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Changes in the fish species composition in the coastal zones of the Kuroshio Current and China Coastal Current during periods of climate change: Observations from the set-net fishery (1993–2011)



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ABSTRACT

 $Changes \, in \, fish \, distribution \, and \, migration \, patterns \, have \, occurred \, in \, mid- \, and \, high-latitude \, oceans \, world-distribution \, and \, migration \, patterns \, have \, occurred \, in \, mid- \, and \, high-latitude \, oceans \, world-distribution \, and \, migration \, patterns \, have \, occurred \, in \, mid- \, and \, high-latitude \, oceans \, world-distribution \, and \, migration \, patterns \, have \, occurred \, in \, mid- \, and \, high-latitude \, oceans \, world-distribution \, and \, migration \, patterns \, have \, occurred \, in \, mid- \, and \, high-latitude \, oceans \, world-distribution \, and \, migration \, patterns \, have \, occurred \, in \, mid- \, and \, high-latitude \, oceans \, world-distribution \, and \, high-latitude \, oceans \, high-latitude \, high$ wide in response to climate change. Since the 1980s, the sea surface temperature (SST) of the southern East China Sea has increased significantly, particularly in winter. The mechanisms behind these changes in migratory fish assemblages are difficult to elucidate from general capture fisheries databases. This study collected a long-term data set of set-net catches, reported from the remote Tung-Ao Bay in northeastern Taiwan to analyze catch composition. Both the total number of species and the Shannon-Wiener index (H') showed an increasing trend, while the cumulative percentages of the top 10 captured fish species decreased annually. These results indicated that in the coastal zone at the front of Kuroshio Current (KC) and China Coastal Current (CCC), increased SST caused fluctuations in the presence of cold-water and warm-water fishes and in the timing of fishing seasons. Additionally, results based on multidimensional scaling (MDS) and cluster analyses showed that the study period could be divided into two clusters, 1993-1997 and 1998-2011, with an 80% similarity value. The boundary of these clusters was consistent with changes in SST. A species composition change analysis of these clusters showed that clustering was associated with changes in the intensities of the CCC and KC, especially in winter seasons. A northward expansion of low-latitude fish species was observed in Tung-Ao Bay, similar to expansion of high-latitude fish species into Polar region.

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1. Introduction

The richness of marine fishery resources can be influenced by both human and natural factors. The human impact has an immediate effect on fishery resources. In comparison, the impact of climate change has been often overshadowed by anthropogenic factors. However, climate change greatly affects population sizes, migration routes, and distribution boundaries of marine organisms (Cushing, 1982; Glantz, 1992). In particular, environmental changes usually influence the species richness of fish and invertebrates and can greatly affect marine biodiversity (Macpherson, 2002). Trenberth et al. (2007) found that global SST in average increased 0.067 °C each year during the period of 1901–2005. The impact of this magnitude of change on marine fishery resources should not be

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underestimated. Cheung et al. (2009) used changes in global species richness in combination with climate change models to predict that increases in SST will result in the migration of many species toward the south and north poles and the local extinction of some species in tropical and sub-polar regions. A study by Perry et al. (2005) revealed that fish species at the southern and northern edges of the North Sea are migrating northward. In the past 22 years, the number of fish species continued to increase in the North Sea. The newly added species consisted primarily of small fish that normally live in southern regions; in the meantime large fish typically distributed in northern regions decreased (Hiddink and Hofstede, 2008).

The increase in SST near Taiwan is highly significant. Studies by Liu and Zhang (2013) showed that, over the past 100 years, the SST of the East China Sea (ECS) and waters around Taiwan increased by more than $2.7\,^{\circ}\text{C}$. A study in the surrounding waters of Taiwan (119–123° E/21–26° N) by Chen (2002) even reported that the trend in SST during the period of 1982–2001 had an increase of $0.56\pm0.11\,^{\circ}\text{C}/\text{decade}$, significantly higher than the global increase (0.11 $\pm\,0.03\,^{\circ}\text{C}/\text{decade}$). Few previous studies have been conducted about the impact of climate change on specific fish species and

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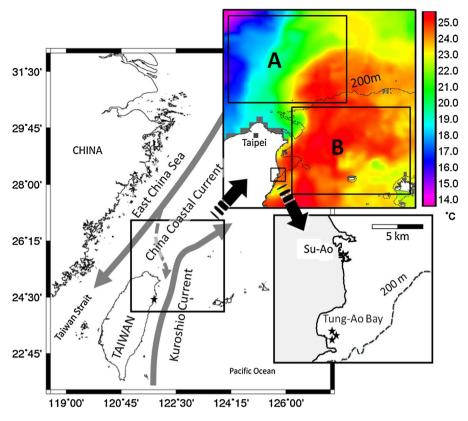


Fig. 1. The locations of the 3 groups of set-net samples used in this study (indicated by asterisks), the surrounding ocean current systems, and zones A and B from which sea surface temperature (SST) data were selected (SST image was taken in February 2012).

fisheries in this region. For example, the increase in SST has gradually affected the abundance of larval anchovies in the coastal waters southwest of Taiwan due to an influx of *Engraulis japonicas*, carried by the China Coastal Current (CCC), and *Encrasicholina heteroloba* and *Encrasicholina punctifer*, carried by the Kuroshio Current (KC) (Hsia et al., 2004; Hsieh et al., 2009). Other examples include reduced numbers of wintering migratory gray mullet (*Mugil cephalus*) from the Taiwan Strait to the south, as well as a shift of catch location of this species to the north (Lu et al., 2012), and cold damage to cage aquaculture fish around the Penghu Islands in the central Taiwan Strait (*Chang et al.*, 2013). Due to a lack of long-term and systemic sampling and monitoring, it is difficult to observe regional changes in fish species composition. More direct results could be obtained from long-term observations at a fishery location without disturbance from too many factors.

Tung-Ao Bay is a semi-enclosed bay located in northeastern Taiwan (Fig. 1). Due to its remote location, Tung-Ao Bay is almost unaffected by environmental pollution and human activities. The main KC, a warm current, flows outside this bay year-round, and the colder CCC invades the bay in winter; thus, cold and warm currents merge and carry marine organisms from different water systems into this area. There are three long-term sets of 2-trap set-nets within the bay, of which the location, mesh size, and fishing gear structure are fixed. Changes in fishing conditions are primarily determined by natural factors. Over the 20 years previous to 2012, the average annual catch has ranged from 258 to 731 tons (mean = 551, standard deviation = 153) without increasing or decreasing trend beyond annual fluctuations. Set-nets are a completely passive type of fishing gear with a fixed fishing effort and complicated standardization of fishing effort is unnecessary.

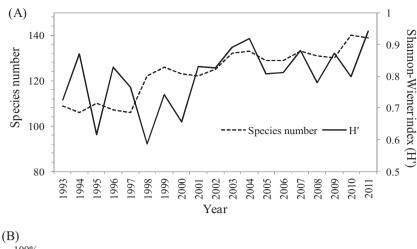
Catch and change in species composition can be used to monitor changes in the exploitation of fishery resources and changes in coastal ecosystems (Inoue and Watanabe, 1986; Yamane, 2008).

Tung-Ao Bay is a sub-tropical coastal bay adjacent to the transition zone from deep ocean to ECS shelf. The composition of fish species caught in the bay may provide information about the response of regional fish communities in the western Pacific marginal waters to increase in global SST. In this study, we collected daily catch records and conducted shoreside fish measurements of the fishery landing of set-nets at Tung-Ao Bay, then combined with remote sensing SST data to observe the response of fish assemblages in the coastal zones of the KC and CCC to the environmental variability under climate change during the past two decades (1993–2011).

2. Materials and methods

We collected daily catch data from a set-net fishery (a total of three groups of set-nets) at the remote Tung-Ao Bay in northeastern Taiwan from 1993 to 2011. During this period, there were 183 species captured. The common and scientific names of each species were compiled and confirmed according to the Fish Database of Taiwan (http://fishdb.sinica.edu.tw/). There were 164 fish species confirmed. The unconfirmed species occurred rarely and the likelihood of catching unidentified species was very low. The numbers of confirmed fish species in each year were calculated, and changes of their presence were observed.

Catch data consisted of weights and/or numbers; only weight of mass-caught fish species were recorded. To estimate the numbers of mass-caught fish species, shoreside sampling measurements were taken from 2010 to 2012 to calculate the average weight per month, which was used to convert weight into number of fish caught monthly for each year. Changes in biodiversity were determined by comparing the Shannon-Wiener index (Shannon, 1948) for each year and each month. The Shannon-Wiener index was



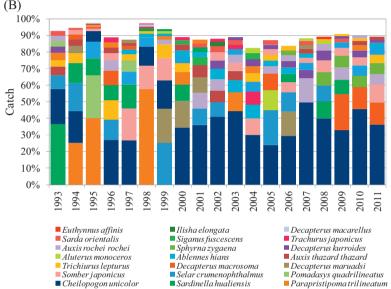


Fig. 2. Variations in the species biodiversity of the catches during each year: (A) species number and Shannon–Wiener index, and (B) the cumulative catches of the top 10 species of the year.

calculated using data for fish species and numbers caught with the following formula:

$$H' = -\sum_{i=1}^{S} \frac{n_i}{N} \log \frac{n_i}{N} \tag{1}$$

N, number of fish of all species in the catch; n_i , number of the ith species; and S, number of species in the catch.

To avoid damage, set-net operators in Tung-Ao Bay remove their nets during the typhoon season (approximately July-September) and suspend fishing activities for 3 months each year. To ensure consistent time periods of catch data in each year, the above formula was used to analyze data obtained between January and June and between October and December.

To compare structural changes in fish species composition, PRIMER 6 (Plymouth Routines in Multivariate Ecological Research) software was used to perform a multivariate cluster analysis (Clarke and Gorley, 2006). The Bray–Curtis similarity index (S_{jk}) was used to calculate similarity distance matrix (Eq. (2)), and the non-metric multi-dimensional scaling (MDS) (Kruskal, 1964) method was used to convert the matrix into a spatially structured diagram. Finally, cluster analysis (Clarke and Green, 1988) was used to determine

and interpret the composition of fish assemblages among years within clusters

$$S_{jk} = 100 \left(1 - \frac{\sum_{i=1}^{p} |y_{ij} - y_{ik}|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})} \right)$$
 (2)

 y_{ij} , the number of the *i*th species of fish in the catch in the *j*th year; y_{ik} , the number of the *i*th species of fish in the catch in the *k*th year; and p, the total number of species.

The similarity percent (SIMPER) was used to identify the major representative fish species in each cluster and the fish species that affected clustering changes (Clarke, 1993; Clarke and Warwick, 2001). First, the Bray–Curtis dissimilarity index was calculated ($\delta_{jk}(i)$) to determine differences between the sample points based on the fish species present in each catch. This value was averaged over species and divided by the sum δ of all species to calculate the percentage of dissimilarity caused by each fish species (contribution, %). The major species in the catch that led to differences in the fish assemblages in the catch were also identified.

$$\delta_{jk}(i) = 100 \frac{\left| y_{ij} - y_{ik} \right|}{\sum_{i=1}^{p} (y_{ij} - y_{ik})}$$
(3)

$$contribution(\%) = 100 \frac{\overline{\delta_i}}{\sum_{i=1}^p \overline{\delta_i}}$$
 (4)

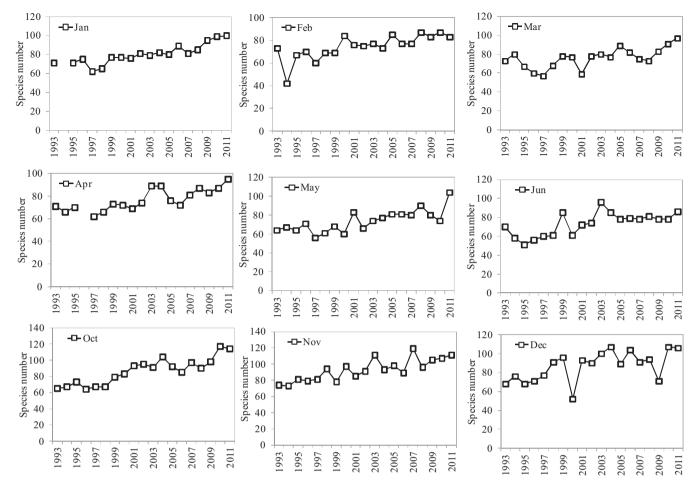


Fig. 3. The number of species caught from January to June and from October to December in each year.

During the study period, SST data from the waters surrounding Tung-Ao Bay were obtained from the National Oceanic and Atmospheric Administration website (NOAA: http://las.pfeg.noaa.gov/oceanWatch/). The Pathfinder Version 5.0 SST Advanced Very-High Resolution Radiometer (AVHRR) database, containing data from an NOAA series of satellites, was used to obtain SST before 2008; data from 2009 to 2011 were obtained from the Aqua satellite database, which relies on a Moderate Resolution Imaging Spectroradiometer (MODIS). SST data were obtained for the area between 24° N–27° N and 121° E–124° E (Fig. 1) from 1990 to 2011. Some extreme values observed in the downloaded data were usually due to cloud blockage; thus, the SST in these areas could not be measured and was excluded from our analysis. The excluded areas of bad data were less than 15% and 5% of the total area in winter and summer, respectively.

Off the northeastern Taiwan, the KC flows closer to the 200 m isobath, mostly in winter, and away from it in summer (Matsuno et al., 2009). The CCC, mainly driven by winter monsoon, intensely interacted with KC in winter. As the strength of KC and CCC are the two major factors that cause environmental changes in the study area, we used a proxy of current intensity by SST. The area was divided into zones A (25.5–27° N and 121–123° E) and B (24–25.5° N and 122–124° E). The mean monthly SST of zones A and B for each year was obtained, and an SST time series was plotted for each season and used to perform Spearman rank correlation analysis of catches of dominant species. The differences in the SST between the two zones were calculated and used as an indicator of fluctuations of intensity in the KC and CCC (Fig. 1). Zone A was primarily affected by the CCC, while zone B was affected by the KC. A smaller difference

in temperature between zones A and B indicated a weaker intensity of CCC invasion into Tung-Ao Bay or stronger intensity of KC.

3. Results

3.1. Changes in fish composition and diversity indices

The numbers of fish species recorded in the catches each year ranged from 106 to 140, with a yearly increasing trend (Fig. 2A). The number was increased from 106–110 species in 1993–1997 to 122–126 in 1998–2002, 129–133 in 2003–2009, and approximately 140 in 2010–2011. There was also an increasing trend in the total number of fish species per month (Fig. 3), especially in colder months, with the greatest increases in the number of fish species observed between December and April.

Variation in the biodiversity index (H') (solid line in Fig. 2A) ranged from 0.58 to 0.94, lowest in 1998 and highest in 2011, with an increasing trend of 0.09/decade. The colder months (December–April) showed a stronger increasing trend in H' (Fig. 4), while in January and March, there was a linear increasing trend each year (p < 0.05). In the other months, all the indices showed an increasing trend of 0.005–0.008/decade. Only in May did the index show a significant yearly decreasing trend (p < 0.05), with a decrease of 0.1/decade.

The cumulative percentages of the top 10 fish species (different from year to year) in the catch per year are shown in Fig. 2B. The average percentage of the top 10 fish species was 93% during 1993–2001 but decreased to 87% during 2002–2011, indicating a yearly increasing trend of the number of dominant species. The

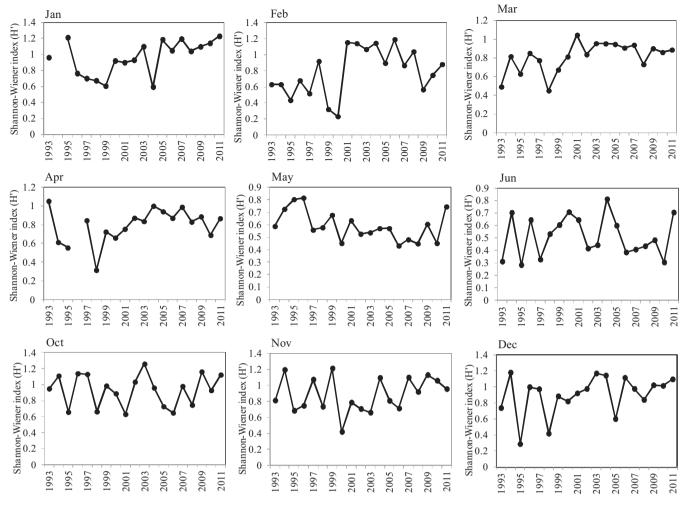


Fig. 4. Variations in the monthly Shannon-Wiener index for each year.

percentage of the top 10 species in the catch was highest in 1995, at 97% of the total catch, and lowest in 2004, at approximately 82%. Variations in the percentage of the top 10 species per month during the study period are shown in Fig. 5. In January, catch of the top 10 species was accounted for 91% of the catch during 1993–2001 but decreased to 85% during 2002–2011, while the percentages during December, February, March, and April decreased from 92%, 96%, 97%, and 97% to 87%, 89%, 94%, and 95%, respectively. The percentages in May, June, October, and November did not show significant changes. May was an unusual case; although the percentage of the top 10 species did not change significantly, the percentage of Limpid-wing flyingfish in the catch increased significantly.

The yearly and monthly time serials derived from the catch data, including number of fish species caught, H' and cumulative percentages of the top 10 fish species, showed that the fish assemblage structures were changing from low to high diversity. Such change was particularly significant in winter months due to decrease in mass-caught winter migratory species.

3.2. Changes in dominant species

The percentage of the top 10 species was accounted for 82–97% of the total catch per year (Fig. 2B). There were 21 dominant species appeared in the top 10 species (Table 1). Eleven of these dominant species are associated with reefs, including nine pelagic fish, and one benthopelagic species. Of the nine pelagic species, five

were cold-water species that arrived in Tung-Ao Bay with the CCC. and four were warm-water species that arrived with the KC. To observe changes in the dominant species over time, species that appeared among the top 10 species of a year for more than 10 times were considered to be dominant species, including limpidwing flyingfish, bigeye scad (Selar crumenophthalmus), chicken grunt (Parapristipoma trilineatum), spotted mackerel (Scomber australasicus) (may have been mixed with chub mackerel, Scomber japonicus), bigeye barracuda (Sphyraena forsteri), bullet tuna (Auxis rochei rochei), frigate tuna (Auxis thazard thazard), Largehead hairtail (Trichiurus lepturus), flat needlefish (Ablennes hians), and redtail scad (Decapterus kurroides). The linear regression analysis of the changes in the numbers of these species per year showed that the numbers of limpid-wing flyingfish ($R^2 = 0.35$, p < 0.01), bullet tuna ($R^2 = 0.17$, p < 0.05), and redtail scad ($R^2 = 0.23$, p < 0.05) increased significantly over time, while spotted mackerel ($R^2 = 0.38$, p < 0.01) and largehead hairtail ($R^2 = 0.23$, p < 0.05) showed significant decreasing trends; changes in other species were not significant (p > 0.05) (Fig. 6).

3.3. Annual variability in fish assemblages

The MDS and cluster analyses of variability in fish assemblages over a 19-year period identified 2 clusters, 1993–1997 and 1998–2011, with a similarity of 80% (Fig. 7A). The average dissimilarity between these two periods, determined by the SIMPER

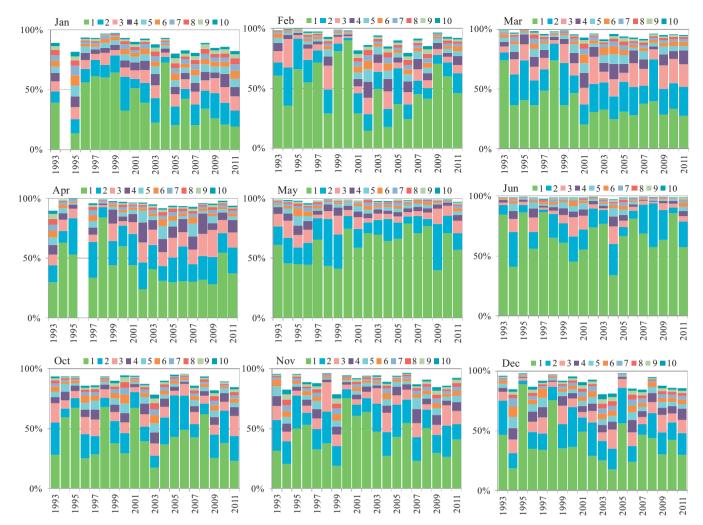


Fig. 5. Monthly cumulative percentages of the top 10 species caught of the year. The number and color of the bar of each year represent the contribution of the fish species in the year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 1Top 10 fish species caught in each year from 1993 to 2011 period. Most species were in the top 10 in multiple years.

Common name	Species name	Habitat	Number of year	Associated Current	Catch in weight (%)	Cumulated catch (%)
Bigeye scad	Selar crumenophthalmus	Reef	19		5.1%	5.1%
Limpid-wing flyingfish	Cheilopogon unicolor	Pelagic	19	KC	6.5%	11.6%
Bigeye barracuda	Sphyraena forsteri	Pelagic	16	CCC	1.8%	13.4%
Largehead hairtail	Trichiurus lepturus	Benthopelagic	15		8.0%	21.5%
Bullet tuna	Auxis rochei rochei	Pelagic	14	KC	9.1%	30.5%
Frigate tuna	Auxis thazard thazard	Pelagic	13	KC	6.2%	36.8%
Flat needlefish	Ablennes hians	Reef	12		2.4%	39.2%
Spotted mackerel	Somber autralasicus	Pelagic	12	CCC	4.7%	43.9%
Redtail scad	Decapterus kurroides	Pelagic	11	CCC	0.7%	44.6%
Chicken grunt	Parapristipoma trilineatum	Reef	10		4.9%	49.5%
Striped bonito	Sarda orientalis	Pelagic	9		13.4%	62.9%
Japanese scad	Decapterus maruadsi	Reef	7		3.6%	66.5%
Shortfin scad	Decapterus macrosoma	Reef	7		1.4%	67.9%
Jack mackerel	Trachurus japonicus	Pelagic	6	CCC	0.3%	68.2%
Crocodile needlefish	Tylosurus crocodilus crocodilus	Reef	6		3.2%	71.4%
Unicorn leatherjacket filefish	Aluterus monoceros	Reef	5		3.5%	74.9%
Moontail bullseye	Priacanthus hamrur	Reef	3		3.0%	77.9%
Mottled spinefoot	Siganus fuscescens	Reef	3		0.8%	78.6%
Mackerel scad	Decapterus macarellus	Reef	1		0.3%	79.0%
Kawakawa	Euthynnus affinis	Pelagic	1	KC	3.9%	82.8%
Torpedo scad	Megalaspis cordyla	Reef	1		0.3%	83.1%

Note. KC, Kuroshio Current; CCC, China Coastal Current; Habitat, based on records in FishBase (http://www.fishbase.org) and Shao and Chen (2004); Associated current, based on fishermen's recognition and local knowledge.

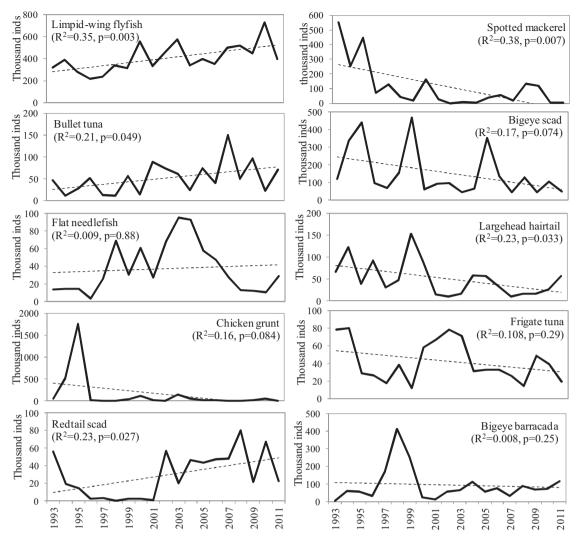


Fig. 6. Numbers of dominant species (in thousands of individuals) caught each year. The dotted line represents the results of the linear regression between annual catch in number and year.

dissimilarity analysis, was 20.1%, and 27 species had contributions greater than 1%. Decreases in richness were attributed to changes in the following fish species: moontail bullseye (*Priacanthus macracanthus*), Chinese herring (*Ilisha elongata*), spotted mackerel, Japanese scad (*Decapterus maruadsi*), nibbler (*Girella leonina*), and chicken grunt (Table 2). Of these, Spotted mackerel and Chicken grunt were considered dominant species (Table 1). The other species contributing to increased richness were all lesser dominant species, except for flat needlefish. Therefore, in addition to the decrease in the average richness of major dominant species, the increase in the average richness of lesser species was also an important factor leading to significant variability in the fish assemblages during the two time periods.

An analysis of the similarity percentage contribution with SIM-PER showed that the similarities in the 1993–1997 and 1998–2011 clusters were 87.2% and 85.2%, respectively. The top 10 contributing species had a high repeatability (Table 3). However, the species contributing to the high average richness in these two periods still experienced significant changes. Of the representative species, frigate tuna and moontail bullseye in the 1993–1997 periods were replaced by flat needlefish and kawakawa (*Euthynnus affinis*) in the 1998–2011 periods.

3.4. Analysis of SST changes

The SST of the waters adjacent to northeastern Taiwan (i.e., average SST in zones A and B, see Fig. 1) showed an increasing trend during the period 1990–2011. Deviations in SST, defined as yearly average of monthly SST anomalies (baseline = 1990–2011), changed from negative to positive after 1997 (Fig. 7B). SST significantly increased after 1998, which was the same year found to be the dividing line between the two clusters in the MDS analysis. The average SST time series for each season is shown in Fig. 8A. Based on the linear regression analysis, SST showed an increasing trend in all four seasons, with season 1 having the greatest temperature change (p < 0.05) followed, in order, by seasons 2, 4, and 3. Temperature increased more rapidly in relatively colder months and more slowly in warmer months, indicating that the temperature differences between warm and cold months became smaller and that seasonal differences became less significant.

The differences in average temperatures between zone A and zone B was greatest in season 1 (January–March) and least in season 3 (July–September) (Fig. 8B). The temperature differences between zones A and B showed decreasing trends in all seasons (Fig. 8B). In season 1 it decreased by 0.24 °C/decade and had the most significant

Table 2Fish species contributing to assemblage differences during the 2 time periods (1993–1997 and 1998–2011; only species with contributions greater than 1% to the dissimilarity were included).

Common name	Species name	Habitat	Contribution (%)	Comparison
Needlescaled queenfish	Scomberoides tol	Reef	3.91	+
Flat needlefisha	Ablennes hians	Reef	3.02	+
Moontail bullseye	Priacanthus hamrur	Reef	2.17	+
Shortfin scad	Decapterus macrosoma	Reef	2.12	+
Moontail bullseye	Priacanthus macracanthus	Reef	1.94	_
Smooth hammerhead	Sphyrna zygaena	Reef	1.89	+
Jack mackerel	Trachurus japonicus	Reef	1.82	+
Shrimp scad	Alepes djedaba	Reef	1.78	+
Mackerel scad	Decapterus macarellus	Reef	1.76	+
Whip stingray	Dasyatis akajei	Demersal	1.73	+
Bali sardinella	Sardinella hualiensis	Pelagic	1.73	+
Yellowfin seabream	Acanthopagrus latus	Reef	1.57	+
Longtail tuna	Thunnus tonggol	Pelagic	1.43	+
Chinese herring	Ilisha elongate	Reef	1.41	_
East Asian fourfinger threadfin	Eleutheronema rhadinum	Reef	1.4	+
Yellow-lined grunter	Pomadasys quadrilineatus	Reef	1.33	+
Mottled spinefoot	Siganus fuscescens	Reef	1.29	+
Spotted Spanish mackerel	Scomberomorus niphonius	Pelagic	1.24	+
Red-eye round herring	Etrumeus teres	Reef	1.18	+
Spotted mackerela	Scomber australasicus	Pelagic	1.18	_
Chinese seerfish	Scomberomorus sinensis	Pelagic	1.1	+
Yellow drum	Niber albiflora	Benthopelagic	1.09	+
Thresher shark	Alopias superciliosus	Demersal	1.04	+
Japanese scad	Decapterus maruadsi	Reef	1.04	_
Moonfish	Mene maculate	Reef	1.03	+
Nibbler	Girella leonine	Reef	1.01	_
Chicken grunt ^a	Parapristipoma trilineatum	Reef	1	_
Cumulative contribution (%)			43.21	

^{+,} Comparison indicates species that the average richness during the 1998–2011 period was higher than that during the 1993–1997 period; –, comparison indicates species that the average richness during the 1998–2011 period was lower than that during the 1993–1997 period.

decreasing trend (p < 0.05), followed by season 2 (April–June) with a decrease of 0.15 °C/decade. Therefore, the trends in wintertime SST and SST differences imply a regional climatic changes characterized by significant coastal warming and more frequent KC intrusion in the study area during the past two decades.

4. Discussion and conclusion

The number of species in the set-net catches from northeastern Taiwan and the biodiversity indices based on these catch data showed increasing trends, while the cumulative percentages of the top 10 species showed decreasing trends (Figs. 2–5). The results of the MDS and cluster analyses showed that our study period could be divided into two clusters, 1993–1997 and 1998–2011, with a dissimilarity of about 20%. There were two major factors contributing to these results: first from the dominant species, including decreased numbers of cold-water pelagic fish, such as spotted mackerel and jack mackerel (*Trachurus japonicus*), and increased

numbers of warm-water pelagic fish, such as limped-wing flyingfish and kawakawa, second from the increased numbers of species primarily associated with reefs. Meanwhile, the remote sensing SST data indicate significant coastal warming in the study area. The changes found in fish assemblage and in SST are discussed below.

4.1. Change of dominant species and coastal warming

The decrease of catch in the dominant species had decisive effect on the H' index. If the six most dominant species with decreasing trends (Fig. 6 and Table 1) were excluded from the catch, H' showed an increase of 0.03/decade, which showed significantly different from the H' calculated without exclusion of these dominant species (0.09/decade). Apparently, the reduced migration of dominant species to the study area is a major factor contribute to the elevated H' index.

Water temperature affects growth, feeding, and reproduction of fish, as well as changes the suitability of marine habitats, thus

Table 3The average similarity of the species compositions in each time period (only the top-10 species from each time period were included).

Common name	Species	1993–1997	1998-2011
Limpid-wing flyingfish	Cheilopogon unicolor	2.82	2.47
Spotted mackerel	Somber japonicus	2.68	1.68
Bigeye scad	Selar crumenophthalmus	2.62	2.13
Largehead hairtail	Trichiurus lepturus	2.43	1.9
Frigate tuna	Auxis thazard thazard	2.31	0
Chicken grunt	Parapristipoma trilineatum	2.28	1.79
Moontail bullseye	Priacanthus hamrur	2.22	0
Bullet tuna	Auxis rochei rochei	2.21	2
Bigeye barracuda	Sphyraena forsteri	2.19	2.06
Flat needlefish	Ablennes hians	0	1.94
Striped bonito	Sarda orientalis	2.17	1.77
Kawakawa	Euthynnus affinis	0	1.75
Cumulative contribution (%)	-	23.93	19.49

^a Indicates major dominant species that were among the top 10 catches for more than 10 times in 19 years.

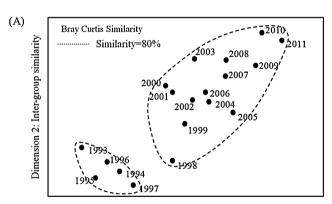
 Table 4

 Correlation analysis (Spearman rank correlation coefficients) between the dominant species and annual average sea surface temperature (SST) in zones A and B.

Dominant species		Spearman correlation	
Name	Scientific name	Coefficient (r)	<i>p</i> -value
Limpid-wing flyingfish	Cheilopogon unicolor	0.57	0.01*
Bigeye scad	Selar crumenophthalmus	-0.17	0.49
Chicken grunt	Parapristipoma trilineatum	-0.42	0.04*
Spotted mackerel	Scomber australasicus	-0.53	0.02*
Bigeye barracuda	Sphyraena forsteri	0.18	0.45
Bullet tuna	Auxis rochei rochei	0.12	0.63
Frigate tuna	Auxis thazard thazard	0.13	0.59
Largehead hairtail	Trichiurus lepturus	-0.49	0.03*
Flat needlefish	Ablennes hians	0.42	0.04^{*}
Redtail scad	Decapterus kurroides	0.09	0.76

^{* 0.01 &}lt; p < 0.05.

leading to changes in the distribution and richness of fish species (Thomas et al., 2004; Wood and McDonald, 2008). As the migration of the six mass-caught species was mostly associated with CCC or KC (Table 1), therefore the increase trend in SST played an important role on the change of mass-caught species during the study period. The temperature differences between zones A and B decreased during 1993–2001, especially during the coldest months of season 1 (Fig. 8). This change indicates that the intensity of the CCC became weaker, a change that could cause the observed decrease in the number of fish in the catch during season 1. Among the major contributors to the variation during these two periods, bigeye barracuda, bigeye scad, striped bonito (*Sarda orientalis*), largehead hairtail, spotted mackerel, and chicken grunt all showed decreasing trends (Table 3), although only the decreasing trends for



Dimension 1: Inter-group similarity

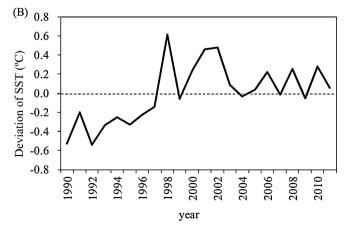
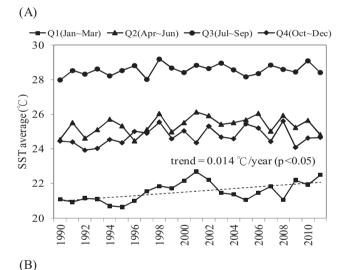


Fig. 7. (A) MDS plot of fish assemblages in Tung-Ao Bay from 1993 to 2011. (B) Changes in the sea surface temperature (SST) deviation value from 1990 to 2011 in zones A and B (see Fig. 1).

largehead hairtail and spotted mackerel were significant (p<0.05; Fig. 6). There was a significant negative correlation between SST and the catch numbers of chicken grunt, spotted mackerel, and largehead hairtail (Spearman rank correlation, p<0.05; Table 4). However, the catch numbers of limpid-wing flyingfish and flat needlefish showed increasing trends (Fig. 6) and were positively correlated with SST (p<0.05). Both were warm-water species, and the former was considered to be an indicator species that migrated northward with the KC.



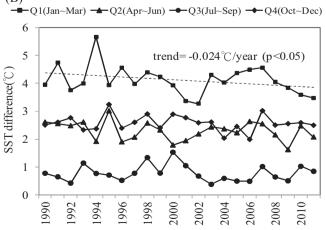
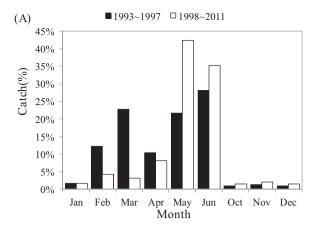


Fig. 8. (A) Time series of the average sea surface temperature (SST) for each season (Q1–Q4) in zones A and B. (B) Time series of the SST differences in each season (Q1–Q4) in zones A and B.



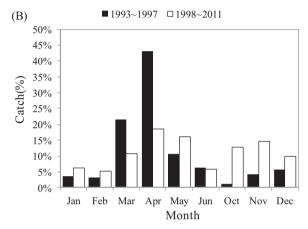


Fig. 9. Comparison of monthly catch percentage during 1993–1997 and 1998–2011 for (A) pelagic fish and (B) reef fish.

4.2. Change of non dominant species and coastal warming

Analysis of the SIMPER dissimilarity contribution among groups showed that 27 of the fish species during the two periods had contributions greater than 1% (Table 2). Among these species, only three were dominant species, including flat needlefish, spotted mackerel, and chicken grunt, while the rest were not. Therefore, change in the richness of lesser dominant species also contributed to the variations in species assemblage in these two periods. The numbers of these non-dominant species increased in catches of all these fishes, with the exception of moontail bullseye, Japanese scad, Chinese herring, and nibbler.

The fish species that caused significant variations in the assemblage structures during the two time periods were primarily reef fish, which comprised 16 of the 27 species with contributions greater than 1% to the dissimilarity (Table 2). Different species of fish in the same area will affect each other through competition for food and habitat. A significant reduction in competitors or predators will cause increases in the numbers of other species (Wootten, 1992; Choi et al., 2007). Although the numbers of reef fish in the catches per year varied widely but without significant trend. This was likely due to constraints caused by the aforementioned biomass compensation.

High monthly catch percentages were concentrated in March and April before 1998, while after 1998 but became more scattered after 1998 (Fig. 9B). SST increased more rapidly in colder months (January–March) and more slowly in warmer months (July–September) (Fig. 8). In the study area, the variation in SST in each season became less pronounced and might lead to a dispersion of the seasonal catch numbers of reef fish. Additionally, the

increase in SST reduced species catch richness, which was concentrated in March and April, induced structural changes in the reef fish assemblages and caused the disappearance of seasonal catch concentrations

4.3. Pelagic fish and current system

The numbers of pelagic fish in the catches were relatively stable throughout the years. However, the changes in the catch numbers during season 1 (January-March) decreased significantly, while that in season 2 (April-June) increased (Fig. 9A). The trends of change in catch number might be due to fluctuations in the intensities of the CCC and KC. The surface migratory species in season 1 primarily migrated southward with the CCC, and the weakening of cold water might have affected the numbers of fish, including spotted mackerel, jack mackerel, and largehead hairtail, that migrated to this area. The surface migratory species in season 2 were mostly warm-water species, such as limpid-wing flyingfish and mahi-mahi (Coryphaena hippurus), among others, that migrated northward with the KC. The number of limpid-wing flyingfish increased significantly each year and was positively correlated with the average annual SST ($r_s = 0.559$, p < 0.05). Increase in KC intensity might increase in catch number as well as the H' index decrease in May.

Significant intrusion of the KC into the ECS shelf occurred from autumn through winter and was associated with monsoon events (Liu and Gan, 2012; Tang and Yang, 1993; Chuang and Liang, 1994). The frequencies of KC intrusions have likely steadily increased in the past decades, consistent with the theory of a more efficient spreading of heat from the KC, as evidenced by the observed coastal warming (Oey et al., 2013). As shown in Figs. 7 and 8, the SST off northeastern Taiwan showed an increasing trend and the temperature gradient between zones A and B were lessening during the past 20 years, especially in winter season. The phenomenon observed from SST is consistence with the result from these studies. The ocean currents affect temperature and consequently change fish habitat as well as cause long-term changes in SST therefore is important for the fish species migrated in the Tong-Ao Bay fishing ground.

5. Conclusion

In summary, set-nets in Tung-Ao Bay were placed in an area affected by both the KC throughout the year and invading water of the CCC; thus, winter catch compositions had a certain percentage of cold-water, mass-caught species. Because the SST gradually increased, the catch compositions showed fluctuations between the cold-water and warm-water species. There was a gradual, significant increase in the fish species diversity index, indicating that there was a northward expansion of low-latitude fish species into the bay. Taiwan is at the southern migration boundary of many cold-water fish species, and the expansion of high-latitude fish to Polar regions (Perry et al., 2005; Daw et al., 2009) may also occurs here. The set-nets in this region were retrieved daily, except during typhoon seasons. Therefore, the changes of migratory fish assemblages, which can be easily masked by human factors, could be identified in the catch data. Of course, factors that affect changes in fish assemblages are complex. In addition to natural factors, effects of other fishery activities should also be considered (Tian et al., 2011). In particular, the captured species, together with other fishery activities, might have interaction with the set-net catch.

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