Hydrobiologia
DOI 10.1007/s10750-009-9829-2

PRIMARY RESEARCH PAPER

A spatial analysis of trophic composition: a case study of hairtail (*Trichiurus japonicus*) in the East China Sea

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Received: 24 November 2008 / Revised: 22 March 2009 / Accepted: 18 May 2009

Abstract The spatial distribution of fish on feeding grounds is an important factor in determining their prey composition. Of the factors that may influence the spatial distribution on the feeding ground and subsequent diet composition is the fish maturation stage. Using hairtail (*Trichiurus japonicus*) as an example, we evaluated the impacts of gonad development stage on diet composition. Hairtail supports one of the most valuable and largest fisheries in the East China Sea. As one of the top predators, it plays an important role in the ecosystem. We analyzed hairtail stomach samples collected on their feeding grounds from a fisheries-independent survey program in September 2005. Our analyses suggest that females in their third maturity stage tended to feed more intensively. Fish were the most important preys for hairtail, accounting for 72.6% of the total stomach contents in weight. The four most important fish species were juvenile hairtail (25.2%), Japanese scad (11.4%), Japanese jack mackerel (7.7%), and small yellow croaker (5.9%), suggesting strong cannibalism. A cluster analysis suggests that hairtail could be divided into three groups in their spatial distribution based on their diets: one group with similar percentages of fish and crustacean preys mainly distributed in the south of East China Sea far from the coast; one group mainly consuming fish and distributed over the north of East China Sea near the coast; and the third group consuming mainly crustacean species mainly distributed in the open sea. We hypothesize that gonadal development stage of hairtail may determine their movement from spawning ground to feeding ground, and subsequently spatial distribution on the feeding ground, which in turn results in different feeding intensities and prey compositions.

Keywords *Trichiurus japonicus* · Prey composition · Feeding migration · Gonadal maturity · Spatial distribution · East China Sea

Introduction

Feeding activities provide fish with necessary nutrition and energy to support their maintenance, growth, reproduction, and subsequently the development of the populations (Beverton & Holt, 1957; Backiel & Le Cren, 1978; Persson & De Roos, 2006). The study of feeding activities and factors influencing them is thus critically important in our understanding of the dynamics of fish populations. Much effort has been put on the

Handling editor: Robert Bailey

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Published online: 15 June 2009

studies of fish prey compositions that show fish feeding characteristics and analyze habitat environments and inter- and intra-species trophic interactions (Shaw & Jenkins, 1992; Hovde et al., 2002; Martins et al., 2006).

Feeding ground is an ideal sampling location for studying fish feeding activities because it provides the information on typical feeding characteristics. The gut content composition tends to correspond strongly with the prey composition in the environment (Floeter & Temming, 2003; Hinz et al., 2005; Calbet et al., 2007). Thus, the spatial location of fish on the feeding ground may be critical in determining the prey composition. For example, Islam et al. (2006) found that a single species dietary habit at the upper river in Chikugo estuary for Japanese temperate bass and a multi-species dietary habit were dominated by the common coastal copepods in the lower estuary. Spatial variations in the abundance of some major prey species could cause regional differences in diet composition, and such information can lead us to a better understanding of the ecology and feeding habits of the predator in question (Hovde et al., 2002).

Reproductive activity is an important part of life circle determining recruitment and population dynamics (Stearns, 1992; McGraw & Caswell, 1996; Li et al., 2007). Marteinsdottir et al. (2000) found that egg production, based on abundance, size, and age composition of spawning cod, might vary extensively among different spawning areas. Choices of the geographical location of spawning might influence the offspring survival (Cushing, 1990; Hutchings & Myers, 1993). Thus, information about the distribution of spawners, in conjunction with spatial and temporal variations in oceanic and environmental conditions, might help understand recruitment processes critical for the assessment and management of commercially important fish species (Marteinsdottir et al., 2000). The spatial analysis of both feeding and reproducing activities is thus important.

Feeding and reproduction are two different physiological needs for fish. The two life history processes interact with each other because they develop simultaneously. For examples, mature fish engage in feeding activity while their gonads develop in the same time. Most studies, however, dealt with feeding or reproduction separately (Shaw & Jenkins, 1992; Floeter & Temming, 2003; Hinz et al., 2005). Few studies considered both the processes and their interactions (Garrido et al., 2008).

Feeding migration usually starts after spawning, and the gonad of fish also recovers and/or develops for the next spawning (Ter et al., 2007). Due to variations in the timings of gonadal maturation and spawning, the timing of starting feeding migration tends to vary among individual fish. Thus, spatial location of fish on the feeding ground may vary among fish of a given population, depending on their temporal schedule of gonadal maturation and feeding. Such variations in spatial location may result in differences in prey compositions among fish of a given population. In this study, using hairtail (*Trichiurus japonicus*) as an example, we evaluated potential links between their prey compositions, gonadal maturation stages, and spatial distribution on the feeding ground.

Hairtail is one of the most important fish species, both economically and ecologically, in the East China Sea (Chen & Zhu, 1984; Nakamura & Parin, 1993; Chakraborty et al., 2007), and always supports the most valuable and largest fishery in China. China landed about 70–80% in the total hairtail catch around the world (Ling et al., 2005). As one of the top predators, the hairtail plays an important role in the ecosystem (Duarte & Garc, 1999). Typical reproductive activity of hairtail in the northern East China Sea reaches the peak between May and June (Deng & Zhao, 1991; Luo, 1997). Individuals only begin the feeding migration after they finish spawning activity (Yan et al., 2004; Ter et al., 2007).

In this study, based on hairtail stomach samples taken over a large spatial area (i.e., feeding ground) from a fisheries-independent survey program in September 2005, spatial variations in prey compositions and gonadal maturation stages of hairtail on the feeding ground were evaluated. The information derived was used to address the objective of this study, which is to identify possible links between gonadal maturation, prey composition, and spatial distribution of hairtail on their feeding ground. Hairtail on the feeding ground would then be classified into different groups based on the identified prey composition and spatial distribution.

Materials and methods

Study area and sampling protocol

Hairtail samples were collected in a fisheries-independent survey in the East China Sea from September

19 to 26, 2005. The survey was conducted by pair bottom trawlers with power of 183.25 kW each, and average trawling velocity of 2n mile h^{-1}. The size of the net mouth is 100 × 4 m, and the mesh size of cod end is 2.5 cm. The survey covered the area from 27°00′ to 32°00′ N latitude and 122°00′ to 127°00′ E longitude. The survey had a systematic sampling design with sampling stations evenly distributed with a 30′ interval between every pair of sampling sites and 1 h of towing duration for each sampling site. For each sampling site with hairtail, we randomly sampled 10–30 hairtail for stomach samples in this study. In total, we sampled effective stomach samples for 229 hairtail (Table 1) from 16 sampling stations (Fig. 1).

Sample analysis

Once sampled, each specimen was measured for the basic biological information, such as length, weight, sex, gonad maturity, and stomach fullness. For each sampled fish, the gonad maturity was classified into one of the six stages defined below: 1, immature; 2, developing or recovering spent; 3, maturing; 4, mature; 5, ripe; and 6, spent (Davis, 1985; Chen, 1997; Kwok & Ni, 1999). The macroscopic and histological characteristics for each maturity stage were referred to the above-cited literatures. The stomach fullness was recorded on a scale of 0 (empty) to 5 (full) (Chen, 1997; Hajisamae et al., 2003). The stomach samples were immediately removed and wrapped with medical bandage, marked, and put into 5% formaldehyde solution for the later laboratory analysis.

In laboratory, stomach samples were removed from formalin and soaked in water for 1–2 days before being processed (Drazen et al., 2001). The surface water of stomach was removed with absorbent paper, and the total stomach was weighed. Stomach contents were then transferred into a Petri dish, and the empty stomach was weighed. The weight of stomach contents was calculated from the difference between the empty stomach weight and stomach content weights. The identification and analysis of stomach contents might take long times, resulting in the evaporation of moisture. Thus, it was necessary to adjust the measured weight of identified items into the original wet weight. This was done by multiplying the weight of identified items by a coefficient which is the ratio of the original total stomach content weight (i.e., wet weight) versus the final total stomach content weight (after loss of moisture).

The process for prey identification/classification proceeded using the following procedures. After weighing, the prey items were separated and grouped by taxa and then identified to species if possible. In the case of highly digested items or items that cannot be identified to species levels, they were grouped to a higher category. Preys from taxa that were difficult to identify were sent to appropriate taxonomists for specific identification or verification. After identification, the wet weight and number of individual prey were counted for each group. All the identifications were done under a binocular microscope, and the items were weighted to 0.001 g.

Table 1 The number of samples for each station

Station no.	Count of samples	Station no.	Count of samples
1	23	9	13
2	10	10	18
3	19	11	15
4	21	12	10
5	21	13	11
6	16	14	8
7	14	15	9
8	12	16	9

Data analysis

The feeding intensity was estimated from the average of stomach fullness of all the samples at each sampling site. Based on the feeding intensities of all the stations, the contour of feeding intensity was derived using a computer program written in the R software (R Development Core Team, 2008).

In order to test whether there was a difference between male and female hairtail in feeding intensity, a paired Student t test was conducted on the total 16 sets (16 sampling sites in total) of paired feeding intensities of males and females. Female hairtail were divided into groups by different gonadal maturity stages, and the average stomach fullness of all the samples in each group was used as feeding intensity and compared among groups. Relative quantity of each species in stomachs was quantified with the three normally used measures: (1) the weight percentages (%W) of each prey item in all the stomachs in a sampling site or the survey; (2) the percentage in

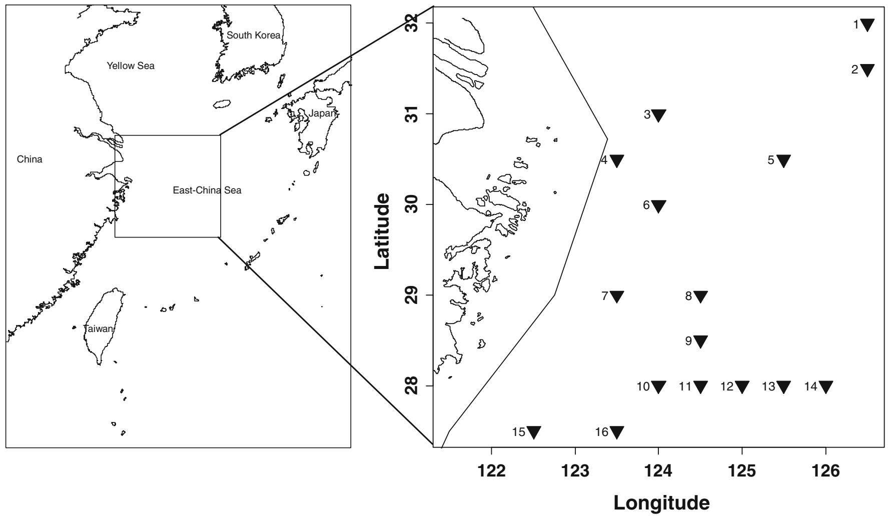

Fig. 1 The spatial distribution of sampling stations: "*downward triangle*" denotes the stations with the station number on the top left

number (%*N*) of each prey item in all the stomachs in a sampling site or the survey; and (3) the percentage in frequency of occurrence (%*F*), based on the number of stomachs in which each food item occurred in relation to the total number of stomachs sampled at a sampling site including empty stomachs (Jacobsen & Hansen, 2001).

Based on the main categories of preys (i.e., pisces, crustacea, cephalopods, and others), the distribution of prey composition in weight was analyzed to identify the compositions of preys for different locations. Each site corresponded to a set of proportions of preys, and the proportion data of 16 sites were put together to construct a matrix. Based on this matrix, a cluster analysis was conducted for evaluating the spatial variations in prey composition. We did a cluster analysis using the following procedure: (1) the data in the matrix were standardized by dividing each matrix entry by its station total (and multiplied by 100) to avoid comparison based on different volume for every station; and to weigh the contributions of common and rare species, all the data were applied to a fourth root transformation (Clarke & Warwick, 2001); (2) a similarity matrix was calculated using the Bray–Curtis measure on the standardized and transformed data (Bray & Curtis, 1957); and (3) based on the similarity matrix, a hierarchical agglomerative clustering was implemented with group average cluster mode.

Based on the grouping of sampling sites determined in the above cluster analysis, a SIMPER analysis was conducted (Clarke & Gorley, 2001). The SIMPER analysis examines the contribution of each species to the average Bray–Curtis dissimilarity between groups of samples, and determines the contribution to similarity within a group. In this study, it was used in identifying the amount of contribution each prey made to the similarity within a group. Similar to the above cluster analysis, it was necessary for the data to be standardized and then transformed using the fourth root transformation (Clarke & Warwick, 2001).

Results

Spatial distribution of hairtail abundance and feeding intensity

The contour of hairtail abundance (catch in number per hour) in the survey area is presented in Fig. 2. The plot showed that the highest abundance in the survey was located in the area of 123°30′ E longitude and 30°00′ N latitude. Two areas with relatively low abundance were located at 126°00′ E longitude, 30°30′ N latitude and 124°30′ E longitude, 29°00′ N latitude, respectively (Fig. 2).

The contour of feeding intensity in the survey area is presented in Fig. 3. The contour plot showed that the feeding intensity was relatively higher for the area located at 124°00′ E longitude and 31°00′ N latitude. The feeding intensity decreased gradually away from the area of high feeding intensity. The *t* test showed that there was no significant difference in feeding intensity between males and females ($P = 0.137$).

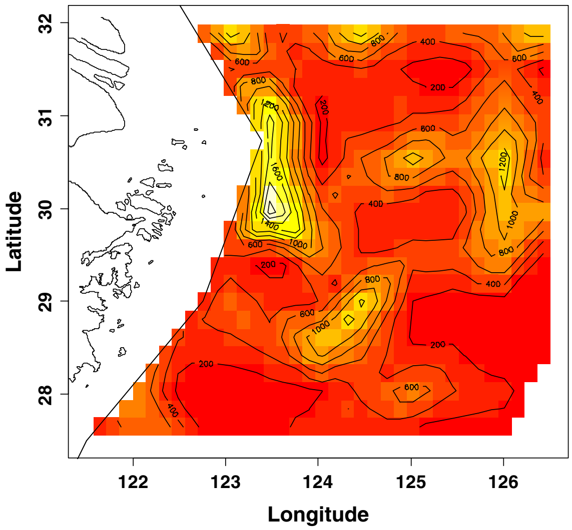

Fig. 2 The spatial distribution of hairtail abundance. The *lines* are the contours of abundance, and the *number* between the lines denotes the abundance

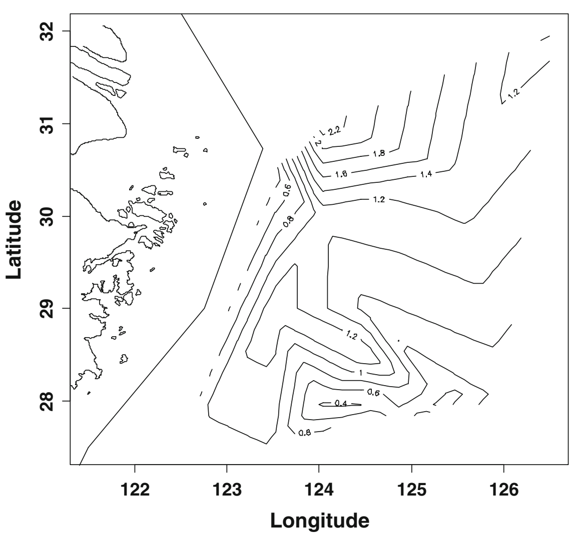

Fig. 3 The spatial distribution of feeding intensity. The *lines* are the contours of feeding intensity, and the *number* between the lines denotes the feeding intensity value

Variation in feeding intensities and distribution among gonadal maturity stages

The results for the comparison of feeding intensity among gonadal maturity stages are shown in Fig. 4. The individuals in the third stage of gonadal maturity had relatively higher feeding intensity than those

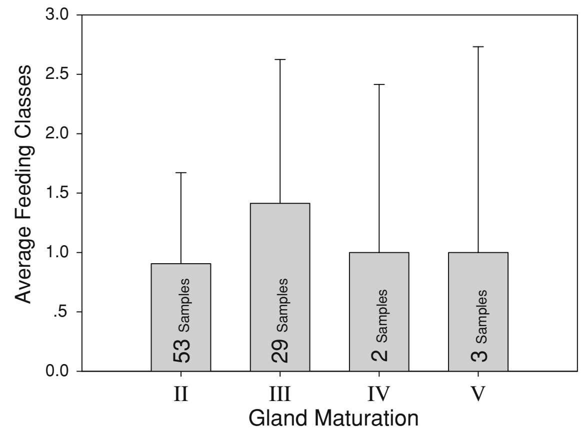

Fig. 4 Comparing feeding intensities of hairtail of different maturation stages. The *vertical line* is standard deviation

individuals in the other maturity stages. Due to the time starting feeding migration after spawning, the maturity stages in IV and V were rare (totally five individuals among the samples), and they were not typical in the targeted population in the survey. Thus, a Student t test was conducted only between maturity stages II and III. Before the t test, F test was conducted to test whether the variances of the two stage groups were equal, and the result showed that the variances were not equal. Therefore, a t test assuming unequal variances was conducted, and the result showed that there was a significant difference in the feeding intensity between maturity stages II and III ($P = 0.024$).

The hairtail in different maturity stages tended to have different spatial distributions (Fig. 5). Fish in stage II had the widest distribution, and fish in stage III tended to be in more northern area with less in the south comparing to those of stage II. The number of fish in stages IV and V was small, and they were all distributed in the north of 30°30′ N latitude.

Prey composition analysis

During the feeding migration, the preys could be divided into four groups: pisces, crustacea, cephalopods, and urochorda. In total, there were 36 species identified in the stomach contents (Table 2).

Pisces were found to be the most important food for hairtail in this study. Their percentage in stomach contents was only 7.8% in number, but reached 72.6% in weight. The percentage of pisces frequency

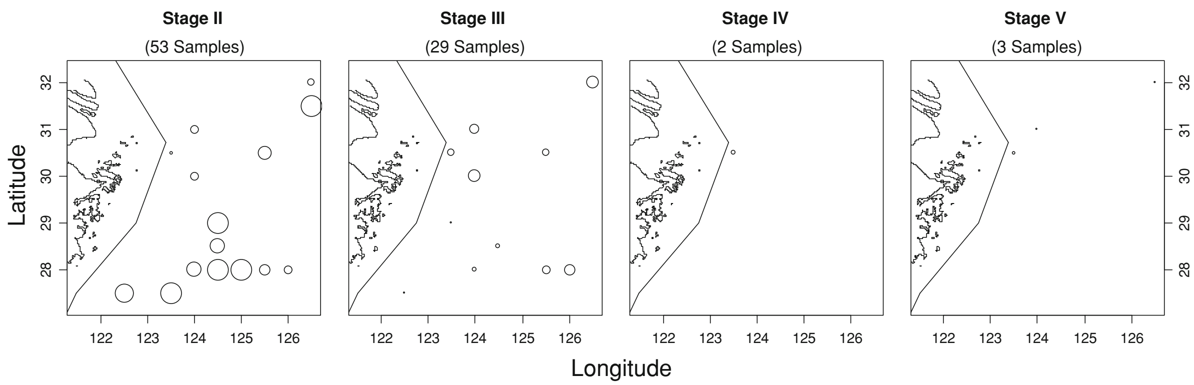

Fig. 5 The spatial distribution of female hairtail of different maturity stages. The *size of circle* is proportional to the percentage of individuals in a specific maturity stage for females at the sampling site

in stomach contents was also high, reaching 55.6%. The top four most important fish species in weight were juvenile hairtail (25.2%), *Decapterus maruadsi* (11.4%), *Trachurus japonicus* (7.7%), and *Larimichthys polyactis* (5.9%). The percentages of other food items were all no more than 5.0% in weight.

The most frequent prey item was the unidentified fish, reaching 35.1% in frequency. Other frequently occurred fish species in stomach included *Myctophum pierotum* (11.6%), *Champsodon capensis* (6.7%), and juvenile hairtail (3.1%). The percentages of the rest organisms were all less than 3.0% (Table 2). The proportion of fish species in number was similar to the above in frequency.

Crustacean species were also important for hairtail during the feeding migration. Although the percentage of crustacean species was only 25.1% in weight, the percentages for both number and frequency were highest, reaching 90.3% and 66.7%, respectively. The most frequent prey organism was mysidacea species (29.3% in frequency), and other frequently occurred crustacean species in stomach included stomatopoda (27.1%), euphausiacea (24.9%), decapods (19.1%), amphipoda (12.9%), and the percentages of sergestidae and copepoda were both less than 10% in frequency. The proportion of crustacean species in number was also similar to the above in frequency. The other two food groups (i.e., cephalopods and urochorda) were not so important, with both only taking 2.1% of the stomach contents in weight.

The preys in the stomach of hairtail could be classified into three ecological groups: nekton, zooplankton, and benthic fauna. Their percentages in weight in the stomach contents were 74.7%, 23.1%, and 2.1%, respectively. This study shows that the hairtail in the East China Sea targeted a wide range of species with nekton being their most important preys.

Distribution of prey composition

For almost all the sites north of 29°00′ N latitude, except for site 2, the percentages of pisces species were more than 50% (Fig. 6). However, for the sites south of 29°00′ N latitude, except for sites 11 and 12, the preys were mainly composed of crustacea species, all more than 50% in percentage.

The result of cluster analysis showed that 16 stations could be divided into three groups (Fig. 7). The distribution of the three groups was different: Group 1 was mainly distributed in the south of East China Sea far from the coast; Group 2 was distributed over the north of East China Sea near the coast; and Group 3 was mainly distributed in the open sea (Fig. 8).

The results of SIMPER analysis were listed in Table 3. The average biomass of Group 2, whose distribution corresponded to the relatively high feeding intensity area, was significantly higher than the other two groups (Fig. 2), and Group 3 was the lowest. The contribution of each prey species to the similarity within group was significantly different from that among groups. In Group 1, crustacea species had contributions similar to pisces species. In Group 2, the contribution of pisces species was most important, much more than that of crustacea species. In Group 3, crustacea species were the most important preys, followed by cephalopods species and pisces species.

Table 2 The prey composition of *Trichiurus japonicus* in the East China Sea

Prey items	Percentage of weight (%)	Percentage of number (%)	Percentage of frequency (%)
Pisces	72.6	7.8	55.6
Trichiurus japonicus	25.2	0.8	3.1
Decapterus maruadsi	11.4	0.04	0.4
Trachurus japonicus	7.7	0.04	0.4
Larimichthys polyactis	5.9	0.1	0.9
Engraulis Japonicus	4.5	0.04	0.4
Myctophum pierotum	4.4	2.0	11.6
Champsodon capensis	4.1	0.7	6.7
Caelorinchus multispinulosus	1.5	0.04	0.4
Kentrocapros aculeatus	0.4	0.04	0.4
Gobiidae spp.	0.1	0.2	1.8
Unidentified fishes	7.4	3.8	35.1
Crustacea	25.1	90.3	66.7
Decapod	2.9	10.8	19.1
Plesionika izumiae	1.2	0.4	3.1
Crangon affinis	0.5	0.04	0.4
Portunus trituberculatus larve	0.3	5.8	4.9
Scylla serrata larve	0.1	0.7	3.1
Eriocheir sinensin larve	0.04	0.3	1.8
Unidentified decapod	0.8	3.5	8.0
Sergestidae	1.0	1.6	8.9
Acetes chinensis	0.4	0.8	4.9
Lucifer faxonii	0.3	0.2	1.8
Lucifer intermedius	0.3	0.4	1.8
Lucifer hansem	0.1	0.2	0.9
Stomatopoda	10.1	24.6	27.1
Stomatopoda larve	10.1	24.6	27.1
Euphausiacea	5.7	23.5	24.9
Pseudeuphausia sinica	1.7	9.5	8.4
Euphamia pacifica	1.3	5.6	5.8
Oxycephalus clecasi	0.02	0.04	0.4
Pseudeuphausia sinica	0.01	0.04	0.4
Unidentified euphausiacea	2.7	8.3	12.0
Mysidacea	5.3	26.2	29.3
Acanthomysis longirostris	1.7	9.1	6.7
Siriella sinensis	0.2	2.0	4.9
Neomysis awatschensis	0.04	0.3	1.3
Oxycephalus clecasi	0.01	0.04	0.4
Unidentified mysidacea	3.3	14.8	16.9
Amphipoda	0.2	3.3	12.9
Themisto gracilipes	0.1	2.3	5.8
Oxycephalus clecasi	0.1	0.7	7.1
Simorhynchotus antennarius	0.01	0.2	0.9
Lycaea pulex	0.004	0.04	0.4
Unidentified amphipoda	0.001	0.04	0.4

Table 2 continued

Prey items	Percentage of weight (%)	Percentage of number (%)	Percentage of frequency (%)
Copepoda	0.04	0.3	1.8
Phaenna spinifera	0.01	0.04	0.4
Corycaeus japonicus	0.003	0.2	0.9
Unidentified Copepoda	0.03	0.04	0.4
Cephalopods	2.1	0.7	4.9
Abralia multihamata	0.3	0.2	0.4
Unidentified cephalopods	1.8	0.5	4.4
Urochorda	0.003	0.04	0.4
Fritillaria pellucida	0.003	0.04	0.4
Unidentified parasite	0.1	0.9	3.6
Other thing	0.1	0.3	2.7
Empty			10.7

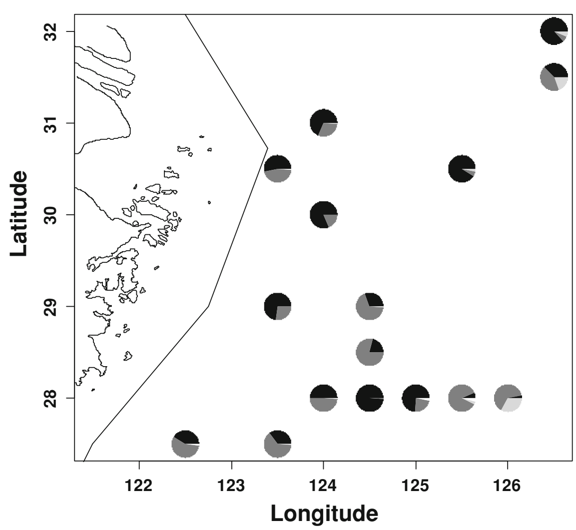

Fig. 6 The spatial distribution of diet weight composition for Pisces (*black*), Crustacea (*deep grey*), Cephalopods (*light grey*) and others (*white*)

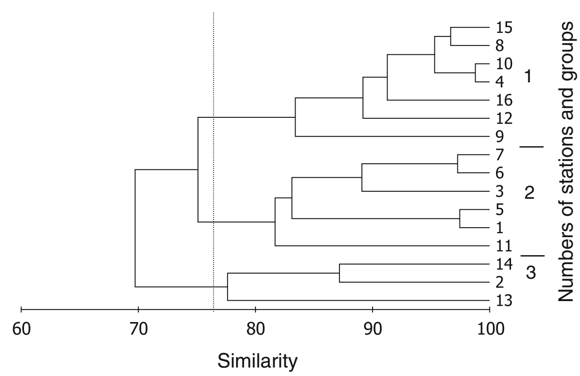

Fig. 7 Cluster analysis of diet composition

Discussion

Feeding habitat near the mouth of Yangtze estuary

The analysis of the distribution of hairtail feeding intensity revealed that there was an area in which hairtail were concentrated for feeding. This area was defined in 124°00′ E longitude and 31°00′ N latitude, and is part of the Yangtze River estuarine fishing grounds (Fig. 2). This area of high feeding intensity was also identified and confirmed by previous studies, which suggested that after finishing spawning migration hairtail would aggregate in the Yangtze River mouth for feeding, resulting in the formation of River mouth fishing ground (Deng & Zhao, 1991). The Yangtze River estuary was identified as one of the most important feeding grounds for hairtail with abundant food supplies for many fish species (Deng & Zhao, 1991; Chen et al., 1999).

The area around the Yangtze River estuary was influenced by three water masses: Yangtze River freshwater, Taiwan Strait warm water, and North Jiangsu coastal cold water (Gao & Wang, 2008). The Yangtze River carries rich sediment to the estuary from upstream, and the meeting of waters

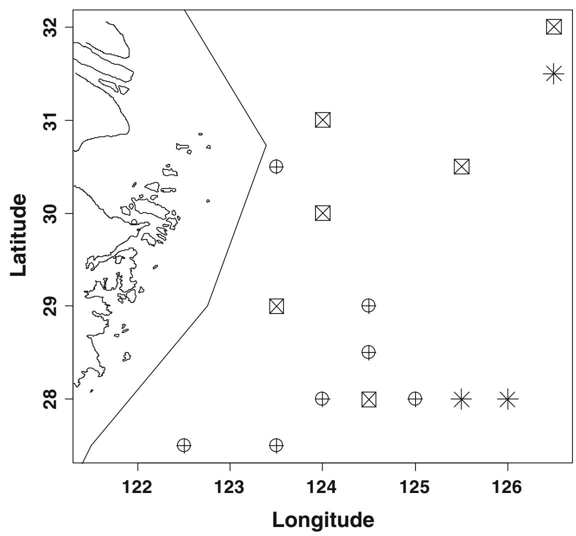

Fig. 8 The spatial distribution of the three groups defined in the cluster analysis (Fig. 7). "⊕"is for group 1, "⊠" for group 2, and "✳" for group 3

of the two different temperatures: Taiwan Strait warm water and North Jiangsu coastal cold water, brings diverse and dynamic environments suitable for many organisms. This results in abundant primary producers, and subsequently making this area a major fishing ground (Luo et al., 2008). Some surveys in autumn around the estuary reported that the dominant species included small yellow croaker, Japanese scad and Japanese jack mackerel (Li & Cheng, 2005; Li et al., 2006). All these species were the main preys for hairtail found in this study.

Characteristics of prey composition

The analysis of the hairtail prey composition during its feeding migration showed that fish was the most important component in hairtail diets, reaching 72.56% in weight. Of the fish species in the diets, the top one was juvenile hairtail, suggesting strong cannibalism by the hairtail. Studies in 1960s found that the major foods of hairtail were crustaceans such as euphausiacea (Chen & Zhu, 1984). The survey in 2002 found that the major foods were fish, but of which the juvenile hairtail did not appear in the diets in large quantity and most fish species were juvenile fishes of other species (Lin et al., 2006). In this study, fish were also found to be the most important diet, but with juvenile hairtail being most abundant. It seems that the increasing cannibalism occurred recently and that cannibalism is part of hairtail's life history process. The occurrence of cannibalism for fish is often associated with certain life history strategies (Amundsen, 1994; Baras, 1999; Takeyama et al., 2002). With the increased sizes, fish trophic level can be enhanced by having more choices on its preys (Persson & De Roos, 2006). For example, adult fish can eat their juvenile fish. It was found that the intensity of cannibalism of catfish tended to be high in a low population density environment (Baras et al., 1999; Stoner, 2004). We speculated that with the increase in fishing pressure, the ecosystem of the East China Sea had changed greatly, and many preys for hairtail had decreased in abundance or even disappeared (Jin & Tang, 1996; Xu & Jin, 2005). This resulted in an increase in the frequency of low

Table 3 The SIMPER analysis (Clarke and Warwick 2001) of prey compositions for the three groups classified in the cluster analysis (Fig. 7)

Groups	Average similarity	Species	Average abundance	Average similarity	Similarity/SD (similarity)	Contribution %	Cumulative %
1	89.91	Crustacea	2.81	41.15	8.20	45.76	45.76
		Pisces	1.84	38.44	20.85	42.75	88.52
		Other	0.04	10.33	1.49	11.48	100.00
2	85.34	Pisces	24.49	54.27	10.10	63.59	63.59
		Crustacea	5.12	27.50	4.20	32.22	95.81
		Cephalopods	0.53	3.57	0.48	4.19	100.00
3	80.81	Crustacea	1.76	37.86	14.33	46.85	46.85
		Cephalopods	0.52	23.19	3.55	28.70	75.55
		Pisces	0.55	19.76	10.32	24.45	100.00

population density environment, and subsequently leading to an increased intensity of cannibalism. This hypothesis needs to be tested in the future studies.

Distributional characteristics of prey composition

The cluster analysis suggests that sampling stations could be divided into three groups with different spatial distributions: one group was in the south of East China Sea far from the coast; one group was in the north of East China Sea near the coast; and the third group was in the open sea. Diet compositions differed among the groups. Individuals of the first group fed similar percentages of fish and crustacean with crustacea being slightly more than pisces. For the second group, pisces were most abundant, followed by crustacean species. For the third group crustacean species were most abundant in the diets, followed by cephalopods and pisces. Thus, different groups that were distributed in different areas had different diets. It is generally known that the location of fish determines the availability of preys, and subsequently their prey composition (Shaw & Jenkins, 1992; Floeter & Temming, 2003; Hinz et al., 2005). Thus, to explain the variations in prey compositions identified in this study, we need to identify what causes the spatial variability of these three groups of hairtail.

An interesting relationship between feeding intensities and gonad development was found in this study: the average feeding intensity of hairtail that were in stage III of gonad maturity was obviously higher than that of the fish in the other stages of gonad maturity. The Student *t* test suggests significant differences in the feeding intensity between maturity stages II and III. Other fish species were also found to aggregate in different areas based on their gonad maturity stages (Gonzalez-Gurriaran et al., 1998; Morais et al., 2003; Liu et al., 2007). We hypothesized that the hairtail of different gonad maturity stages might be aggregated in different areas, which resulted in differences in the feeding intensities. The analysis of the distribution of fish in different maturity stages (Fig. 5) is consistent with this hypothesis. Thus, we conclude that hairtail of different maturity stages had different spatial distributions, which resulted in differences in food availabilities, and subsequently different feeding intensities. The hairtail of stage II might come from two sources, one had just spawned this year, and the other just reached their first maturity and ready to spawn next year (Chen, 1997; Bancroft et al., 2002; Li et al., 2007). The fish of the first type had finished spawning and migrated to the feeding ground from spawning ground. These fish were unlikely to arrive at the feeding ground at the same time. Some of them might be still on their way to the feeding ground, and some had already arrived (Deng & Zhao, 1991). However, the fish of the second type were not from the spawning ground. This might explain why hairtail of stage II had the widest distribution (Fig. 5). After spawning, fish migrated to the feeding ground with gonad starting to develop again for the next spawning season. This might explain why the distribution of fish of stage III was more in northern areas (Fig. 1).

Environmental variables such as temperature influence not only the timing and duration of the fish spawning season, but also the abundance and distribution of their preys. The interactions among these factors are, however, complicated and difficult to be isolated. This study focuses on the relationships among the feeding, spawning, and spatial distribution of hairtail. Environmental factors such as temperature were considered as background which influences all life history processes and prey distributions considered in this study, and their impacts on a single life history process are not discussed in this study. Future studies need to evaluate how environmental drivers may intervene possible interactions between spatial distribution of hairtail and their preys in different life history stages.

Due to the high cost of survey and time-consuming sample process, the sampling process was not repeated in this study. This may lead to the question regarding the robustness of the outcome derived in this study. Thus, the results derived from this study should be treated as a working hypothesis to explain what were observed in the spatial variations in prey compositions of hairtail with different maturation stages. This working hypothesis will be tested in the future with data from repeating this sampling program. Although we used the hairtail as an example in this study, the hypothesis we developed in this study with respect to the relationships between feeding, spawning, and spatial distribution can also be applied to other fish species, leading to a better understanding of interactions of different fish life history processes.

In summary, we conclude that physiological differences, such as spawning in this study, resulted in different spatial distributions among the fish of different gonadal development stages. Such a difference in spatial distribution was likely to result in different habitats, which in turn resulted in different feeding intensities and different prey compositions.

Acknowledgments We would like to thank Prof. Siming Zheng and Prof. Guoliang Dai for their help in identifying some preys that were difficult to identify. Thanks are also due to all scientific staff and crew for their assistance in collecting data during the surveys. A special thank goes to Rongkang Zou and Lanyin Ling for their help in lab sample analyzing and data entry, respectively. This study was conducted under the auspices of the Key and Open Laboratory of Marine and Estuarine Fisheries of the Ministry of Agriculture of China (Open Fund: 1-04-02), National Science and Technology Support Plan (2007BAD43B01) and the Chinese Ministry of Agriculture Assessment of Marine Fisheries Resources Programme. We also would like to thank the anonymous reviewers and Associate Editor Bailey for helpful and constructive comments which greatly improved the initial manuscript.

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