Chaetognaths in the diet of Pacific saury (*Cololabis saira*) in the northwestern Pacific Ocean

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Abstract — The feeding of Pacific saury (*Cololabis saira*) on chaetognaths was investigated off the east coast of Japan. 58.1% of the saury examined contained chaetognath remains. Most saury contained only a couple of chaetognaths, but about one-third of the saury had over 100 in their gut—suggesting encounters with chaetognath swarms. The chaetognath *Sagitta elegans* was commonly ingested, and the mean calculated length of *S. elegans* ingested by saury was significantly larger than the mean length of *S. elegans* collected by net from the water, indicating selectivity of larger prey sizes by saury. *Sagitta elegans* ingested at the Oyashio region feeding grounds in July were significantly larger than those ingested in the mixed/transition water off Sanriku in November. Correlation analysis of saury size versus ingested *S. elegans* size suggests that saury at the Oyashio feeding grounds in July do not eat *S. elegans* of lengths directly proportional to the saury's length. But, saury do seem to select *S. elegans* directly proportional to their own body length in the region of the Subarctic Front. Though size of saury and *S. elegans* affects predator-prey interactions, additional unknown factors are also recognized as being influential.

Key words: Pacific saury, Chaetognaths, Oyashio, Kuroshio, feeding

Introduction

The northwestern Pacific Ocean off the east coast of Japan is an exceptionally dynamic area that is highly productive with a commercial fishing harvest of great economic value (Chikuni 1985). The northern region contains the cold southward flowing Oyashio Current formed from a mixture of Okhotsk Sea and Bering Sea waters, while the southern region is comprised of the warm Kuroshio Current that flows north from the equator. Where these two currents meet and mix a Transition Zone is formed between roughly 36° and 40°N, which stretches east into the Pacific Ocean beyond 160°E (Oguma et al. 2002, Yasuda 2003).

The Pacific saury (*Cololabis saira*) is a pelagic fish species widely distributed through the waters off eastern Japan, and is one of the most important commercially harvested fishes. The life cycle and annual migration of saury has been well studied (Watanabe et al. 1997, Kosaka 2000) and can be summarized as follows: A) spawned juveniles and over-wintered adults travel north from the Kuroshio region, pass through the Kuroshio-Oyashio Transition Zone and reach the feeding grounds in the Oyashio region; B) the saury spend summer feeding in the Oyashio region, often in proximity to the Kurile Islands, as juveniles continue maturing; C) in early fall, the saury begin a southward migration to return to the winter spawning grounds in the Kuroshio region, passing again through the Transition Zone.

Saury feed on zooplankton and several studies have been conducted over the years to investigate their feeding habits. Though the studies collected much useful information about crustaceans in the saury diet, they did not always properly account for other zooplankton such as chaetognaths. Chaetognaths are highly abundant carnivorous zooplankton that generally rank second in abundance (behind copepods) among all marine zooplankton groups in the world's oceans (Feigenbaum and Maris 1984). Though they are recognized as a prey item for fish species (Kooka et al. 1998, Brodeur et al. 2000), their soft body is easily digested making them difficult to include in gut content analysis and they are often overlooked or ignored during feeding studies. Some early studies were able to enumerate chaetognaths in the saury gut and give some recognition to their importance as a dietary component (Hotta and Odate 1956, Odate 1977). However,

other studies (Taka et al. 1980, 1982) presented very little information on their role in saury diet——most likely due to the difficulty in spotting and collecting chaetognath remains in gut contents.

In recent years, technological advancements in analytical equipment and improved laboratory conditions have allowed for much better recognition of chaetognaths in the diet of saury, as well as an increased sense of their importance (Ito et al. 2004, Sugisaki and Kurita 2004). But, the work is by no means complete and there is also much to be done with respect to predator-prey interactions, such as prey selection. This study attempts to address these deficits by the use of a novel technique for collecting quantitative data on ingested chaetognaths: careful extraction, numeration and analysis of their minute, digestion-resistant hooks from saury guts. The purpose of this paper is to enhance understanding of the role of chaetognaths in saury diet, as well as provide insight into predator-prey interactions between them.

Method

Sampling

Samples were collected during 7 cruises conducted by the Tohoku National Fisheries Research Institute (TNFRI) between February 2000 and July 2001, as well as July 2005. This study used samples from 31 of the stations surveyed, covering several different water masses across a relatively wide area: Kuroshio region water, Oyashio region water, Eastern Oyashio water, Oyashio water near the Kurile Islands, Oyashio water off Kushiro, Oyashio water near the Subarctic Front, mixed/transition water off Sanriku and mixed/transition water in the East Transition Zone (Fig. 1).

Pacific saury (*Cololabis saira*) were collected by both mid-water trawl and drifting gill net. Mid-water trawling was conducted according to the protocols outlined by Ueno et al. (2004) (net type: NST-99-K1, cod-end mesh: 18 mm, line out: 180–200 m, boat speed: 5 kt, sampling depth: 20 m, duration: ~60 min). Drifting gill nets were 38 m long and 7 m deep, with a mesh size between 30 and 43 mm, and were set for 2 hours duration. In addition, drifting gill nets were used for time-series sampling of saury during three cruises: WK0002, KY0007 and TK0009. Chaetognaths (*Sagitta elegans*) were collected along with other zooplankton by vertical hauling of NORPAC plankton nets from a depth of 20 m (mouth diameter: 45 cm, length: 180 cm, mesh size: 100 and 330 μm) (Motoda 1994). Full details of cruises and sampling are located in Table 1.

After collection, saury body length and weight was measured, and then the guts were removed and stored in a 10% buffered formalin and seawater solution. Zooplankton samples were rinsed into the cod end of the NORPAC nets
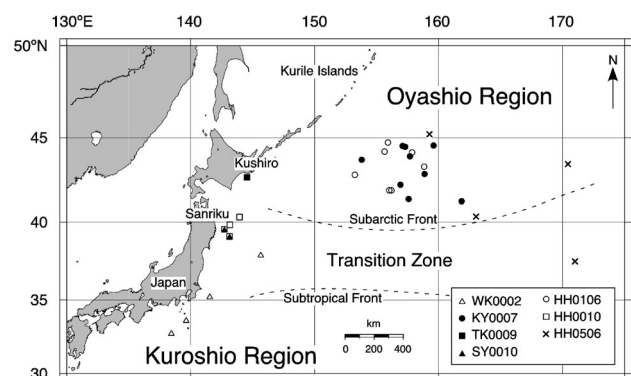

Fig. 1. Map of the study site and sampling locations—Oyashio and Kuroshio regions east of Japan (northwestern Pacific Ocean).

Table 1. Cruise and relevant sampling information.

Cruise No.	Vessel	Date	No. of Stations[1]	Water-Region[2]	Gear[3]
WK0002*	Wakataka-maru	2/2000	4	Kuroshio	Gill Net
KY0007*	Kaiyo-maru	7/2000	9	Oyashio (+Kurile Islands)	Gill Net
TK0009*	Tankai-maru	9/2000	1	Oyashio off Kushiro	Gill Net
HH0010*	Hokuho-maru	11/2000	4	Mixed/Transition off Sanriku	Gill Net, NORPAC
SY0010	Shoyo-maru	11/2000	2	Mixed/Transition off Sanriku	Mid-Water Trawl
HH0106*	Hokuho-maru	7/2001	7	Oyashio (+Kurile Islands)	Gill Net, Mid-Water Trawl, NORPAC
HH0506	Hokuho-maru	7/2005	1	Oyashio near Subarctic Front	Mid-Water Trawl, NORPAC
	Hokuho-maru	7/2005	1	Eastern Oyashio	Mid-Water Trawl, NORPAC
	Hokuho-maru	7/2005	1	Oyashio near Kurile Islands	Mid-Water Trawl, NORPAC
	Hokuho-maru	7/2005	1	East Transition Area	Mid-Water Trawl

[1] The number of stations is the number used for this study, it is not neccesarily the total number of stations for each cruise.

[2] Cruises KY0007 and HH0106 sampled throughout the Oyashio Region with some stations in proximity to the Kurile Islands.

[3] Pacific saury (*Cololabis saira*) were collected by gill net and mid-water trawl. Chaetognaths (*Sagitta elegans*) were collected by NORPAC net.

* These cruises also supplied data for Sugisaki and Kurita (2004).

and then fixed with a 10% buffered formalin and seawater solution.

Laboratory Analysis

Pacific saury gut content analysis began with cutting open the guts and emptying the contents into a 270 ml capacity glass dish. Approximately 150 ml of tap water was then added to dilute the contents, creating an aqueous solution of saury gut contents. Portions of the gut content solution was transferred to a smaller dish and examined with a stereomicroscope. Chaetognath remains were separated and collected for further analysis. Chaetognath remains consisted of undigested pieces of their body as well as the hard, chitinous grasping spines (hooks) that surround their mouths. The soft chaetognath body is easily digested, therefore the most common evidence of chaetognaths found in saury guts were the minute digestion-resistant hooks.

During analysis of HH0506 cruise samples, sub-samples were divided out and examined when initial observations made it obvious that the number of hooks in the gut was several hundred or more. Sub-samples were created by extracting and analyzing 13 ml measurements of the aqueous solution of gut contents, and this process was repeated until at least 50 hooks were recovered. The total hook number for the sample was then extrapolated mathematically using the ratio of the sub-sample volume and the total gut content volume.

In cases where the gut contents were largely undigested, numeration of ingested chaetognaths could be done with the body fragments collected. In cases of highly digested contents, the number of collected hooks was used for chaetognath numeration according to: 16 hooks for one chaetognath. This value was based on common averages for the species found in the guts: *Sagitta elegans*, *S. scrippsae*, *S. nagae* and *S. enflata*.

The hooks of *S. elegans* were easy to identify by their distinctive red-brown coloration. A sub-sample of *S. elegans* hooks from each gut was gathered and the overall length of the hooks measured. These hook lengths were used to calculate the overall body length of ingested *S. elegans* according to the following equation:

$$Y = (X + 0.151)/0.038$$

where X is hook length and Y is overall body length (Terazaki 1993).

The Product Moment Correlation Coefficient (*r*) was calculated to determine correlations between the length of saury and the calculated length of ingested *S. elegans*. This was done for all cruises except WK0002 (*S. elegans* were not ingested in that region) and TK0009 (only 2 saury with chaetognaths remains in the gut were recovered). For comparative purposes, *S. elegans* were sorted from the zooplankton samples and the overall body length (front of the head to the end of the tail, excluding fin) was measured.

To check for prey size selectivity by the saury, a *t*-test was used according to Fowler et al. (1998) to compare the mean body length of *S. elegans* collected by NORPAC net at 14 stations during 3 cruises (HH0106, HH0010 and HH0506) against the mean calculated length of *S. elegans* ingested by saury at the same stations. For cruise HH0506, during sampling of the Oyashio water near the Kurile Islands, the station of *S. elegans* net collection was slightly separated from the station of saury collection. However, an ANOVA performed on the log-transformed body length data for net collected *S. elegans* revealed no statistically significant difference (P= 0.31) in mean *S. elegans* body length anywhere in the Oyashio water during cruise HH0506. Therefore, the distance between the stations was deemed negligible. (According to Fowler et al. (1998), the net collected *S. elegans* body length data was determined to require normalization for accurate ANOVA, and thus was log-transformed for normalization.)

A comparison of the calculated body length of ingested *S. elegans* was made between the Oyashio water feeding grounds (cruises HH0106 and KY007) in July and the mixed/transition water off Sanriku (cruises HH0010 and SY0010) in November. For cross-referencing, a comparison was also done with saury body length. These comparisons were used to look for differences in prey size at different periods during the saury annual migration. Since the data failed homogeneity of variance tests, non-parametric Kruskal-Wallis tests were used to compare median length in the data sets. Further non-parametric analysis in the form of Mann-Whitney U-tests was applied to the calculated body length data of ingested *S. elegans*.

Additional analysis of size and selectivity for predator and prey was conducted by comparing both saury body length and ingested *S. elegans* calculated body length within different regions of the Oyashio current during cruise HH0506. Non-parametric Kruskal-Wallis tests analyzed saury length and chaetognath length in Oyashio water near the Kurile Islands (45.20N, 159.25E), in Eastern Oyashio water (43.47N, 170.46E) and in Oyashio water near the Subarctic Front (40.34N, 163.01E).

Because the station in the East Transition Zone (37.51N, 171.00E) of cruise HH0506 yielded only a single saury with chaetognath remains in the gut, that region was not included in any statistical analysis involving cruise HH0506.

Unless otherwise noted, all statistical analysis was conducted with Statview version 5.0.1, Macintosh edition (SAS Institute Inc., Cary, NC, USA).

Results

Ingestion counts and characteristics

289 saury guts were examined and 168 (58.1%) of them

Table 2. Ratio of total Pacific saury examined to those with chaetognaths in the gut.

Cruise No.	Date	Water-Region	No. of Saury	Saury w/ Chaetognaths	Per Cent Ratio
WK0002	2/2000	Kuroshio	14	14	100.0
KY0007	7/2000	Oyashio (w/Kurile Islands)	51	31	60.8
TK0009	9/2000	Oyashio off Kushiro	7	2	28.6
HH0010	11/2000	Mixed/Transition off Sanriku	17	13	76.5
SY0010	11/2000	Mixed/Transition off Sanriku Oyashio (w/ Kurile Islands)	14	10	71.4
HH0106	7/2001		36	18	50.0
HH0506	7/2005	Oyashio near Subarctic Front	30	20	66.7
	7/2005	Eastern Oyashio	50	13	26.0
	7/2005	Oyashio near Kurile Islands	50	46	92.0
	7/2005	East Transition Area	20	1	5.0
			289	168	58.1

contained chaetognath remains. The percentage of saury with chaetognath remains in the gut varied widely between cruises, from 5% to 100% (Table 2). Most saury from the July 2005 cruise (HH0506) had evidence of only 1 or 2 ingested chaetognaths in their gut, except for the Kurile Island saury that ingested multiple numbers of chaetognaths, with one saury having as many as 65 chaetognaths in its gut, and another as many as 91. In the samples from the 2000 cruises, there was even greater evidence of multiple chaetognaths per saury; of 70 saury containing chaetognaths from those cruises, 29 of them had over 100 chaetognaths in their gut. Those 29 were collected in the mixed/transition water off Sanriku in November.

Time series samples in 2000 (February, July and September from cruises WK0002, KY0007 and TK0009, respectively) revealed the largest proportion of saury containing chaetognath remains was collected between 18:00 and 24:00 (40.7%). The next largest was between 12:00 and 18:00 (34.5%). In one-third of the saury containing chaetognaths, the remains were located in the foregut; this was especially common between 12:00 and 18:00. Saury were found to ingest both crustaceans and chaetognaths after sunset (nighttime), but they ingested mostly chaetognaths between 6:00 to 18:00 (daytime; before sunset) when the crustaceans had migrated out of the surface layers. The common types of crustaceans found in saury guts were: *Neocalanus* copepods, *Euphasia pacifica* and *Themisto amphipods*. Throughout the course of analysis, a general trend was noticed whereby the amount of chaetognaths in the guts decreased in the presence of large numbers of crustaceans in the gut. However, this apparent inverse relationship was only a qualitative visual observation, and no specific crustacean counts were taken.

In the Oyashio water and mixed/transition water, the most common and abundant chaetognath found in saury guts was *S. elegans*. There were also some remains of *S. scrippsae*, however in very small quantities. In the Kuroshio water, the chaetognath species *S. nagae* and *S. enflata* were
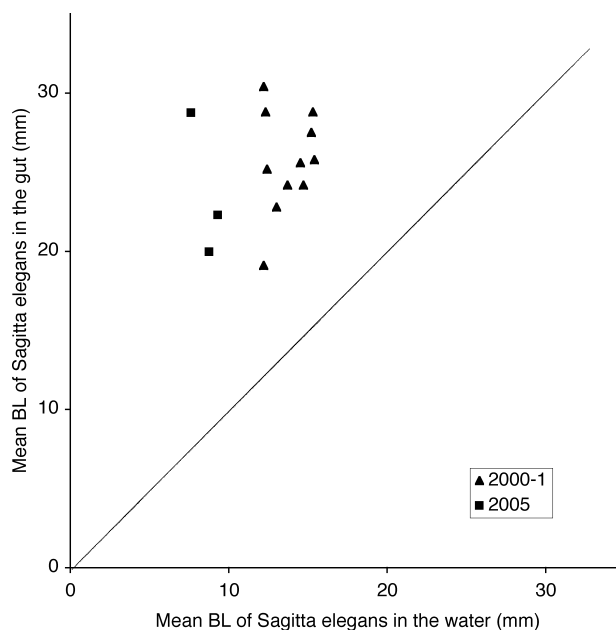
Fig. 2. Comparison of body length (BL) for *Sagitta elegans* in the water and in saury guts, for the years of 2000-1 and 2005.

recovered from saury guts. The Kuroshio region was the only location where chaetognath remains were found in all the saury examined.

Predator and prey size

During both 2000–2001 and 2005 sampling, the calculated mean length of *S. elegans* recovered from gut contents (25.24±0.91 mm) was longer than the mean length of *S. elegans* recovered from the water by NORPAC net (12.61±0.67 mm) (Fig. 2). A *t*-test confirmed the difference to be statistically highly significant (F±1.84, t±11.12, P<0.01), which demonstrates that saury select larger than average *S. elegans* (compared to other *S. elegans*).

Along the saury migration route, a Kruskal-Wallis test revealed no significant difference in median body length

Table 3. Results of Mann-Whitney U-tests to compare median body length of ingested *Sagitta elegans* between the Oyashio water in July and mixed/transition water near Sanriku in November. Three of the four cases tested were statistically significant. Refer also to Fig. 3.

Region & Median Length		U	P	Status
Oyashio	Sanriku			
[22.2 mm–HH0106, July 2001] ×	[18.8 mm–HH0010, Nov. 2000]	49.0	0.18	Not Significant
[22.2 mm–HH0106, July 2001] ×	[18.5 mm–SY0010, Nov. 2000]	16.0	0.01	Significant
[25.7 mm–KY0007, July 2000] ×	[18.8 mm–HH0010, Nov. 2000]	29.0	<0.0001	Significant
[25.7 mm–KY0007, July 2000] ×	[18.5 mm–SY0010, Nov. 2000]	5.0	<0.0001	Significant
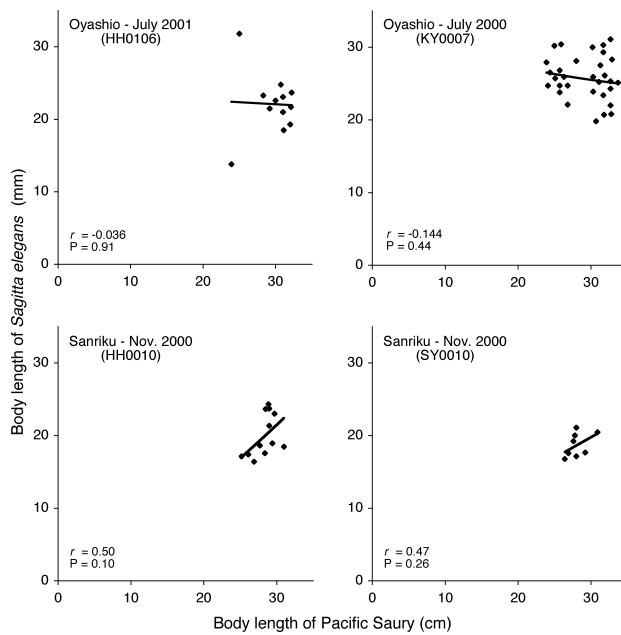
Fig. 3. Body length comparison of Pacific saury and ingested *Sagitta elegans* from the Oyashio water (cruises HH0106 and KY0007) in July and the mixed/transition water off Sanriku (cruises HH0010 and SY0010) in November. Trendlines shown, along with results of Product Moment Correlation Coefficient analysis (r and P).

among saury from the Oyashio water in July and mixed/transition water near Sanriku in November (K=3.6, P=0.31). However, the difference in median body length of ingested *S. elegans* was found to be statistically highly significant (Kruskal-Wallis test, K=32.2, P<0.0001). Further analysis by Mann-Whitney U-tests, revealed a statistically significant difference in median body length of ingested *S. elegans* in 3 out of 4 comparisons between the Oyashio water in July and mixed/transition water near Sanriku in November (Table 3), suggesting that larger *S. elegans* were being eaten in the Oyashio region feeding grounds during July (Fig. 3).

Analysis of predator and prey length in the Oyashio water during cruise HH0506 showed that the median length of saury near the Kurile Islands and in the Eastern Oyashio water did not differ significantly, but the saury near the Subarctic Front were significantly smaller than both of them (Kruskal-Wallis test, K=12.8, P=0.0016) (Table 4). Further-

more, though the saury near the Kurile Islands and Eastern Oyashio water were essentially the same size, the median length of chaetognaths they ingested was significantly different. *Sagitta elegans* ingested in the Eastern Oyashio water were significantly larger than those ingested near the Kurile Islands or the Subarctic Front (Kruskal-Wallis test, K=19.6, P=0.0001) (Table 4). No correlation was found between saury length and ingested *S. elegans* length in the Oyashio water near the Kurile Islands ($r=-0.06$, P=0.68), and while a positive correlation was noted in the Eastern Oyashio water, it was not statistically significant ($r=0.40$, P=0.18) (Fig. 4). A statistically significant positive correlation between saury length and ingested *S. elegans* length was found at the Subarctic Front ($r=0.56$, P=0.01), the only location where a significant correlation was found during this study. Samples from cruises HH0010 and SY0010 (mixed/transition water off Sanriku in November) showed a positive length correlation, but it was not statistically significant; no correlation was apparent from cruises KY0007 and HH0106 (Oyashio water feeding ground in July) (Fig. 3).

Discussion

Considering that nearly 60% of the saury examined had evidence of chaetognaths in their gut, saury predation on chaetognaths off Japan is obviously common and wide spread. However, given the variety of zooplankton species that previous research has established as prey for saury (Hotta and Odate 1956, Odate 1977, Taka et al. 1980, 1982, Sugisaki and Kurita 2004), it is not totally clear how much saury depend on chaetognaths and what type of impact a flux in chaetognath population would have on saury. Sugisaki and Kurita's (2004) work established that chaetognaths comprise 16% of the wet weight of saury gut contents off Sanriku and 29% of the wet weight in the Kuroshio region to the south. At nearly one-third (29%) of the total gut contents, chaetognaths could be considered an important dietary component. It is believed that the importance of chaetognaths in saury diet increases in the absence of suitable euphausiid prey (the preferred food item) as saury move south out of the Oyashio region and into the Transition Zone and Kuroshio region

Table 4. Results of Kruskal-Wallis tests on the median length of Pacific saury and ingested *Sagitta elegans* among the three areas (Kurile Islands, Subarctic Front, and eastern Oyashio) in the Oyashio Region during cruise HH0506 in July 2005. Refer also to Fig. 4.

Organism	Median Length			K	P	Status
	Kurile Islands	Subarctic Front	Eastern Oyashio			
Pacific saury	29.9 cm	23.9 cm	29.7 cm	12.8	0.002	Significant
Sagitta elegans	19.5 mm	21.3 mm	27.9 mm	19.6	<0.0001	Significant
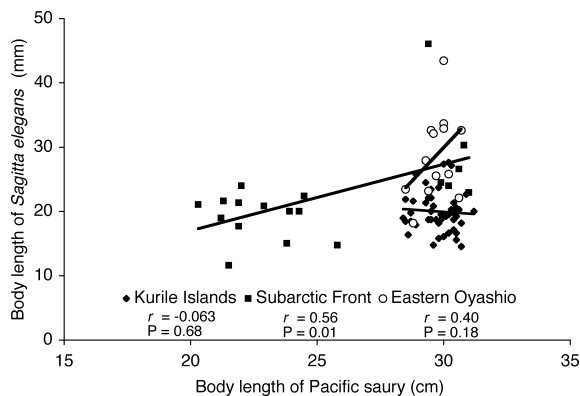
Fig. 4. Body length comparison of Pacific saury and ingested *Sagitta elegans* from the Oyashio region (cruise HH0506, July): near the Kurile Islands, near the Subarctic Front and Eastern Oyashio. Trendlines shown, along with results of Product Moment Correlation Coefficient analysis (*r* and P).

(Sugisaki and Kurita 2004). This concept is supported by our finding that 100% of saury collected in the Kuroshio region had chaetognath remains in the gut. However, since saury show considerable adaptability to the available prey resources—percentages of copepod wet weight also increased in the euphausiid-poor Kuroshio region (Ito et al. 2004)—critical dependence by saury on chaetognaths, or any other singular prey item, is highly debatable.

Certainly there are instances when saury feed very heavily on chaetognaths, as is evidenced by the gut samples that contained greater than 100 individuals. While this was not always the case, there were enough such saury specimens recovered to suggest that saury might occasionally come across aggregate swarms of chaetognaths where they can be easily ingested in high numbers. Chaetognath swarms have been reported since at least the 1950's (Bieri 1959) and they obviously present a useful feeding situation for their predators. However, the forming and dispersal of such swarms is not regular enough for saury to rely on for timing of their feeding activities.

A more reasonable explanation for the high numbers of chaetognaths found in saury guts might be vertical migration. According to the time series data, the largest proportion of saury with chaetognaths in the gut were collected from 18:00 to 24:00. Much previous feeding research suggests that saury feed most actively at dusk and the early hours of the night

(Hotta and Odate 1956, Odate 1977, Sugisaki and Kurita 2004), which corresponds with the vertical migration of some chaetognath species into the surface layers where they become available prey. The cold water species *S. elegans* is known to migrate periodically (King 1979, Sullivan 1980) as do several warm and mixed-water species (Johnson et al. 2006).

Of course vertical migration is not limited to chaetognaths, and the movement of other zooplankton can affect their occurrence in saury diet. Sugisaki and Kurita (2004) found differences in migration timing into and out of the surface layer between chaetognaths and crustaceans to create different periods of encounter with saury; thus leading to alternating consumption. This study noted a similar pattern with chaetognaths becoming a central dietary item during the daytime as crustaceans migrate more regularly and completely out of the surface layers. In addition, there was a general trend of alternate or inverse consumption of saury on crustaceans and chaetognaths throughout the study that did not appear to be regularly governed by the time of day—the cause of which can only be speculated as some type of preference or selectivity (passive or active) on the part of the saury. Furthermore, Sugisaki and Kurita's research (2004) revealed some seasonal inverse selectivity by saury on chaetognaths and crustaceans (especially amphipods), however an overall cause for such selection (other than vertical migration) remains unknown.

Selectivity of prey by saury can also be recognized within a single species, *S. elegans*—in this study statistical analysis demonstrated that saury have a very clear preference for *S. elegans* of above average length. Moreover, Figure 2 suggests that saury select *S. elegans* with lengths approximately 20 mm or greater. The simple explanation for the mean length of *S. elegans* in the gut being so much larger than that of *S. elegans* in the water is: nutrition. Larger prey items should have a higher caloric content and are therefore more nutritious for the predator. However, there is a possible influence by passive selection (large prey may be easier to detect) and feeding success probabilities (larger prey may be easier to catch). While the data in this study is insufficient to say with any certainty why saury select *S. elegans* of above average length, we do know this activity occurs.

Understanding prey size selectivity between regions and

seasons includes a few more variables and is even more difficult. The larger *S. elegans* eaten in the Oyashio water in July compared to mixed/transition water off Sanriku in November could have been caused by either saury selection or the sizes of available *S. elegans*. Supposing selection by saury was the causative factor, one could argue that saury striving for calories in the seasonal feeding ground (Oyashio region during July) are selecting for larger *S. elegans*, which would be a more nutritious food source. And if the saury then began being less selective and eating less actively as they migrated through the Sanriku region in November towards the seasonal spawning grounds, then that could potentially result in larger *S. elegans* eaten in the Oyashio water compared to the mixed/transition water off Sanriku. However, this theory does not fit well with the correlation analysis between saury length and *S. elegans* length conducted in this study (Fig. 3). The lack of correlation in the Oyashio water for July implies that during the feeding season saury do not eat *S. elegans* of lengths directly proportional to the saury's own body length. In a certain sense these saury eat indiscriminately: as they increase in length they don't necessarily choose proportionally larger *S. elegans*, the larger saury simply eat a greater range of sizes among the available *S. elegans* above ca. 20 mm length. Furthermore, the positive correlation noted off Sanriku (though not statistically significant) implies that saury are, for that season and location, selecting larger sized *S. elegans* that are proportional to the saury's own body length. They may be more selective as they seek to conserve energy while traveling through low productivity waters towards the spawning grounds, not risking energy expenditure to go after prey unless the potential nutritional reward is high enough. In this case, it is also important to consider predator-prey interactions. Basically, feeding interactions can be separated into four events: encounter, attack, capture-handling and ingestion (Hunter 1972, Beyer 1980). The probability of success by planktivorous fish at any one of these events is mathematically complex and can be influenced by zooplankton (prey) size (Drenner 1978, Vinyard 1980, Heath 1993, Caparroy et al. 2000). To the best of our knowledge, evasion capabilities of chaetognaths in response to planktivorous fish have not been laboratory tested. However, if larger sized *S. elegans* (proportional to saury size) are easier to locate and feed on, or if they offer the best energetic cost-benefit ratio, it is logical that saury would select them en-route to the spawning grounds. The opposite should occur in the summer feeding grounds (Oyashio region near Kurile Islands): the more productive waters would be more abundant with prey and the saury would be actively trying to acquire as much food as possible. Therefore, the *S. elegans* ingested would not necessarily be in direct proportion to the saury body length, which is what the correlation data suggests for all years of this study (Fig. 3 and 4). Thus it is unlikely that saury selectivity is the causative factor behind the ingestion of larger sized *S.*

elegans in the Oyashio water in July compared to mixed/transition water off Sanriku in November.

The more plausible causative factor is the differences in size of *S. elegans* available to saury with respect to the *S. elegans* life cycle and local water conditions. A review of the literature shows that *S. elegans* are widely reported to have differing spawning periods and generation lengths at different locations (Sameoto 1971, King 1979, Tiselius and Peterson 1986, Nishihama and Hirakawa 1997). For example, Kotori (1999) found *S. elegans* in the North Pacific off Hokkaido to have maximum mean abundance from late July to early August, and some of his study years show more large sized individuals in the summer compared to other seasons. However, research conducted at Ocean Station P in the eastern North Pacific by Terazaki and Miller (1986) revealed no notable difference in abundance or body length between July and November. So, the length difference between Oyashio water in July and mixed/transition water in November could be resultant from localized differences in the life cycle of *S. elegans*.

Another aspect to consider is the hydrographic conditions at the two locations. While the water in the Oyashio region has some degree of isolation and consistency, the mixed/transition water near Sanriku is a dynamic mixture of both cold Oyashio water and warm Kuroshio water. It is not uncommon for warm-core rings of Kuroshio water, as well as pockets and streamers, to move through the mixed/transition water area, and previous research in a warm-core ring has suggested they are detrimental to *S. elegans* (Johnson and Terazaki 2003). Therefore, it could simply be that *S. elegans* in the mixed/transition water are not developing as large as those in the Oyashio water, irrespective of season.

Regardless if the root cause is life cycle or water conditions, *S. elegans* off Sanriku in November are most likely smaller than their July Oyashio counterparts and this is accounting for the length difference among the ingested samples recovered from saury guts. A similar situation was recorded in previous work with another saury prey item: euphausiids. Sugisaki and Kurita (2004) noted that the euphausiids off Sanriku in the autumn were smaller than those available in the Oyashio water in the summer, and as such saury were ingesting euphausiids of differing size at each location and season.

However, neither chaetognath size nor saury size alone can be the deciding factor as to which sizes of prey are selected by saury. The data collected in this study makes a strong argument that additional, influential factors must be present. Throughout the Oyashio water in 2005, the length of net collected *S. elegans* was essentially the same at all stations studied, and saury size near the Kurile Islands and in the Eastern Oyashio water was also basically the same. In spite of this, the length of *S. elegans* recovered from their guts was significantly different. So, additional factors must

exist but the question of what they are and how they influence prey selection must be left for future study.

In light of the questions and dilemmas raised by this study, future study of saury and chaetognath interactions should focus more on the Kuroshio region spawning ground where evidence suggests that chaetognaths are a much more important dietary component. Furthermore, it should be useful to design experiments (laboratory or in situ) that can reveal the underlying cause of the feeding selectivity recognized in this paper.

Acknowledgements

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