japanese anchovy
Engraulis japonicus



Pacific round herring
Etrumeus teres



Japanese jack mackerel
Trachurus japonicus



White croaker
Pennahia argentatus

Non-growth-selective predator



Japanese sea bass
Lateolabrax japonicus



Greater amberjack
Seriola dumerili



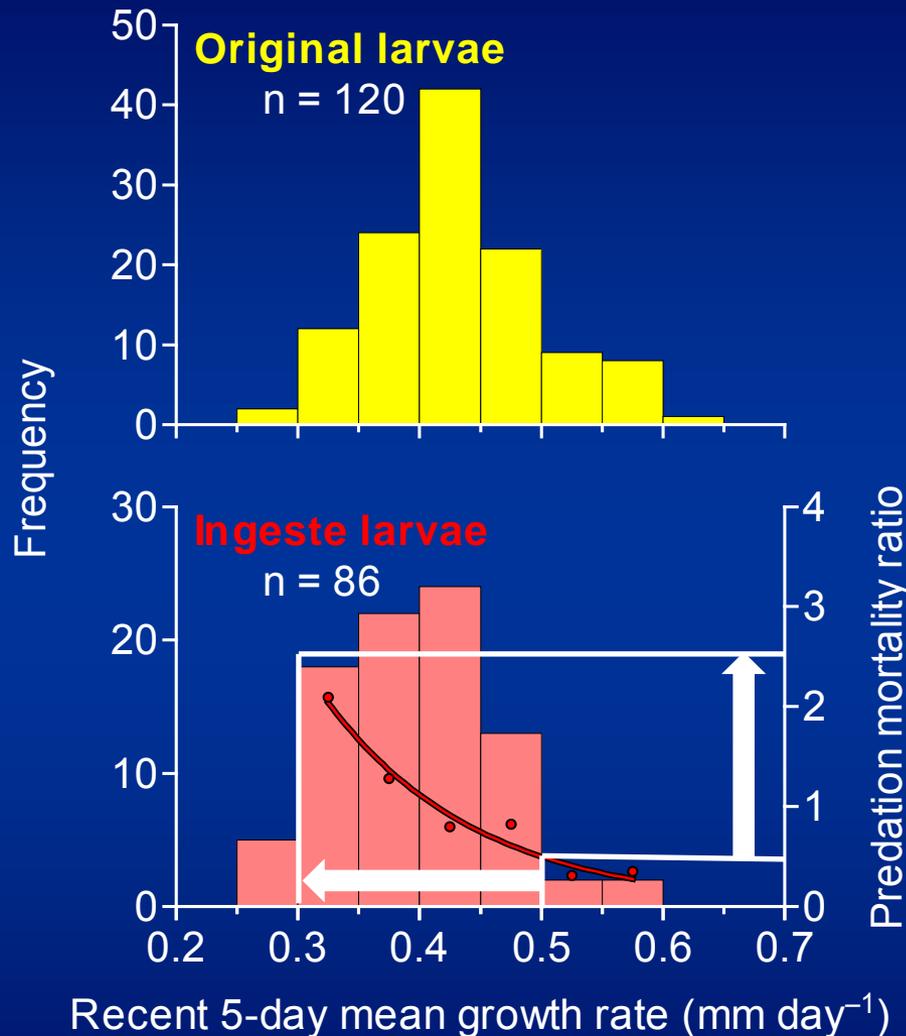
Skipjack tuna
Katsuwonus pelamis



Chub mackerel & Spotted mackerel
Scomber japonicus & *S. australasicus*

Predator-specific growth-selective predation on anchovy larvae.

Relative predation mortality

Takasuka et al.
(2007) MEPS

Predators:
Pacific round herring
Japanese jack mackerel

Growth decline:
0.20 mm day⁻¹
(0.50 to 0.30 mm day⁻¹)

Predation mortality
ratio increased
from **0.5** to **2.5**

Instantaneous
predation mortality
multiplied by **ca. 5 times**

Frequency distributions of growth rate compared between **ingested larvae** and **original larvae** with an index of relative predation mortality.

Advance

Takasuka et al. (2007) MEPS
Robert et al. (2010) FS

Growth-selective predator



Japanese anchovy
Engraulis japonicus



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Etrumeus teres



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Katsuwonus pelamis



Chub mackerel & Spotted mackerel
Scomber japonicus & *S. australasicus*

Predator-specific growth-selective predation on anchovy larvae.

- What is a consequence of cumulative survival probability when larval shoals encounter different predators?
- Dynamics of growth-based survival mechanisms.

Field sampling

- Anchovy larvae were sampled repeatedly with an interval of *ca.* 2 weeks from multiple cohorts in a coastal fishing ground.

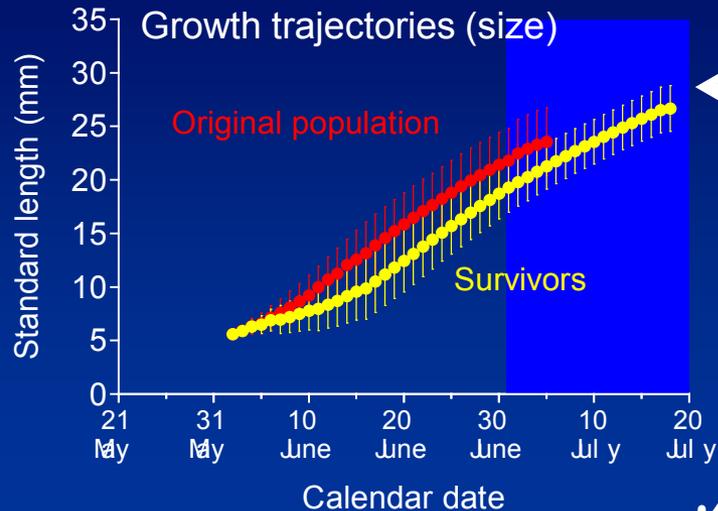
Samples

- The larvae collected at the first sampling: **original population**
- The larvae collected at the later sampling: **survivors**



Mechanism tests

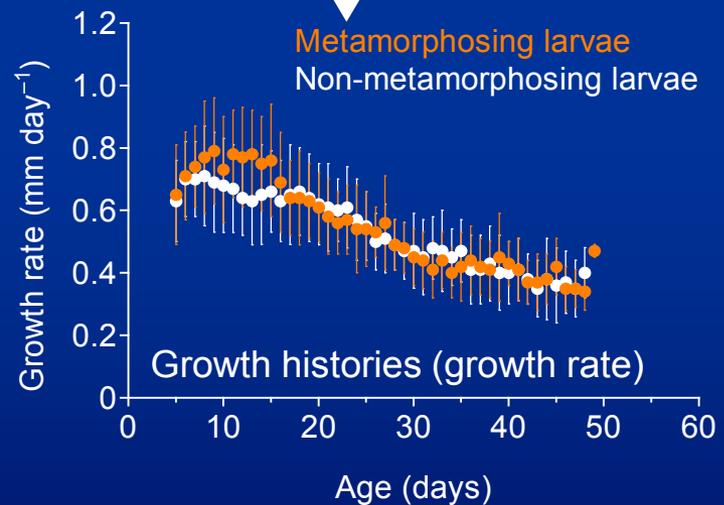
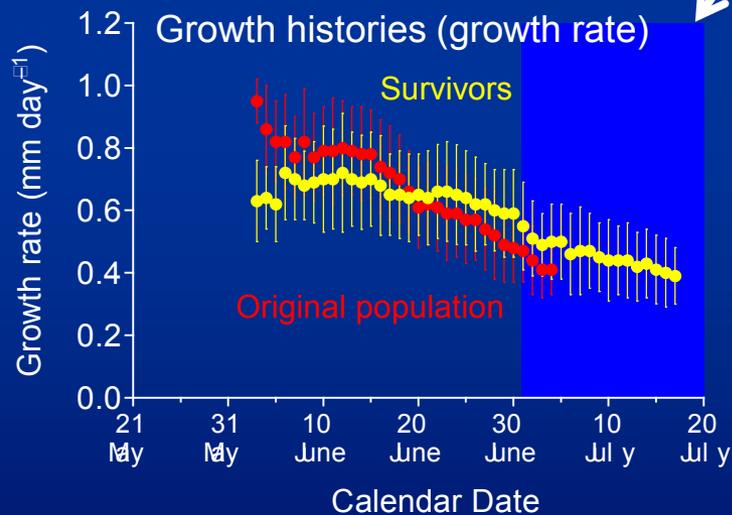
Takasuka *et al.* (2017)
CJFAS



“Bigger is better” test

“Growth-selective predation” test

“Stage duration” test



Three mechanisms tested based on the characteristics of the **survivors** vs the **original population** for multiple cohorts.

Mechanism tests

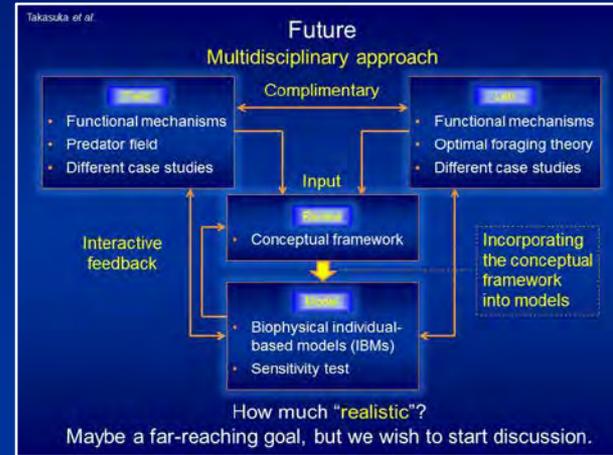
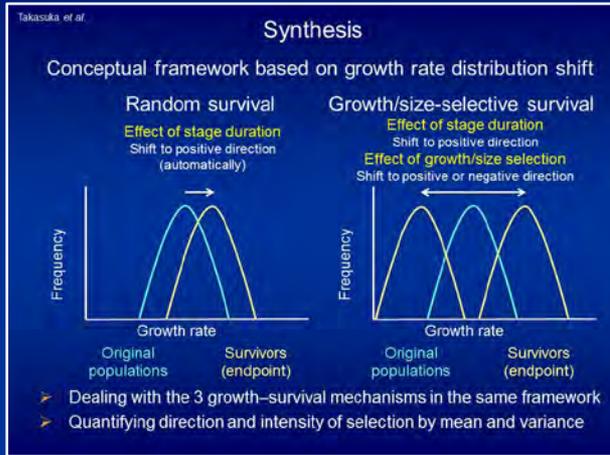
Takasuka *et al.* (2017)
 CJFAS

Summary of the test results of the 3 functional mechanisms for the short-term survival processes of multiple cohorts (9 seasonal cohorts & 18 pairs of SV and OP).

Sample	Cohort Season and year	Pair		Survival period (d)	Bigger is better	Growth-selective predation	Stage duration
		Original	Survivors				
A	Autumn 2003	OP	SV-1	10	NS	NS	–
		OP	SV-2	20	NS	NS	–
		SV-1	SV-2	10	NS	Effective	–
B	Spring 2004	OP	SV-1	12	Contrary	Effective	Effective
		OP	SV-2	18	Contrary	NS	–
		SV-1	SV-2	6	NS	Contrary	–
C	Summer 2004	OP	SV	11	NS	NS	–
D	Autumn 2004	OP	SV	7	Contrary	Effective	–
E	Winter 2004	OP	SV	29–38	Effective	Effective	–
F	Spring 2005-1	OP	SV-1	9	Contrary	NS	Effective
		OP	SV-2	21	Contrary	Effective	–
		OP	SV-3	31	Contrary	Effective	–
		SV-1	SV-2	12	Effective	Effective	–
		SV-1	SV-3	22	Effective	Effective	–
		SV-2	SV-3	10	NS	NS	–
G	Spring 2005-2	OP	SV	10	NS	Effective	–
H	Winter 2005	OP	SV	17	NS	Contrary	–
I	Summer 2001	OP	SV	13–17	NS	Effective	NS

Under discussion

How can we incorporate conceptual frameworks into IBMs?



Is there any special characteristics in growth–survival dynamics of small pelagic fish?

(small pelagic fish vs large pelagic fish, demersal fish, flatfish, coral reef fish, freshwater fish, etc.)



