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SPECIES COMPOSITION AND DISTRIBUTION OF THE DOMINANT FLYINGFISHES (EXOCOETIDAE) ASSOCIATED WITH THE KUROSHIO CURRENT, SOUTH CHINA SEA

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ABSTRACT. — Flyingfishes (Exocoetidae) are important to Taiwan from an ecological, cultural, and fishery aspect but little scientific information is available regarding the species composition and their distribution. This study documents the species composition of the flyingfishes in the Kuroshio Current off eastern Taiwan, in the South China Sea, the horizontal/vertical distribution of the dominant species and their relationships with major environmental factors. The study is based on a nation-wide in-port sampling programme, a fishery-independent at-sea survey program between 2008 and 2010, and a juvenile at-sea survey programme in 2011. A total of seven genera and 24 species of flyingfishes were collected in the region, including one new record. Six species were considered to be dominant: *Cypselurus poecilopterus*, *Cheilopogon unicolor*, *Ch. cyanopterus*, *Hirundichthys oxycephalus*, *Ch. atrisignis*, and *Parexocoetus brachypterus*. Discrepancies in the horizontal and vertical distribution among the dominant species were observed and discussed. Their distributions were found to be positively related to sea surface temperature and tide level but negatively related to the tidal range (difference of tide levels within one hour).

KEY WORDS. — Flyingfishes, Taiwan, Kuroshio Current, distribution, environmental factors

INTRODUCTION

Flyingfishes (Exocoetidae) are distributed in tropical and subtropical waters, including the Kuroshio Current which flows across the eastern coast of the Philippines and Taiwan and continues northeasterly past Japan where it merges with the easterly drift of the North Pacific Current. The surface waters of the Kuroshio are generally regarded as oligo-trophic and nitrogen-deficient (Chen et al., 2009). However, many economically important pelagic fish species are abundant in these waters such as the dolphinfish (*Coryphaena hippurus*) with annual catches of 9500 tons by Taiwanese fisheries. As mass consumers of zooplankton, flyingfishes are considered an important intermediary within the food web between plankton and predators (Gorelova, 1980; Zuyev & Nikol'skiy, 1981; Nesterov & Bazanov, 1986). Thus, they support dolphinfish stocks as one of the major sources of food (Oxenford & Hunte, 1999; Wu et al., 2006) and are important to the stability of the Kuroshio ecosystem.

Flyingfishes also form an important part of the Tao (Yami) culture (Chen, 2011; Wikipedia contributors, 2011) in Lan-Yu [=Island, off the southeastern coast Taiwan] as the island's important festivals are based on the arrival and departure of the migratory flyingfishes. Artisanal fisherfolks use drive-in net and gillnet fisheries in southeastern Taiwan, and setnet fishery along the southern and eastern coasts. The catches are used for local consumption and as bait for fishing. Wild flyingfish stocks are also a valuable resource to the flyingfish egg fishery, in northern and northeastern Taiwan, mostly for export to Japanese markets. Considering their ecological, economic and cultural importance, the over 60% decline in the catches of flyingfishes in 2006–2007 (Fisheries Agency, 1999–2009) has caused serious concerns to fishery managers on the fish stock status and consequent criticisms from conservation groups and the Lan-Yu aboriginals on the overfishing and inadequate management of the resource (Buchan, 2007; Hung, 2007). However, fisherfolks and fishery managers only refer to flyingfishes as a single taxon that migrates from the south of Taiwan to the north of Taiwan for spawning (Hung, 2008). Due to the lack of information on species composition of the catch and their spatial distribution, it is thus difficult to ascertain the impact per species in the different locations.

Distribution studies of new and existing species of flyingfishes are being undertaken worldwide (Parin & Belyanina, 1998; Parin & Shakhovskoy, 2000; Souissi et al., 2005; Kharin et al., 2007). Fifty two species of flyingfishes from eight genera are currently recognised (Nelson, 2006). Based on surveys for all commercial fishes from 1990 to 1996, 26 species of flyingfishes from seven genera were reported in the waters off Taiwan (Shao, 2009, web published). Except for the aforementioned effort, and that of Chen (1987) on the early life history of the flyingfishes from 1961 to1984, there is little scientific information on this group of fishes in the waters off Taiwan.

This study conducted three sampling programmes between 2008 and 2011 on the flyingfishes in the Kuroshio Current off Taiwan with the following aims; (1) a nation-wide sampling programme in the fishing ports along the eastern and southern coasts of Taiwan, (2) a fishery-independent at-sea survey programme off eastern Taiwan, and (3) a juvenile fish at-sea survey programme in northern waters off Taiwan to document a) the species composition of flyingfishes in that region, and b) the distribution of dominant species based on spatial and environmental factors.

MATERIAL AND METHODS

Sampling targets. — In Taiwan the adult flyingfish resource is mainly utilised by three fisheries: drive-in net, setnet, and gillnet fisheries. The sampling programmes (in-port sampling and at-sea survey) covered two drive-in net (D), four setnet (S), and three gillnet (G) fisheries in the Kuroshio Current off these locations (refer to Fig. 1); Ping-Tung [=County, PT], Lan-Yu [=Island, LY, also known as Orchid Island], Lu-Dao [=Island, LD, also known as Green Island or Lyudao], Tai-Tung [=County, TT], Hua-Lien [=County, HL] and I-Lan [=County, IL], for different time periods. A three-character code composed of a two-character abbreviated location codes and one-character gear code was used to denote the sampling location and the type of gear used.

Port sampling programme. — The major drive-in net fishery is located at near-shore waters (< 4 km from the coastline) off Ping-Tung (PTD, Fig. 1, based in Ho-Bihu town) in the south and southeast coast of Taiwan. Fisherfolks at this location utilise nets with mesh sizes of 0.9 cm. This site lands the highest catches for flyingfishes; approximately 148 mt, or 1.1 million fishes in Mar. to Jun.2009, representing about half of the overall national catches in Taiwan for that fishing season. Catches by species for the seasons of 2008, 2009, and 2010 were obtained from two vessels. The number of individual fishes was obtained by dividing the total weight (in kg) by the average weight of the species caught. Species composition was then estimated from the catch data and verified through monthly random sampling in port. Species that were misidentified by fishermen were also adjusted during in-port sampling sessions. An additional sampling of a small-scale drive-in net fishing vessel in Lan-Yu using a 1.3-cm mesh net was conducted in May 2009.

Sampling sessions of near-shore setnet fishing ports (the mesh size is about 3 cm) were conducted in Ping-Tung (PTS) and I-Lan (ILS, included two setnets) between Apr.2008 and Jun.2010; in Tai-Tung (TTS) between Apr.2008 and Jun.2009; and in Hua-Lien (HLS) between Apr.2009 and May 2010. Most of the sampling sessions were carried out during the fishing seasons between the months of March and June for all years and in all areas. No visits were made during the typhoon seasons between July and October of each year. In general, one visit during off-seasons or two visits during in-seasons were made each month to each setnet location (except for Tai-Tung setnet). In general, 30 fish per visit (or all fish if the catch was less than 30 during the off-season) were collected for measurement (fork length to 1 mm) and species and sex identification.

At-sea sampling programme. — An at-sea survey using gillnet was conducted in Lu-Dao (LDG, Fig. 1) on a monthly basis from May 2008 to May 2010. Similar surveys were also made in Hua-Lien (HLG) from Apr.2009 to Jun.2010 and in

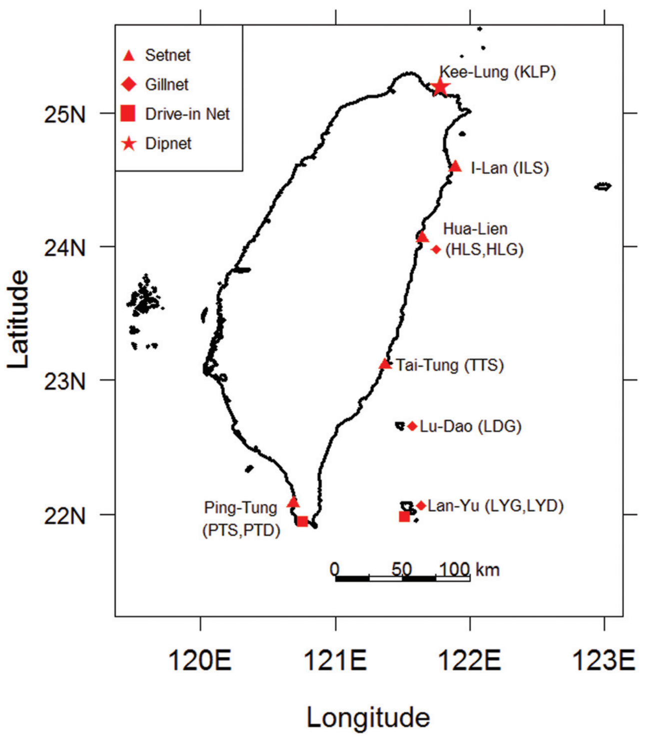

Fig. 1. The six sampling areas and three gear types for the collection of flyingfishes associated with the Kuroshio Current off Taiwan. Codes in parentheses indicate the sampling areas for the first two abbreviated characters, and the gear type in the last character by drive-in net (D), setnet (S), gillnet (G), and dipnet (P).

Lan-Yu (LYG) from Apr. to May 2010 (a pilot programme). Surveys were performed during both fishing and non-fishing seasons to investigate annual patterns in species composition. Three types of gillnets were used in Lu-Dao and Hua-Lien to collect as many different sized fish and species as possible: large (regularly deployed by fisherfolks), medium, and small mesh-sized net with stretched mesh sizes of 5.6 cm, 4 cm, and 2.8 cm, and net lengths of 65 m, 70 m, and 120 m, respectively, and with all nets having a net depth of 3.6 m. In each operation, one large-sized, one medium-sized, and two small-sized mesh nets were used, except for the short-term surveys in Lan-Yu in which only one large net was used. Fifty fish (or all fish if the catch was less than 50) were sampled and brought back to the laboratory for length measurement (fork length, to 1 mm) and species and sex identification.

The survey area in Hua-Lien was 10–15 km away from the Hua-Lien setnet and the survey area in Lan-Yu (over 30 km away off the coast of Taiwan) was in the coastal area off its southwestern coastline. The survey area in Lu-Dao (over 60 km off the coast of Taiwan) was spread out, covering the major fishing grounds off the north and south coasts. For the sake of convenience, these areas were termed as "offshore areas", compared to the "near-shore areas" of the setnet fishing grounds along Taiwan's coastline and the drive-in net fishing grounds off Ping-Tung.

To answer objective 2b, five environmental data were collected during the surveys between May 2008 and Jul.2009 in Lu-Dao and between Apr. and Jul.2009 off Hua-Lien: (1) sea surface temperature (SST, to 0.1°C) at 1 m depth was collected using a Multi-Probe CTD system (YSI model 556); (2) wind speed, which was recorded according to the Beaufort Wind Scale; (3) current speed (km/h) was estimated from the change in time of the central GPS positions (central point of start and end positions) of the deployment and retrieval of the gillnets; (4) tide levels (cm) were obtained from the Marine Meteorology Center of the Central Weather Bureau at the time the retrieval operations started (http://www.cwb.gov.tw/eng/index.htm). To investigate observations of relationship between variation in tidal levels and distribution of the flyingfishes; (5) tidal range was calculated from the difference between in tidal height from when the operations started and the height one hour later. To investigate if there exists species-specific preference for different depths, the net was defined into three vertical zones: upper (0–1.2 m), middle (1.2–2.4 m) and bottom (2.4–3.6 m) for the surveys off Lu-Dao from May 2008 to Jul.2009. Catches were subsequently recorded at the vertical depth.

Juvenile sampling programme. — An at-sea survey for juvenile fish using dipnet (P) was conducted around Kee-Lung Island [=Island] located in north of Kee-Lung [=county, KL] during Jul. to Oct.2011 (Fig. 1). This place is in the major fishing ground of flyingfish egg fishery. The collection of juvenile fish was conducted in the night during 2100–0000 hours with 4000 watt aqua-lamp in the water for one hour, twice a month. Since this sampling was only for four months period in a specific area and only for juvenile fish, the result was only for documenting the species that occurred around Taiwan and was not used in the discussion of the distribution of dominant species.

Species identification. — Flyingfishes are only differentiated into two broad categories of 'large' and 'small' in fisheries catch records, with no species determination. Collected fishes were identified using keys from two main sources; Parin (1999) for adult fish, and Chen (1987) for juvenile fish. Aizawa (2002) was also referenced, especially for the species that were reported present in Japan.

Data analyses. — Catch data from different fisheries sites are not directly comparable due to differences in selectivity among the different sampling gear employed. Using the above standardised sampling method for each fishery, the total number of fish samples and the species composition for each location/gear strata were calculated separately in order to identify the dominant flyingfish species in the Kuroshio Current off Taiwan and to study their horizontal distribution.

For studies of vertical distribution and relationship with environmental factors, a density index (or catch rate) for the at-sea surveys using gillnets was defined as $C/(T\times A)$, where C is the catch (number of fishes, including those immediately released), T is the time (min) that the nets were in the water for fishing (= the difference in time between the end of deployment and the start of retrieval), and A is the total area (km^2) of the nets in the water (= netting length × width). As currents may cause nets to drift, the actual net length at sea was estimated from the distance between start and end positions of deployment instead of the summation of all the net lengths. The start and end GPS positions, as well as the time, for both the deployment and retrieval were recorded for this purpose.

The Kruskal-Wallis and Duncan's multiple comparison tests (Siegel & Castellan, 1988) were used to elucidate the relationships between the density index and two factors: vertical catch layer and mesh size. The Principle Components Analysis (PCA) (Stevens, 1996) was used to explore the possible preference of the dominant species for the five environmental factors noted. A generalised linear model (GLM) was then applied to study the relationship of density distribution with the environmental factors. Since the quantity of the data from at-sea surveys was not sufficient to develop a relationship by species, a general one was developed for the major dominant species under the condition that the PCA result does not show a species preference. Before applying the GLM, a commonly used logarithmical transformation was applied to the density index to stabilise the variances and normalise the residuals (Spencer & Collie, 1997; Chang et al., 2011). The transformation also took into account the fact that the relationships between the density indices and environmental variables are not linear (Khohiattiwong et al., 2000). The environmental data were binned to reduce noise in the analysis, i.e., SST by 0.5°C bins, tide level and one-hour tidal range by 5 cm bins, current speed by 0.5 km/hour, and wind speed by Beaufort scale. The statistical analyses were performed using Statistica™ (StatSoft USA, version 8) and the R statistical system (version 2.11.1).

The GLM analysis is to find the variables that have statistically significant effect on the log-transformed index. However, it is conceptually difficult to interpret the change of density index in logarithm scale, while the original catch data is associated with the number of sampling trips and thus should not be interpreted alone. Therefore, to provide the correlations of density with significant environmental variables, a monthly catch proportion per trip (i.e., proportion of a month's catch to the overall catch of the sampling period adjusted by number of trips per month) was calculated from survey data for comparison with the monthly change of statistical significant environmental factors.

RESULTS

Species and size composition. — A total of 4918 fish were sampled by the two main sampling programmes (in-port sampling and at-sea survey), comprising seven genera and 21 species. The third programme (juvenile fish survey) collected 239 fish, comprising six genera and 11 species. Altogether there were seven genera and 24 species found in the Kuroshio Current off Taiwan. The name of the species in the samples and the species composition by location/gear strata are shown in Table 1. Six of the 24 species (bold-face scientific name in Table 1) contributed to species compositions higher than 10% each in one of the location/gear stratum and were marked as 'the dominant species' in this region (excluded the sampling result from juvenile fish surveys). The six dominant species in order of dominance were: *Cypselurus poecilopterus*, *Cheilopogon unicolor*, *Ch. cyanopterus*, *Hirundichthys oxycephalus*, *Ch. atrisignis*, and *Parexocoetus brachypterus*.

Fig. 2 shows the size range of the six dominant species. Majority of *Ch. unicolor*, *Ch. cyanopterus*, and *Ch. atrisignis* were larger than 25 cm with one clear single size mode, while the other three were shorter (Fig. 2). This suggests that the major species in the large flyingfish category are *Ch. unicolor*, *Ch. cyanopterus*, and *Ch. atrisignis* (25–33 cm), and the major species in the small category are *Cy. poecilopterus*, *H. oxycephalus*, and *P. brachypterus* (10–23 cm). For all the dominant species, the females were larger than the males (Fig. 3).

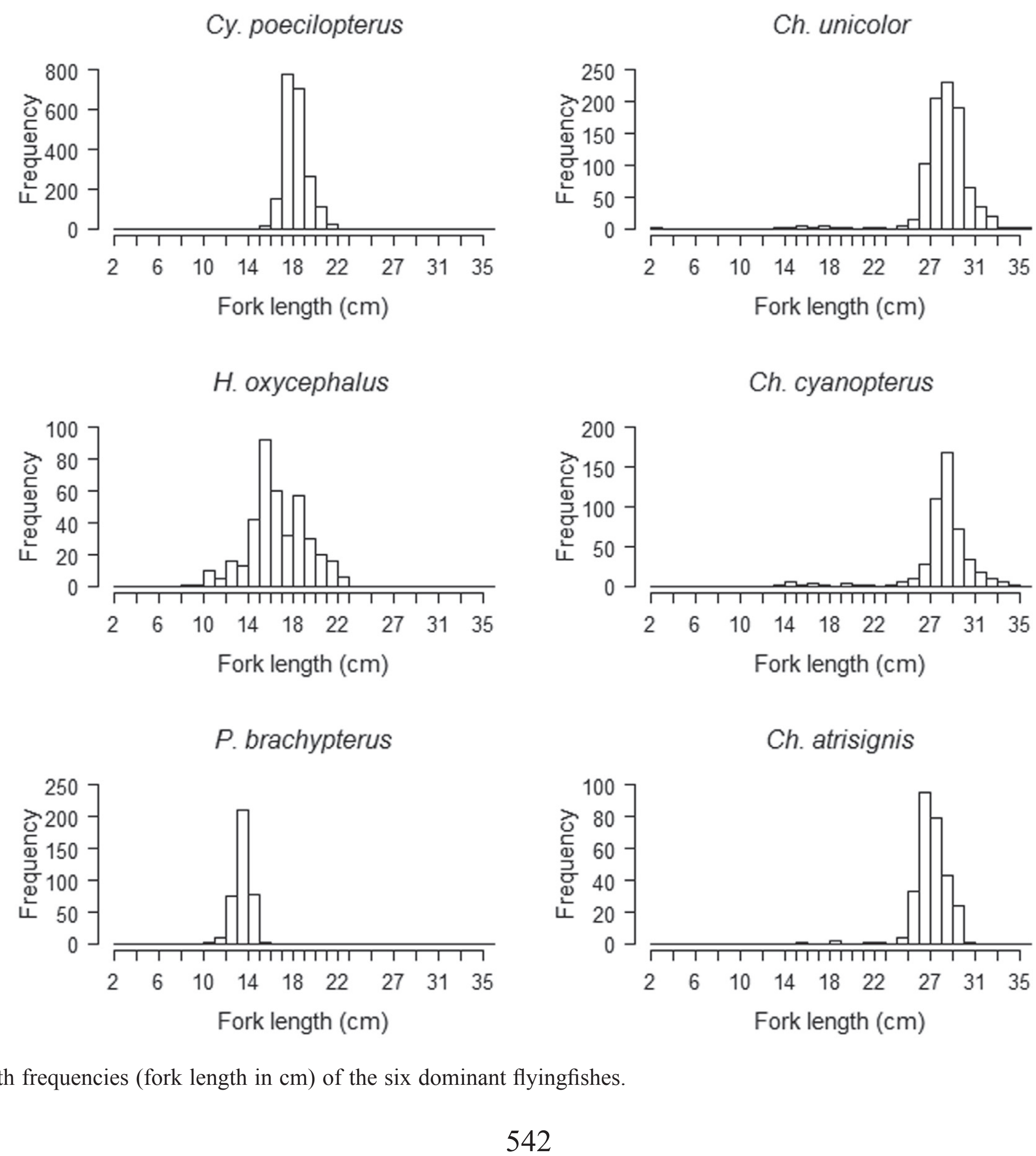

Fig. 2. Length frequencies (fork length in cm) of the six dominant flyingfishes.

Table 1. Flyingfish species, and species composition by location and gear type (three-character code), collected from the Kuroshio Current off Taiwan by in-port sampling and at-sea survey programmes between Apr.2008 and Jun.2010, and by juvenile surveys during Jul–Oct.2011. Scientific names for the dominant species are in bold face.

Species	Location & gear type code[V]										
	PTS	**PTD**	**LYD**	**LYG**	**LDG**	**TTS**	**HLS**	**HLG**	**ILS**	**KLP***	**Total[§]**
Cheilopogon abei					2%			1%			21
Cheilopogon agoo						8%			6%	0%	83
Cheilopogon arcticeps				1%	1%			2%	1%		33
Cheilopogon atrisignis		**56%**	**62%**	**6%**							**284**
Cheilopogon cyanopterus	**0%**	**15%**	**<1%**	**0%**	**5%**	**28%**	**10%**	**4%**	**23%**		**508**
Cheilopogon cf *furcatus*					1%			0%	0%		10
Cheilopogon cf *heterurus doederleini*										1%	
Cheilopogon spilonotopterus					0%						3
Cheilopogon spilopterus				1%							2
Cheilopogon unicolor	**17%**	**17%**	**29%**	**31%**	**22%**	**25%**	**1%**	**7%**	**21%**	**1%**	**875**
Cypselurus angusticeps					0%						3
Cypselurus hiraii										3%	
Cypselurus naresii	0%			1%	3%			2%			35
Cypselurus poecilopterus	**76%**	**56%**		**5%**	**8%**	**37%**	**88%**	**25%**	**44%**	**14%**	**2187**
Exocoetus monocirrhus					1%					0%	4
Exocoetus volitans					9%			1%	0%	2%	75
Hirundichthys oxycephalus	**0%**	**1%**	**10%**		**35%**			**10%**	**4%**	**4%**	**364**
Hirundichthys rondeletii					0%						2
Hirundichthys speculiger				0%	3%					0%	21
Oxyporhamphus convexus convexus					0%			0%	0%		5
Oxyporhamphus micropterus micropterus					2%						13
Parexocoetus brachypterus	**7%**	**12%**			**2%**	**1%**		**48%**		**2%**	**380**
Parexocoetus mento										46%	
Prognichthys brevipinnis					1%	1%		0%		25%	10
Number of fish sample:	1417	#	21500[#]	379	894	208	431	482	1107	239*	4918
Number of species:	6	6	$	8	19	6	3	12	9	11	24

[V] The first two characters of the code denotes the location (from the south to the north of Taiwan, PT for Ping-Tung, LY for Lan-Yu, LD for Lu-Dao, TT for Tai-Tung, HL for Hua-Lien, IL for I-Lan, and KL for Kee-Lung) and the third character denotes the gear type (S for setnet, D for drive-in net, G for gillnet, and P for dipnet).

* The fish caught by KLP are all juveniles from a short period sampling. The number of fish was not included in the totals of the last column.

[#] Species composition was obtained from fishers and partly verified by in-port samplers for PTD and was estimated by samplers for LYD. The fish samples were not included in the totals of the last two columns.

[$] Some proportion of small flyingfishes was released to sea for LYD and so its number of species is unknown.

[§] Total number of fish sampled, excluding those from PTD, LYD, and KLP.

Horizontal and vertical distributions. — The *Cy. poecilopterus* were the most numerous in most of the sampling location/gear strata (Table 1 and Fig. 4), and occurred mainly in near-shore setnets, and were seldom found in the offshore gillnet surveys areas of Lu-Dao and Lan-Yu. The *Ch. unicolor* flyingfish was the second most dominant species in the region, and the most important dominant species to the local fisheries in terms of biomass due to their abundance and large sizes (Fig. 2). This species was found widely distributed in the Kuroshio Current except in the Hua-Lien area. The *Ch. cyanopterus* flyingfish which has a similar size to the *Ch. unicolor* flyingfish (Fig. 2), was the third most dominant species. It occurred mainly in the catch of drive-in nets and setnets located in the near-shore of eastern Taiwan. Like the *Cy. poecilopterus*, it was seldom found in offshore waters off the coast of Taiwan.

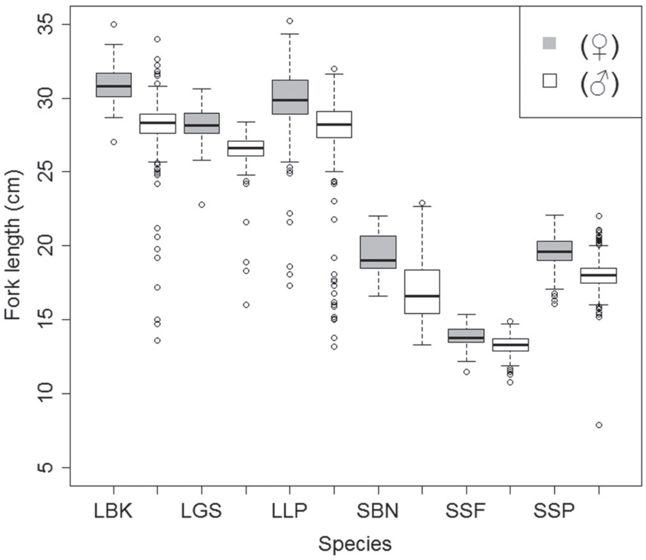

Fig. 3. Boxplots for fork lengths (cm) by sex (grey for female and white for male) for the six dominant species: *Ch. cyanopterus* (LBK), *Ch. atrisignis* (LGS), *Ch. unicolor* (LLP), *H. oxycephalus* (SBN), *P. brachypterus* (SSF) and *Cy. poecilopterus* (SSP).

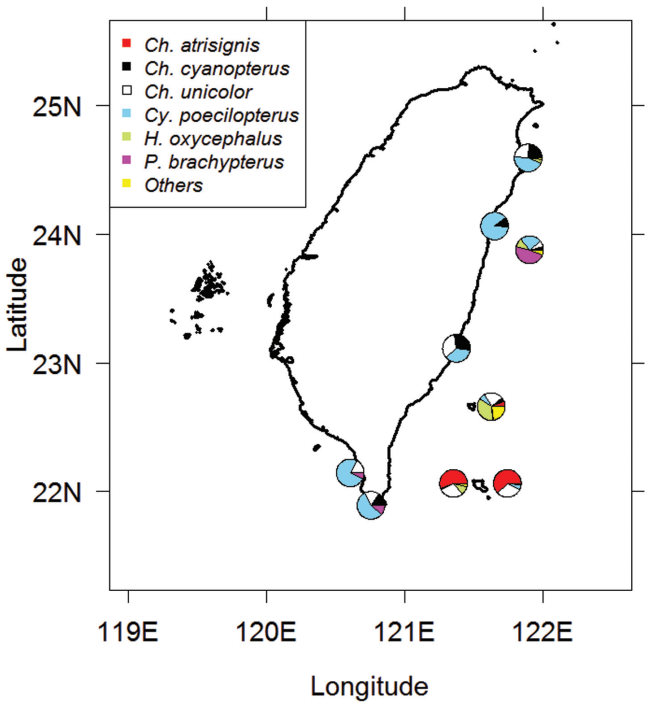

Fig. 4. Flyingfish compositions of the six dominant species by sampling area, collected by in-port sampling and at-sea survey programmes between Apr.2008 and Jun.2010. (Source: Table 1).

The other three dominant species distributed more regionally (refer to Table 1 and Fig. 4): *H. oxycephalus* occurred mainly in Lu-Dao and Hua-Lien gillnets surveys in the offshore waters of Taiwan; *Ch. atrisignis* was found only in the waters off the islands of Lu-Dao and Lan-Yu in any high percentage; and. *P. brachypterus* were well represented in the north Hua-Lien gillnet survey and by a small percentage in the south Ping-Tung drive-in net and setnet fisheries.

The vertical distribution study was based on the data from 151 deployments of gillnet at-sea surveys in Lu-Dao. The monthly density index by vertical catch layer (upper: 0–1.2 m, middle: 1.2–2.4 m, and bottom: 2.4–3.6 m), and mesh size (large: 5.6 cm, medium: 4 cm, and small: 2.8 cm) are shown in Fig. 5; and the relevant statistical tests are tabulated in Table 2. The results suggest that the density was significantly different among the three depth layers ($p = 0.029$). Densities in the upper and middle layers were significantly higher than those in the bottom layer. The vertical distribution of all the dominant species generally covered the three layers, although different species is noted having a different preferred depth layer: *Ch. unicolor*, *Ch. cyanopterus*, *H. oxycephalus* were

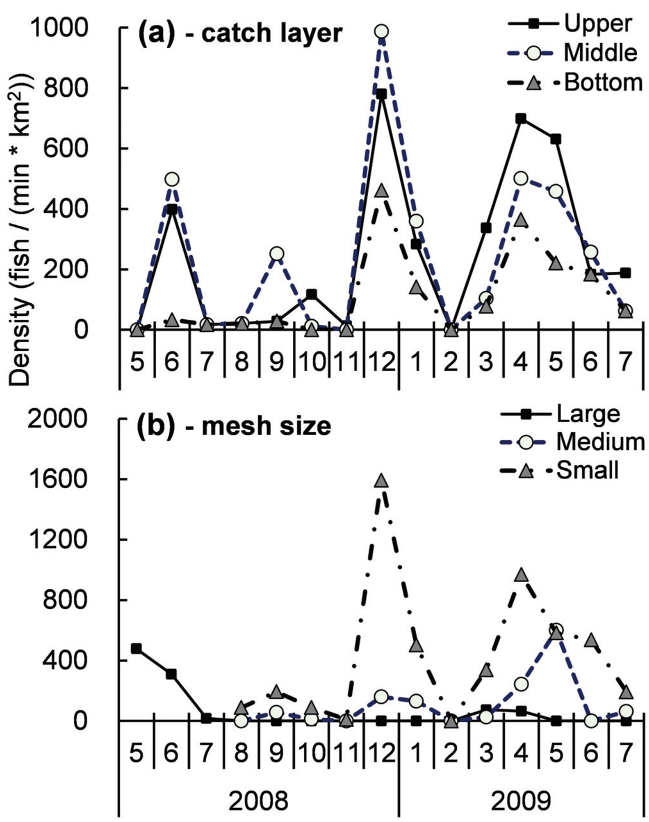

Fig. 5. Monthly flyingfish densities by (a) vertical catch layer (upper: 0–1.2 m, middle: 1.2–2.4 m, and bottom: 2.4–3.6 m), and (b) mesh size of net (5.6 cm, 4 cm, and 2.8 cm for large, medium, and small mesh nets, respectively).

Table 2. Statistical tests of three characteristics on the density index of flyingfish in the surveys: vertical catch depth layer of the net (0–1.2 m, 1.3–2.4 m, and 2.5–3.6 m for upper, middle, and bottom layers, respectively) and mesh size of net (5.6 cm, 4 cm, and 2.8 cm for large, medium, and small mesh nets, respectively). Numbers listed under characteristics are the density index in fish / (min × km^2).

Test item	Characteristics Density index*			p
Depth layer	Upper 266.54^A	Middle 259.06^A	Bottom 112.81^B	0.0290
Mesh size	Large 26.71^B	Medium 144.96^B	Small 426.7^A	<0.0001

* Values indicated with different alphabets have a statistically significant difference.

Table 3. Percentage distribution of flyingfishes by vertical layers of gillnet in the surveys of Lu-Dao for the dominant species in the region.

	Ch. unicolor	*Ch. cyanopterus*	*H. oxycephalus*	*Ch. atrisignis*	*P. brachypterus*	*Cy. poecilopterus*
Upper layer (~1.2 m)	45%	50%	48%	75%	69%	15%
Middle layer (~2.4 m)	47%	46%	41%	25%	17%	41%
Bottom layer (~3.6 m)	8%	4%	11%	0%	14%	44%

more widely distributed and were mostly (about 90%) found in the upper and middle layers (roughly up to 2.4 m depth, Table 3), while the *Ch. atrisignis* was solely (100%) found in these two layers. Most *P. brachypterus* (69%) were caught in the upper layer (above 1.2 m depth). On the other hand, the *Cy. poecilopterus* seemed to be distributed deeper down, and were mainly (85%) caught in the middle and bottom layers (below 1.2 m depth).

Fig. 5 also provides the temporal distribution of the dominant species. Two major seasons can be observed: March to June and December to January. Although not shown in Fig. 5, all six dominant species showed high density in the first season, but only *H. oxycephalus,* was abundant in the second season.

Dominant species distribution in relation to environmental factors. — This analysis was based on the survey data in Lu-Dao and Hua-Lien. Three different mesh sizes were used to maximise catches of different-sized fishes, therefore the effect of different mesh sizes on the density and distribution were tested. The result is shown in Table 2. Altogether 182 gillnet survey deployments were made, including 151 sets in Lu-Dao and 31 sets in Hua-Lien. Table 2 suggested that the density indices were significantly different by mesh size ($p < 0.0001$) (based on Kruskal-Wallis test) and that the index from the small mesh nets was significantly higher than that from the medium and large mesh nets (based on Duncan's multiple comparison test). Small mesh nets retained 76% of the total fish and therefore the data of this size net were considered to be more dependable than that of the other two mesh-sizes for the following analysis.

Among the six dominant species, *Ch. atrisignis* was not present in the Hua-Lien waters, and *P. brachypterus* was found in the Lu-Dao waters only in very low numbers (Table 1). Therefore, for the following environmental relationship analyses based on the survey data, these two species were excluded.

The resultant PCA analysis of the five environmental factors (wind scale, SST, tide level, tidal range, and current speed) associated with the density of the four major dominant species caught by small mesh-size net is shown in Fig. 6. The first two factors (principle components) with eigenvalues exceeding 1.0 explained 57% of the total variance. Factor 1 comprised wind speed, current speed and tidal range as variables (motile featured variables, i.e., changing within a unit of time); and the second component had high loadings with the tide level and SST variables (static state variables).

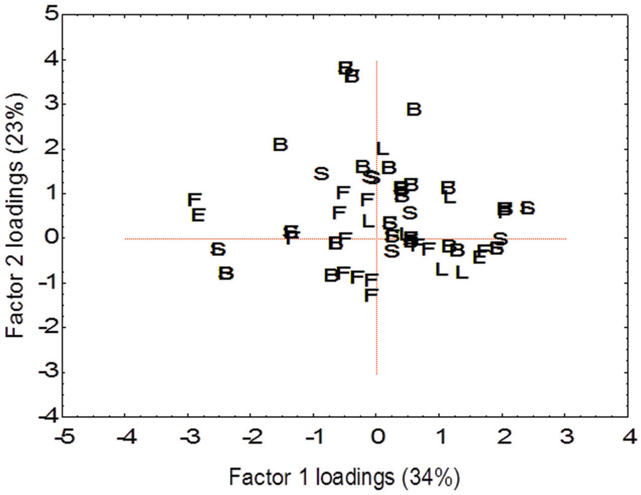

Fig. 6. PCA Factors 1 and 2 projection loadings for environmental factors and dominant species. Labels inside the plot indicates the four dominant species (B: *Ch. cyanopterus*, L: *Ch. unicolor*, S: *Cy. poecilopterus*, and F: *H. oxycephalus*). Each label represents one fish, and different fish of the same species caught in the same environmental conditions may overlap.

No clearly-separate clustering among species can be observed from Fig. 6, suggesting that the four dominant species do not have species specific environmental preferences.

A GLM analysis was performed on the logarithmically transformed density data to derive the general environmental factors affecting the distribution of the four dominant species. The residual distribution (not shown here) conformed well to the log-normal assumption. Table 4 shows the analysis of variance (ANOVA) table, and the result suggests that the distributions of the major dominant species were significantly related to SST ($p < 0.0001$), one-hour tidal range ($p = 0.0004$), and tide level ($p = 0.0100$).

The per trip catch proportion plot (Fig. 7) indicates that there are actually two modes in time range, the first mode from March to June and the second one from December to January. This second mode was noted in Lu-Dao, and almost the entire catch was *H. oxycephalus*. Excluding this second mode which had only one major species, in general, the catch proportion per trip of the four dominant species was positively associated with SST. This finding supports the conclusion from the GLM analysis. The catch proportion was also affected or offset by the other two significant variables, i.e., in the months with tide levels outside the range of –20 to +40 cm and tidal ranges outside the range of ±10 cm seem to have a lower catch proportion per trip even though the SST is high (for example June to August in Fig. 7). The survey data reflected similar phenomenon that the catch rate was low when the tide level or tidal range was too small or too large.

Table 4. Analysis of variances table for the GLM analyses of logarithmically transformed CPUE of the four dominant flyingfish species against the five environmental factors. (Asterisks indicate statistical significance: ** for $p < 0.01$, and *** for $p < 0.001$.)

Factor	**SS**	**F**	**p**
Wind scale	0.981	1.502	0.2234
SST	355.053	543.795	0.0000***
Tide level	8.637	13.228	0.0004***
Tidal range	4.500	6.893	0.0100**
Current speed	0.406	0.622	0.4322
Residuals	63.333		
R^2	0.970		

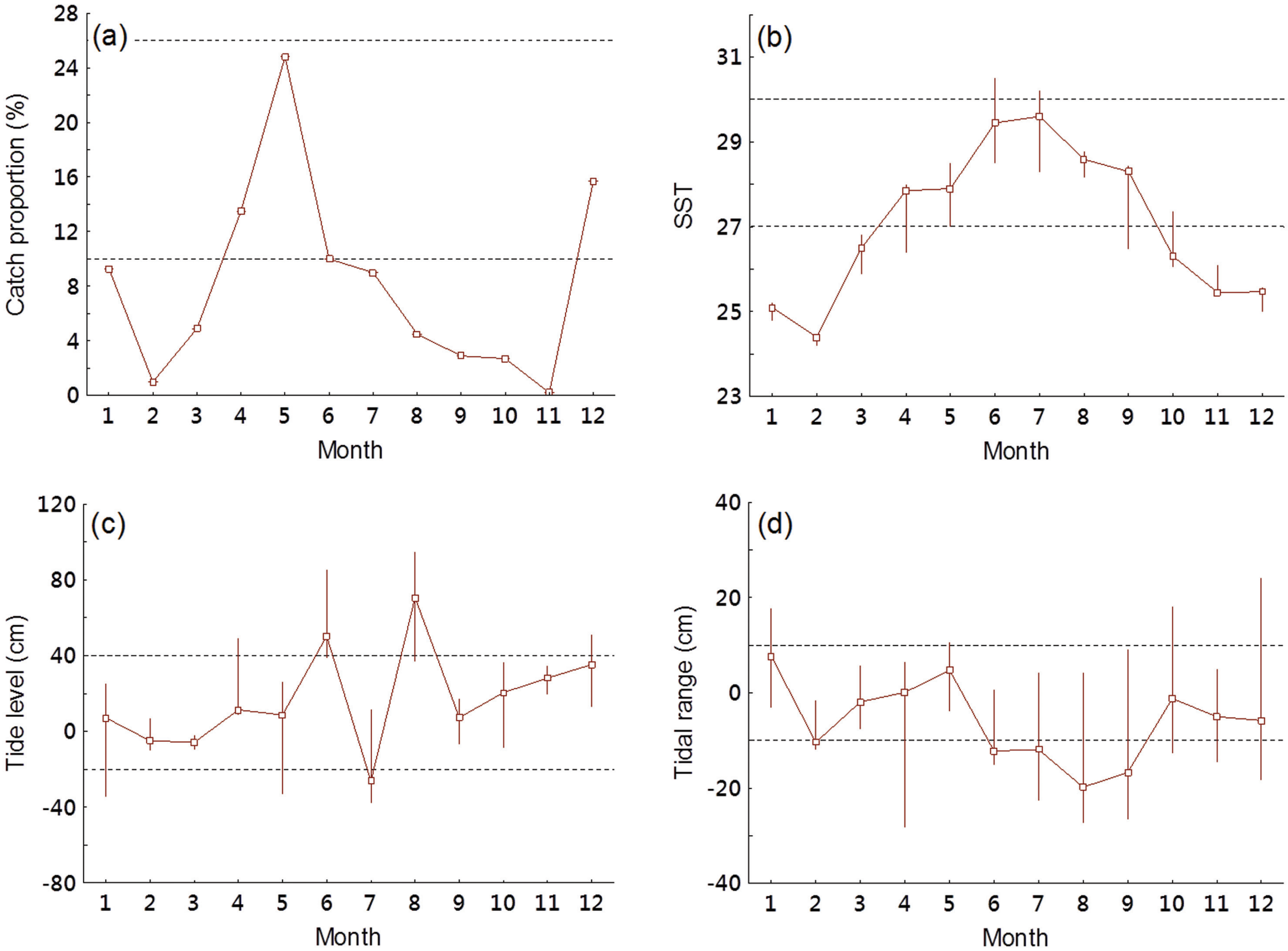

Fig. 7. Monthly median (square dot) with 25th and 75th quartiles (vertical line) for (a) flyingfishes catch proportion (proportion of catch, adjusted by number of trips in the month, to the overall catches of the sampling year), (b) SST (°C), (c) tide level (cm), and (d) tidal range (cm). Tidal range in the plot is the difference of tide level within one hour. Dashed lines indicate roughly the area with high catch proportion (10–26%).

DISCUSSION

Species composition. — Seven genera and 24 species of flyingfishes were documented in the Kuroshio Current off the east coast of Taiwan (Table 1), with six dominant in catches that are important to fisheries in these areas: *Cy. poecilopterus*, *Ch. unicolor*, *Ch. cyanopterus*, *H. oxycephalus*, *Ch. atrisignis*, and *P. brachypterus*. Since Shao (2009) provided the first list of flyingfishes (seven genera and 26 species, referred as the Shao's list) in Taiwan based on surveys 15 years ago, it might be valuable to compare the collections of this study with Shao's list. Here the *Oxyporhamphus convexus convexus* and *O. micropterus micropterus* were classified as flyingfishes (Exocoetidae) according to Dasilao et al. (1997) and Aizawa (2002), although they are excluded from Exocoetidae in Parin (1999), for comparison with Shao's list which also includes these two species.

The present study collected flyingfishes of the same seven genera in Shao's list but not all of the same species: 21 species of this study are also present in Shao's list but three species are here reported as new records. Five species present in Shao's list (*Ch. katoptron*, *Ch. pinnatibarbatus pinnatibarbatus*, *Ch. suttoni*, *Cy. oligolepis*, and *Cy. starksi*) were classified as rare and were not encountered in this study. One possible reason is due to the different spatiotemporal range (the previous work covered additional samplings from the west coast of Taiwan and lasted longer for seven years).

Two (*Ch. heterurus doederleini* and *Cy. hiraii*) of the three species which are new records were collected from juvenile sampling in north of Taiwan, and no adult fishes were thus caught. These two species were reported in Aizawa (2002) to be present in the waters between Japan and Taiwan. The other new observed species is close to *Ch. furcatus* according to Parin (1999) but without the clear pale oblique cross band in the grey pectoral fin as seen in Fig. 1 of Ben Souissi et al. (2005). According to Aizawa (2002), this species is most likely to be *Cy. antoncichi*. This species is provisionally recorded as *Ch. furcatus* in our study.

Horizontal and vertical distributions. — All the dominant species, except *Ch. atrisignis*, were observed throughout the entire eastern coast of Taiwan although specific distributions differed. Lewallen et al. (2011) has grouped flyingfishes into two categories in terms of habitat states: a) 'mero-epipelagic species' that use coastal (continental shelf) waters during some period of their lives, and b) 'holo-epipelagic species' that complete all their life stages in the open ocean (off the continental shelf). Based on these classifications, all six dominant species are classified as mero-epipelagic species in general but with some species-specific exceptions. The followings provide discussions on the horizontal distribution of the six dominant species.

Three species; *Ch. unicolor*, *Ch. cyanopterus*, and *P. brachypterus* were observed in both near-shore and offshore waters (Fig. 4), as per the above classification. However, *Ch. cyanopterus* occurred more in the near-shore waters (Fig. 4) and the *P. brachypterus* occurred more in offshore waters (composed 48% of the catch from HLG, Table 1). Furthermore, *Ch. atrisignis* was found only in offshore waters in this study (Fig. 4), thus contradicting reports of this species occurring in both pelagic open ocean and neritic surface waters (Parin, 1999). This study however, covered only the spawning period and may not be indicative of its distribution throughout the various life stages.

The most abundant species of this study, *Cy. poecilopterus*, (2187 fish of the total sampled 4918 fish) was found mostly in near-shore areas by the setnets and drive-in nets (> 15%, Table 1, Fig. 4). The composition was low in offshore surveys in Lan-Yu and Lu-Dao (< 10%) but, contradictorily, was high in the offshore surveys off Hua-Lien (25%, Table 1) and Kee-Lung (14%). A hatching experiment in 2009 showed that the eggs that support the flyingfish-egg fishery in northeastern offshore waters were laid mostly by the *H. oxycephalus*; with a small percentage contribution by *Cy. poecilopterus* (Chang et al., unpublished data). The female average gonadosomatic index (GSI) of *Cy. poecilopterus* during the fishing season (March to June) was 6.90–9.38 (± 2.92–4.69) in south of Hua-Lien (including) and 3.87 (± 3.18) in north of Hua-Lien. This indicates that this species was spawning in north of Hua-Lien. These observations suggest that the occurrence of *Cy. poecilopterus* in the offshore waters north off Hua-Lien is likely associated with spawning activities.

The last dominant flyingfish species, *H. oxycephalus*, was observed mostly in offshore waters such as LYD, LDG, and HLG (Table 1 and Fig. 4), except for LYG where the gillnet surveys used large mesh nets only. An additional at-sea observation onboard two flyingfish-egg fishing boats off the northeastern Taiwan noted high abundance of *H. oxycephalus* around the straw mats (fish aggregating device and spawning substrata), suggesting that this species was also abundant in the offshore area of northeastern Taiwan. This species should thus be considered a holo-epipelagic species, despite differing accounts that these species occur in near-shore and neritic surface waters (Parin, 1999).

The outcome of the hatching experiment of nine batches of flyingfish eggs collected in the northern flyingfish fishing ground indicated that the major spawner was *H. oxycephalus* (Chang et al., unpublished data). The egg fishery runs from April to July with an annual catch of 228 mt (Fishery Agency, 1999–2009), implying that this species was abundant in northeastern Taiwan during that period. This was also supported by the at-sea observations onboard of flyingfish-egg fishing vessels mentioned above. This species was also observed in high densities in the non-spawning-season from December and January in Lu-Dao (Fig. 5). It is therefore possible to conclude that these fish spend a portion of their life stages in Lu-Dao and then move towards the northern and northeastern coasts of Taiwan to spawn. Alternatively, the fishes that lay eggs in the summer in the northern region belong to a population that is different from the fish that reside around Lu-Dao in the winter time. Further surveys and studies are needed to effectively assess this observation.

The findings on species distribution have implications to the flyingfish management. Sampling results suggest that different fishery was utilising different species groups in different regions, thus management consideration may need to differ by species, rather than treating these fishes as a single taxonomic entity (e.g., Hung, 2008). For example, the egg fishery in northeastern Taiwan uses the eggs of *H. oxycephalus* (< 25 cm) but the gillnet fishery in Lan-Yu uses adult *Ch. atrisignis* (> 25 cm) (Table 1) as food fishes. In addition, *Ch. atrisignis* occurs only in areas south of Lu-Dao (Fig. 5). Therefore, the fisheries in these two areas, and for these two species, are advised to be managed separately.

Nineteen flyingfish species (Table 1) and several juvenile fishes (small fish in Fig. 2) were observed in the Lu-Dao gillnet surveys (LDG, Table 1), more than the Hua-Lien surveys (HLG) that used the same gillnets. This number of species was more than the number from commercial gillnetters in Lu-Dao because our surveys used gears with smaller mesh size and covered the non-fishing seasons (Fig. 4). The high species diversity may emphasize the importance of protecting the ecosystem in the waters off Lu-Dao. The species numbers were low in all setnet fishing grounds, but this number may have bias because setnet fishermen discarded small and low valued fishes in daily catches and stopped operations during typhoon seasons.

The vertical distribution of the dominant species was significantly different (Table 2). Five of the six dominant species were caught in the upper and middle layers of the net (roughly above 2.4 m, see Table 3), while the *Cy. poecilopterus* was mostly (85%) caught in middle and bottom layers (roughly under 1.2 m). This result concurs with the work of Nesterov & Bazanov (1986) which recorded a majority (85.7%) of flyingfish (without separation of species) in the 0–2 m surface layer. Our findings, however, differ from the studies of Khohiattiwong et al. (2000) (on *H. affinis*) and Zuyev & Nikol'skiy (1981) (on an undetermined species) which found that the fishes were generally equally distributed within a depth of 3 m. This may imply that different species have a different preferential depth. On the other hand, Khohiattiwong et al. (2000) indicated that during the peak spawning season more *H. affinis* were recorded at the surface. This study shows that 75% of the *Ch. atrisignis* occurred in the upper layer and over 90% were observed to be gravid when pressing on the gonad position, suggesting that the vertical distribution is likely associated with spawning activities for this species.

Dominant species distribution in relation with the environmental factors. — For the four dominant species, the PCA analysis (Fig. 5) suggests that there is no significant difference in their preferences for environmental conditions. In other words, they have preference for similar environmental conditions, and the GLM analysis (Table 4) indicates that their preferred conditions are associated with SST (positively), tidal range (positively), and tide level (negatively).

Khohiattiwong et al. (2000) concluded that the catch rate (similar to the density index used here) of *H. affinis* is significantly correlated with environmental factors of SST, wind speed, and swell height. Both their work and the present study indicate that the SST is the most significant environmental factor. However the results are contradictory; their work suggests that the catch rate is inversely correlated with SST while the current study showed positive correlation with SST (Table 4 and Fig. 6). These two studies are different in several aspects: (1) target species (one specific species in their study versus four combined species in this study), (2) SST range (26– 29°C versus 24– 31°C), (3) statistical analysing method (Spearman's rank test versus GLM), and (4) number of factors (one single factor versus a combined effect of three factors). At present, the available information is not sufficient to determine the most plausible explanation for the contradiction.

The per trip catch proportion of the four dominant species shows a low catch proportion when the tide level or the tidal range was either too small or too large and a high proportion when the two variables were within a certain low range (Fig. 7). Khohiattiwong et al. (2000) also concluded similar relationship for swell height with catch rate. The data is insufficient to establish a mechanism for these factors on flyingfish distribution. They might be associated with the change in abundance of phytoplankton which is significantly correlated with the tidal range (Balch, 1981).

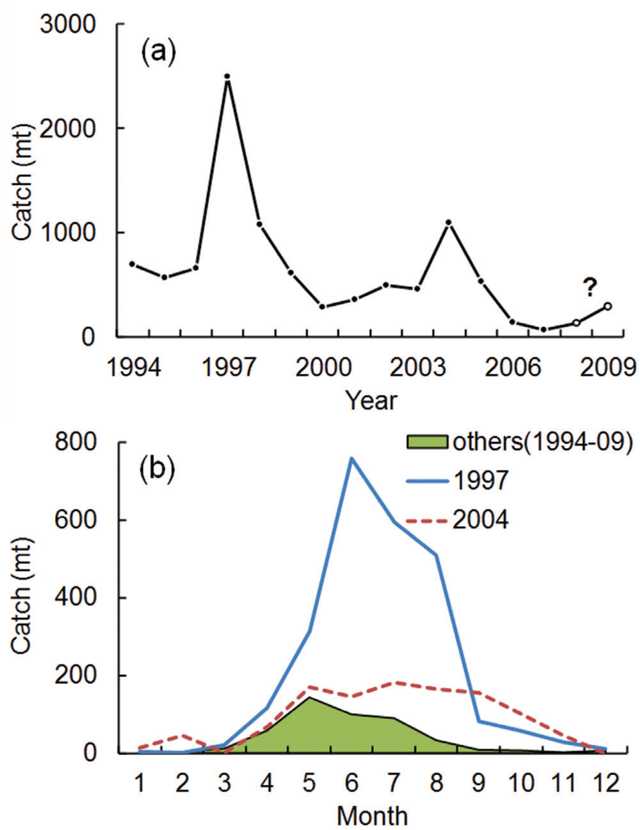

Fig. 8. Annual flyingfish catch in Taiwan from 1994 to 2009 (a), and the monthly catch in three periods: 1997, 2004, and the other years during 1994 to 2009 (normal years) (b) (Source: Fisheries Agency, Taiwan. Data of 2008 and 2009 in (a), empty circles, might be underestimated compared to the sampling data in this study.)

The flyingfish fisheries in the Kuroshio Current off Taiwan show an obvious seasonal variation in catch, similar to that in the Eastern Caribbean (Oxenford, 1994). As indicated in this study and Khohiattiwong et al. (2000), seasonality is correlated with environmental factors. Historically, the catch in Taiwan has two substantial highs in time series: 1997 (four times as high as 1996) and 2004 (two times that of 2003) (Fig. 8a). In these two years, the fishing seasons have shown different patterns from normal years (Fig. 8b, i.e., fishing season lasted longer). In each of these two years, there was an El Niño event that has demonstrated to have some influences on the marine environments of the western Pacific Ocean (Chavez et al., 1999; Connolly & Roughgarden, 1999; NOAA, 2004); and these events might also have contributed to the changes in seasonal patterns.

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