Growth-selective predation hypothesis revisited for larval anchovy in offshore waters: cannibalism by juveniles vs. predation by skipjack tunas

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1 INTRODUCTION

'Growth–mortality' paradigm (hypothesis)
Faster-growing individuals are assumed to be more likely to survive in the sea.

Existing concepts WHY ? …. To date, 3 factors can serve to explain it.

I. **'Bigger is better'** hypothesis: size (negative size-selective mortality)
II. **'Stage duration'** hypothesis: time (high mortality stage duration)
- Growth-survival relationship has been explained indirectly.
- No direct evidence existed to support the growth–predation relationship.

Our previous studies in Sagami Bay (Takasuka *et al.* 2003; 2004)
III. **'Growth-selective predation'** hypothesis: growth rate (*per se*)
- Direct examination of the growth rates of the actually ingested larvae.
- Slower growing larvae were more vulnerable to predation than faster growing larvae, even if they were the same size, at a given moment in the sea.
- Growth rate *per se* had direct impacts on vulnerability to predation.

Larval Japanese anchovy in offshore waters
- Japanese anchovy are distributed and spawn widely in offshore waters.
- Larval anchovy are exposed to multiple predator fields.

In the present study, …

Engraulis japonicus

- The **'growth-selective predation'** hypothesis was revisited for larval Japanese anchovy in offshore waters.
- Cannibalism by juveniles vs. predation by skipjack tunas (*Katsuwonus pelamis*).

2 MATERIALS & METHODS

Field sampling Offshore waters: the western North Pacific **Fig. 1**
- Station A in the Kuroshio Extension region (June 11, 1997)
  Larval anchovy and juvenile conspecifics
- Station B in the Kuroshio-Oyashio transition region (May 15, 2000)
  Larval anchovy and skipjack tunas **Table 1**

Growth and size comparison
- Ingested larvae: the larvae dissected from the stomachs of the predators
- Original larvae: the larvae captured simultaneously with the predators
- Sagittal otoliths extracted from the ingested larvae and original larvae.
- Standard lengths (SLs) of the ingested larvae were restored from otolith radius (OR) data, using the OR-SL relationship of the original larvae.

The larvae dissected from the stomachs of the predators
i.e. the larvae actually ingested by the predators

The larvae captured simultaneously with the predators
i.e. the surviving larvae from the original population

- Standard lengths (mm)
- Recent 5 day mean growth rates directly before capture (mm day^{-1}), which were back-calculated by the biological intercept method

Table 1

Table 1. Sampling information for larval anchovy and predators (juvenile anchovy and skipjack tunas). Standard lengths (SLs) of the ingested larvae were restored from the actually measured otolith radius data. FL: fork length; *n*: number for growth analysis; *n'*: occurrence from the stomach contents of the predators.

Information	Station A		Station B	
Date	11 June 1997		15 May 2000	
Time	19:40–20:20		09:30–17:30	
Location	35°00'N, 144°30'E		38°08'N, 144°34'E	
Predator	Juvenile *Engraulis japonicus*		*Katsuwonus pelamis*	
n	120		9	
Size (mm)	35.7–61.3 (SL)		450–540 (FL)	
Prey (*E. japonicus*)	Ingested larvae	Original larvae	Ingested larvae	Original larvae
n (*n'*)*	33 (85)	100	12 (59)	47
Size (mm)	13.6–20.2	13.1–31.1	22.2–26.2	14.4–27.4

*n: number for growth analysis; n': occurrence from the stomach contents of the predators

Fig. 1

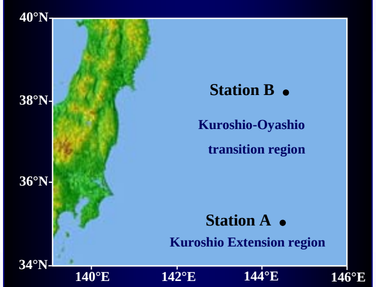

Fig. 1. Sampling stations for larval and juvenile anchovy *Engraulis japonicus* in June 1997 (Station A) and larval anchovy and skipjack tuna *Katsuwonus pelamis* in May 2000 (Station B) in the western North Pacific. Sympatric larval and juvenile anchovy were captured simultaneously by the same tow of a midwater trawl, and larval anchovy and skipjack tunas separately by a neuston net and trolling lines, respectively.

3 RESULTS

Stomach content analysis for predators **Table 1** **Fig. 2**
Cannibalism by juveniles
- A total of 85 cannibalized larvae occurred from 31 of 120 juvenile anchovy of 35.7–61.3 mm (SL); otoliths were extracted from 33 cannibalized larvae.
- A juvenile of 42.8 mm (SL) was the smallest to show cannibalism.
- The SCI values of the cannibals were twice as high as those of non-cannibals.
- Larvae made up 10.0–85.7 % of the stomach content weight for cannibals.

Predation by skipjack tunas
- A total of 59 ingested larvae occurred from 7 of 9 skipjack tunas of 45–54 cm (FL); otoliths were extracted from 12 ingested larvae.

Size-selective predation ('Bigger is better' ?) **Fig. 3**
Cannibalism by juveniles
- The cannibalized larvae tended to be smaller than the original larvae.

Predation by skipjack tunas
- The ingested larvae tended to be larger than the original larvae.

Growth-selective predation ('Growth-selective predation' ?) **Fig. 4**
Cannibalism by juveniles
- The cannibalized larvae had lower recent growth rates than the original larvae in the same larval size range (≦ 20 mm) (Student's t-test, p = 0.005).

Predation by skipjack tunas
- No differences in growth rates were found between the ingested larvae and original larvae in the same larval size range (≧ 20 mm) (p = 0.912).

4 DISCUSSION

Cannibalism by juveniles
- Negative size-selective predation mortality
  'Bigger is better' (also assumably 'stage duration' effects)
- Slower-growing larvae were more vulnerable to cannibalism by juveniles.
  'Growth-selective cannibalism'
- Does cannibalism by juveniles negatively affect the final recruitment? If slower-growing larvae anyway intensively removed by the other predators, intrapopulation removal of such fatal larvae would not be critical. Instead, it will provide a considerable energy source for juvenile conspecifics. This would be rather incidental but rational in terms of net profitability at the population level.

Survivorship of faster growing larvae.

Predation by skipjack tunas
- Positive size-selective predation mortality
  'Bigger is not better' (assumably no 'stage duration' effects)
- Even faster-growing larvae were vulnerable to predation by skipjack tunas.
  'Non-growth-selective predation'

No advantage of faster growing larvae.

Causal background
- Predator-specific **'Growth-selective predation'**. The phenomena are consistent with those detected in Sagami Bay (Takasuka *et al.* 2003).
- Potential for anti-predator behaviors vs. feeding strategies of predators

Fig. 2

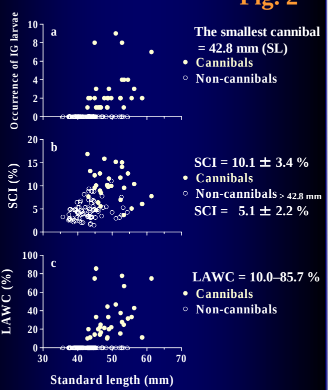

Fig. 2. *Engraulis japonicus*. Ontogenetic features of larval cannibalism by juvenile anchovy. (a) Occurrence of the ingested larvae; (b) stomach content index (SCI); (c) larval anchovy weight contribution to the stomach contents of juveniles in wet weight (LAWC).

Fig. 3

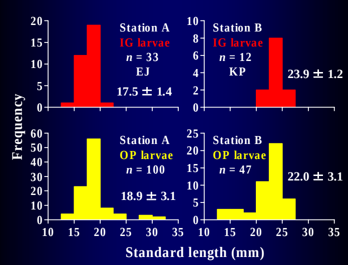

Fig. 3. *Engraulis japonicus*. Comparison of standard length (SL) frequencies between the ingested larvae (IG larvae) and original larvae (OP larvae) for cannibalism by juvenile anchovy (EJ: left) and predation by skipjack tunas *Katsuwonus pelamis* (KP: right). SLs of the 2 ingested larvae groups were separately restored from the actually measured otolith radius (OR) data, using the OR-SL relationships of the 2 original larvae groups.

Fig. 4

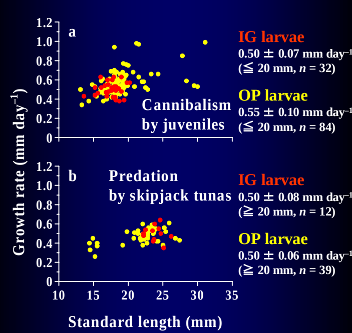

Fig. 4. *Engraulis japonicus*. Comparison of recent 5 day mean growth rates plotted against standard length between the ingested larvae (IG larvae) and original larvae (OP larvae) for cannibalism by juvenile anchovy (a) and predation by skipjack tunas *Katsuwonus pelamis* (b).

Larval cannibalism by juveniles would potentially regulate growth-selective survival as well as survival rate itself during early life history stages of Japanese anchovy, while predation by skipjack tunas would influence survival rate itself but not growth-selective survival.