NOTE

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

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ABSTRACT: The 'growth-selective predation' hypothesis was revisited for larval Japanese anchovy *Engraulis japonicus*, focusing on larval cannibalism by juveniles and larval predation by skipjack tunas *Katsuwonus pelamis*, in offshore waters. Larval anchovy and predators were captured simultaneously in June 1997 and in May 2000 in the western North Pacific. Growth rates estimated through otolith microstructure analysis, as well as somatic sizes, were compared between the ingested larvae from the stomach contents of the predators and the surviving larvae from the original population. Size-selective mortality was directed negatively for cannibalism by juveniles and positively for predation by skipjack tunas. The cannibalised larvae had lower growth rates than the larvae from the original population in the same larval size range. On the other hand, a similar comparison showed no differences in larval growth rates for predation by skipjack tunas. 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.

KEY WORDS: Growth-selective predation hypothesis · Growth rate · Predation mortality · Otolith microstructure · Larval Japanese anchovy · Larval cannibalism · Juvenile · Skipjack tuna

INTRODUCTION

Faster-growing fish larvae are assumed to be more likely to survive in the sea. According to this 'growth–mortality' hypothesis (Anderson 1988), growth rate during early life history stages can be a regulator of recruitment dynamics of fish. Why do faster-growing individuals gain survivorship? To date, 3 factors can serve to explain such a paradigm: size (body size), time (stage duration) and growth rate (*per se* rate) (Takasuka et al. 2003, 2004). The size-based concept has been labelled the 'bigger is better' hypothesis (Miller et al. 1988). This theory postulates the existence of negative

size-selective mortality (i.e. higher mortality for smaller fish). The time-based concept is the 'stage duration' hypothesis (Chambers & Leggett 1987, Houde 1987), which postulates that faster-growing larvae will have a higher development rate and thus experience a decreased cumulative mortality rate by shortening the high mortality larval period. Such survival advantages of higher growth rate have been supported by field investigations (e.g. Meekan & Fortier 1996, Hare & Cowen 1997, Searcy & Sponaugle 2001, Allain et al. 2003, Oozeki et al. 2003). Meanwhile, contrary evidence against negative size-selective mortality has recently presented and apparent size effects may be confused with age or

developmental stage effects (Litvak & Leggett 1992, Pepin et al. 1992, Pepin 1993, Leggett & DeBlois 1994). Also, faster-developing individuals may face up to one predator field, after passing through another. In theory, 2 growth-related scenarios explain the growth–survival relationship indirectly by translating growth rate into size or time. Moreover, until recently, no direct evidence had yet been obtained to identify the direct source of mortality. On the other hand, the recently proposed 'growth-selective predation' hypothesis (Takasuka et al. 2003, 2004) directly links *per se* growth rate with predation mortality. In short, faster-growing larvae will be less vulnerable to predation than slower-growing conspecifics, even if they are the same size, at a given moment in the sea. Thus, growth rates themselves have direct impacts on predation mortality, independently of both size-selective mortality and stage duration.

The 'growth-selective predation' hypothesis was proposed with the first snapshot evidence of the growth–predation relationship for larval Japanese anchovy *Engraulis japonicus* in the shirasu (larval anchovy) fishing ground, just off the coast, in Sagami Bay (Takasuka et al. 2003). However, Japanese anchovy are distributed and spawn widely (Funamoto & Aoki 2002), and larvae are transported offshore and then northward in the western North Pacific (Takasuka & Aoki 2002). The 'growth-selective predation' hypothesis remains to be tested in such offshore waters, where pelagic fish larvae are exposed to multiple predator fields (Sugisaki 1996). One of the top fish predators is the skipjack tuna *Katsuwonus pelamis*, although pelagic juvenile and adult anchovy can also be potential predators (i.e. cannibals). Previous studies on cannibalism in pelagic fish have almost exclusively focused on egg cannibalism (Hunter & Kimbrell 1980, Alheit 1987, Valdés Szeinfeld 1991, 1993, Köster & Möllmann 2000), whereas cannibalism of the larval stage of planktivorous small pelagic species has been

studied much less (but see Brownell 1985, Folkvord & Hunter 1986, Booman et al. 1991).

The present study revisited the 'growth-selective predation' hypothesis for larval Japanese anchovy in offshore waters. We first targeted larval cannibalism by juvenile anchovy, which was then compared to the prey–predator interaction between larval anchovy and skipjack tuna in the western North Pacific.

MATERIALS AND METHODS

Sympatric larval and juvenile Japanese anchovy were both captured simultaneously by the same tow of a frame-type midwater trawl with a mouth area of 16 m^2 and a stretch mesh size of 8 mm (Aoki et al. 2000) in the western North Pacific on 11 June 1997. During nighttime, the net was towed almost horizontally for 30 min at a depth of 10 to 25 m at Stn A on the front of the Kuroshio Extension (Table 1, Fig. 1). During another cruise, larval anchovy were captured by a neuston net with a mouth area of 0.975 m^2 and a mesh size of 0.45 mm (Oozeki et al. 2001) on 15 May 2000. During the daytime, the net was towed horizontally for 10 min at the surface layer 3 times at Stn B in the Kuroshio–Oyashio transition region (Table 1, Fig. 1). Concurrently, we sampled skipjack tunas by trolling lines at the same station. Fork length (FL) of skipjack tuna was measured to the nearest 1 cm on board. Larval and juvenile anchovy were preserved in 90% ethanol, and guts of skipjack tunas in 90% ethanol or 10% formalin immediately after sampling.

Standard length (SL) was measured to the nearest 0.1 mm for each larval and juvenile anchovy. Stomach contents of juvenile anchovy (n = 120) and skipjack tunas (n = 9) were sorted for larval anchovy under a binocular microscope. For juvenile anchovy, stomach content index (SCI%) was calculated as the stomach

Table 1. Sampling information and sample profile for larval Japanese anchovy *Engraulis japonicus* and predatory fish, juvenile anchovy and skipjack tuna *Katsuwonus pelamis*. Ingested larvae: the larvae ingested by the predators, i.e. the larvae dissected from the stomach contents of the predators; Original larvae: the larvae from the original population, i.e. the larvae captured concurrently with the predators. 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

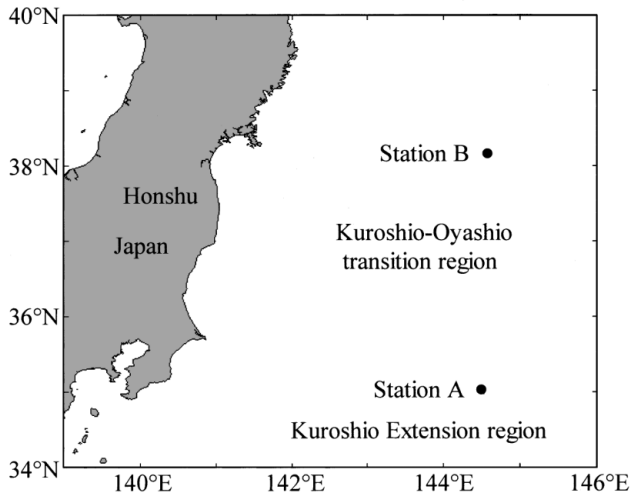| Information	Stn A		Stn B	
Date	11 June 1997		15 May 2000	
Time	19:40–20:20 h		09:30–17:30 h	
Location	35° 00' N, 144° 30' E		38° 08' N, 144° 34' E	
Predator	Juvenile *Engraulis japonicus*		*Katsuwonus pelamis*	
n	120		9	
Size (mm)	35.7–61.3 (SL)		450–540 (FL)	
Prey (*Engraulis japonicus*)	Ingested 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

Fig. 1. Sampling stations for larval and juvenile Japanese anchovy *Engraulis japonicus* in June 1997 (Stn A) and larval anchovy and skipjack tunas *Katsuwonus pelamis* in May 2000 (Stn B) in the western North Pacific

content wet weight divided by body wet weight. In addition, larval anchovy contribution to the stomach content in wet weight (%) was calculated.

The larvae dissected from the stomach contents of the predators should be the larvae actually ingested by the predators (ingested larvae); the larvae captured concurrently with the predators were regarded as the temporarily surviving larvae from the assumed original population (original larvae). This assumption was ensured by the same-tow sampling of the sympatric larval and juvenile anchovy. We separately sampled larval anchovy and skipjack tunas, but collections were made simultaneously.

Sagittal otolith microstructure analysis was conducted to estimate larval growth rates, according to Takasuka et al. (2003). Sagittal otoliths were extracted from both the ingested larvae and original larvae. Maximum otolith radius (OR) and each daily growth increment width were measured to the nearest 0.1 μm, using an otolith measurement system (RATOC System Engineering). Prior to growth calculations, SLs of the ingested larvae were restored from the actually measured OR data using the allometric OR–SL relationship of the corresponding original larvae. This SL restoration process has been validated not to lead to any serious bias in size and growth comparison (see Takasuka et al. 2003 for details). Daily growth rate at each daily age (mm d^{-1}) was back-calculated by the biological intercept method (Campana 1990, Campana & Jones 1992), using an allometric OR–SL formula at the individual level, with SL at the first ring deposition fixed at 5.6 mm (Fukuhara 1983). We adopted recent 5 d mean growth rates directly before capture or predation as

a proxy for survival potential factors. Size-selective and growth-rate-selective predation mortalities were tested by comparing somatic sizes and recent growth rates between the ingested larvae and the corresponding original larvae.

RESULTS

Larval cannibalism was observed for 31 (25.8%) of 120 juvenile anchovy of 35.7 to 61.3 mm SL. A total of 85 larval anchovy (ingested larvae) were dissected from their stomach contents and sagittal otoliths were extracted from 33 ingested larvae for growth analysis (Table 1). The other components of the juvenile stomach contents were mainly copepods such as *Oncaea* and *Sapphirina*, and no fish larvae were observed other than larval anchovy. A juvenile of 42.8 mm SL was the smallest to show cannibalism (Fig. 2). The SCI values were 10.1 ± 3.4% (mean ± SD) for cannibal juveniles (n = 31), which were significantly higher than 5.1 ± 2.2% for non-cannibal juveniles >42.8 mm SL (n = 47) (Welch's *t*-test, p < 0.001). Larval anchovy made up 10.0 to 85.7% (mean = 32.3%) of the stomach contents in wet weight for cannibal juveniles. On the other hand, a total of 59 larval anchovy and 7 unidentified fish larvae occurred from 7 of 9 skipjack tunas of 45 to 54 cm FL and otoliths were available for 12 ingested larval anchovy (Table 1). Almost all of the ingested larvae from both juveniles and skipjack tunas (82 of 85 and 52 of 59) were observed to be at least partially digested.

The restored SLs of the ingested larvae were included in the range of the measured SLs of the corresponding original larvae and the modal SLs seemed similar for both types of prey–predator interactions (Fig. 3). The SL distributions, however, apparently differed between the ingested larvae and original larvae. The mean SL of the ingested larvae was slightly lower than that of the original larvae (17.5 ± 1.4 vs 18.9 ± 3.1 mm) for cannibalism, while the mean SL of the ingested larvae was greater than that of the original larvae (23.9 ± 1.2 vs 22.0 ± 3.1) for predation by skipjack tunas. For cannibalism, 32 of 33 ingested larvae were smaller than 20 mm, in spite of the wider SL range (13.1 to 31.1 mm) of the original larvae (n = 100). For predation by skipjack tunas, conversely, all of the ingested larvae (n = 12) were larger than 20 mm, while the SLs of the original larvae (n = 47) ranged from 14.4 to 27.4 mm. The differences in SLs seemed slight but were confirmed statistically for both comparisons (Mann-Whitney's *U*-test, p = 0.007 and 0.020).

Fig. 4 shows the recent 5 d mean growth rates plotted against larval sizes for growth comparison at the same size. Recent growth rates were positively cor-
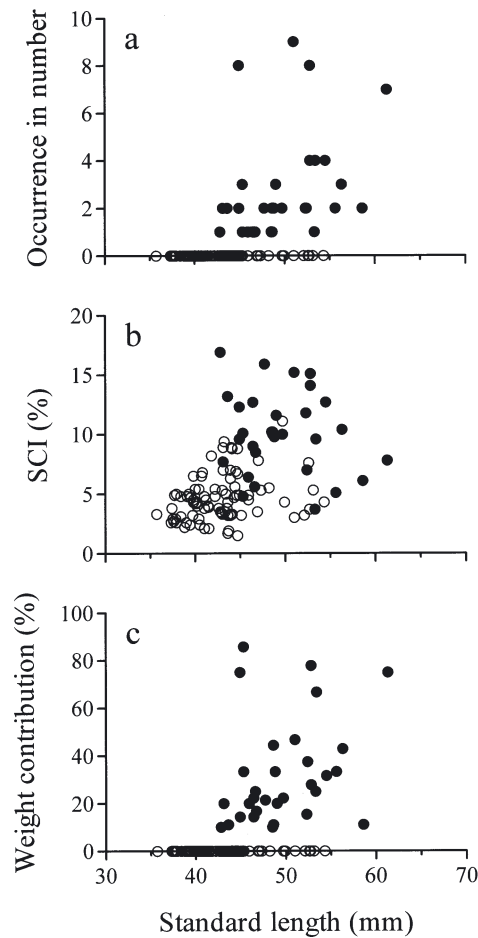
Fig. 2. *Engraulis japonicus.* Ontogenetic features of larval cannibalism by juvenile anchovy. (a) Occurrence of the ingested larvae in number with juvenile size; (b) comparison of stomach content index (SCI) between the cannibal juveniles and non-cannibal juveniles; (c) larval anchovy weight contribution to the stomach contents of juveniles in wet weight. Data are shown separately for the cannibal juveniles (●) and non-cannibal juveniles (○)
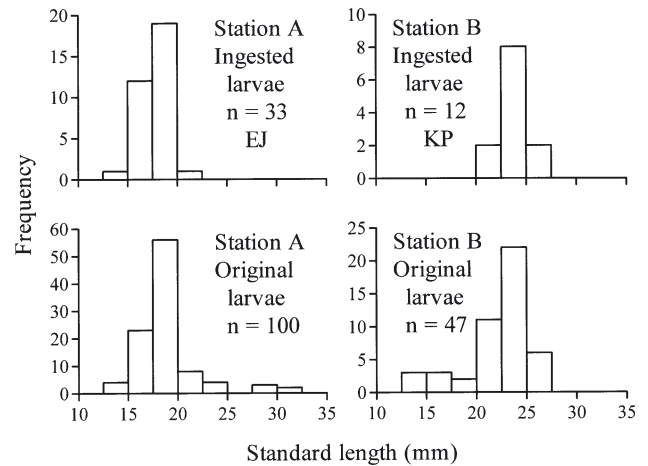

Fig. 3. *Engraulis japonicus.* Comparison of standard length (SL) frequencies between the ingested larvae (upper panels) and the larvae from the original population (lower panels) for cannibalism by juvenile anchovy (EJ: left) and predation by skipjack tunas *Katsuwonus pelamis* (KP: right). Station, sample size and predator (only for the ingested larvae) are indicated in each panel. SLs of the 2 ingested larvae groups were separately restored from the actually measured otolith radius (OR) data, using the allometric OR–SL relationship of the 2 original larvae groups: $SL = 1.447OR^{0.555}$ (n = 100, $r^2 = 0.846$, $p < 0.001$) for the original larvae corresponding to the ingested larvae from juvenile conspecifics and $SL = 1.381OR^{0.563}$ (n = 47, $r^2 = 0.930$, $p < 0.001$) for the original larvae corresponding to the ingested larvae from skipjack tunas

related with larval sizes for the original larvae (linear regression analysis, $p < 0.001$), but not for the ingested larvae ($p > 0.05$), making it impossible to compare regressions. Thus, we compared recent growth rates between the ingested larvae and original larvae within the common SL range. For cannibalism, the recent growth rates of the ingested larvae ≤20 mm (n = 32) were 0.50 ± 0.07 (mean ± SD) mm d^{-1}, which were significantly lower than those of the corresponding original larvae ≤20 mm (n = 84), 0.55 ± 0.10 mm d^{-1} (Student's *t*-test, $p = 0.005$). On the other hand, the similar comparison showed no significant differences in recent growth rates between the ingested larvae ≥20 mm (0.50 ± 0.08 mm d^{-1}, n = 12) and original larvae ≥20 mm (0.50 ± 0.06 mm d^{-1}, n = 39) for predation by skipjack tunas (Student's *t*-test, $p = 0.912$).
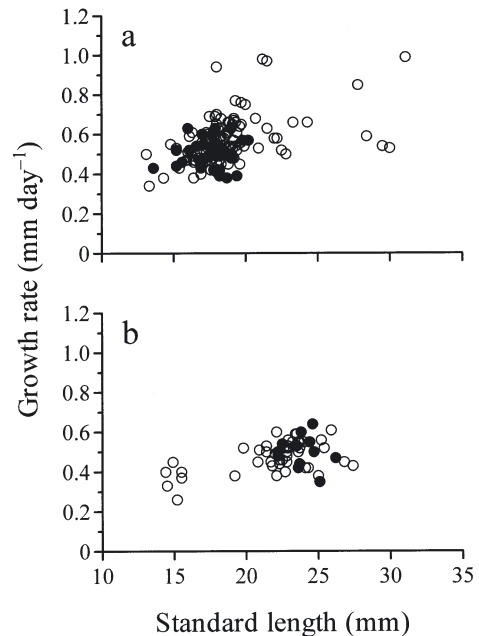

Fig. 4. *Engraulis japonicus.* Comparison of recent 5 d mean growth rates plotted against standard length (SL) between the ingested larvae (●) and the larvae from the original population (○) for (a) cannibalism by juvenile anchovy and (b) predation by skipjack tunas *Katsuwonus pelamis*

DISCUSSION

Size-selective mortality of larval Japanese anchovy was directed negatively for cannibalism by juveniles and positively for predation by skipjack tunas (Fig. 3). A possibility of biases due to selectivity of the gear, such as loss of smaller larvae through the mesh, cannot be completely ruled out, but it would not seriously affect the results, since the original larvae well covered the ingested larvae in size and their minimum sizes were almost the same. We could rule out any critical bias due to predation in the trawl cod-end, because of the rarity of fresh condition larvae (see Takasuka et al. 2003 for details). Brownell (1985) reported that Cape anchovy *Engraulis capensis* of 15 to 35 mm SL could ingest conspecific larvae of almost half of their own size, the largest that the mouth openings could permit, in an experimental condition. This corresponded well to the upper limit of the prey–predator size ratios observed for cannibalism in the present field study (0.46). Such a gape limitation will lead to a survival advantage for larger larvae (Werner & Gilliam 1984, Miller et al. 1988). In addition, no juvenile anchovy suffered from cannibalism, suggesting that individuals developing into the juvenile stage faster will experience a lower cannibalism mortality rate. Larger larvae or juveniles will have broken through the 'window' of vulnerability. In this sense, both the 'bigger is better' and 'stage duration' mechanisms might be in operation in larval cannibalism by juveniles.

The case would be different when larval shoals are attacked by skipjack tunas (Fig. 3): larger larvae would have no size advantage. This would also presumably be true for juveniles as they too would be vulnerable. Thus, neither 'bigger is better' nor 'stage duration' mechanisms would be effective in predation by skipjack tunas. Rather, even the disadvantage of larger body size cannot be excluded. A possible factor leading to the phenomenon that bigger is not always better is the encounter rate; however, larval swimming speed would have virtually no effect when a predator's speed largely surpasses a prey's speed (Bailey & Houde 1989, Litvak & Leggett 1992, Fuiman & Magurran 1994). Thus, conspicuousness of larger larvae (Bailey & Houde 1989) may more effectively contribute to their higher predation mortality rate by skipjack tunas. Such a selection leads to an advantage of more energy gain for a given effort in skipjack tunas.

The ingested larval anchovy had significantly lower recent growth rates than the larvae from the original population in the same size range for cannibalism by juveniles (Fig. 4), providing snapshot evidence to demonstrate the existence of 'growth-selective cannibalism' on larval anchovy by juvenile conspecifics in offshore waters. In contrast, non-growth-selective predation was suggested for the prey–predator interaction between larval anchovy and skipjack tunas, although sample size was rather small. These phenomena are consistent with those detected in the shirasu fishing ground in Sagami Bay, where Japanese jack mackerel *Trachurus japonicus*, Pacific round herring *Etrumeus teres* and Japanese anchovy selected slower-growing larval anchovy, while barracuda *Sphyraena pinguis* and Japanese sea bass *Lateolabrax japonicus* preyed upon larvae randomly (Takasuka et al. 2003). In offshore waters, juvenile anchovy are categorised as the growth-selective predator and skipjack tuna as the non-growth-selective predator.

What leads to such predator specificity? Variations in potential for anti-predator behaviours provides the background for the 'growth-selective predation' mechanism. Slower-growing larvae deteriorate physiologically; thus they have lower responsiveness to predator attacks and swimming ability, and tend to be isolated from shoals, finally becoming more vulnerable to predation (Takasuka et al. 2003). As such, faster-growing individuals may succeed in escaping attacks by a smaller predator (juvenile anchovy) while they cannot escape attacks by an extremely larger predator (skipjack tuna) since variations in larval activities should be nonsignificant against attack performance of skipjack tunas. Predator-specific 'growth-selective predation' should be due to differences in feeding strategy, for example, opportunistic feeding of planktivorous predators versus specialistic feeding of piscivorous predators.

Larval and juvenile anchovy were mixed at a rate of 292 versus 68 (larvae versus juvenile), estimated from a subsample (data not shown). According to the occurrence of 85 larvae from 120 juveniles, our rough estimation led to an expectation that ca. 16.5% of larval anchovy could be cannibalised by juveniles instantaneously. The consumption rate due to cannibalism is expected to be considerable. If so, does larval cannibalism by juveniles negatively affect the final recruitment success? Cannibalism is a focal topic as a density-dependent self-regulator and an adaptation under a trade off between energy gain of predatory conspecifics and mortality of prey conspecifics at the population level (Valdés Szeinfeld 1991, 1993). If slower-growing larvae are also intensively removed by the other predators in offshore waters, intrapopulation removal of such potentially fatal larvae would not, ultimately, be critical to the final recruitment success. Instead, it will provide a considerable energy source for juvenile conspecifics. This may be neither a genetic character nor an acquired adaptation but rather incidental; however, 'growth-selective cannibalism' would be rational in terms of net profitability at the population level in the event.

In conclusion, larval cannibalism by juveniles would potentially regulate growth-selective survival as well as survival rate itself during early life history stages, while predation by skipjack tunas would influence survival rate itself but not growth-selective survival. Predator field and predation pressure are to be estimated in future studies in order to clarify the picture of survival in offshore waters.

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