www.publish.csiro.au/journals/mfr

# Composition and abundance of copepods and ichthyoplankton in Taiwan Strait (western North Pacific) are influenced by seasonal monsoons

Chih-hao Hsieh<sup>A,B</sup>, Chih-Shin Chen<sup>A</sup> and Tai-Sheng Chiu<sup>A,C</sup>

<sup>A</sup>Institute of Zoology, Department of Life Science, National Taiwan University, Taipei, Taiwan 106, ROC.

<sup>B</sup>Present address: Scripps Institution of Oceanography, University of California-San Diego,

California, 92093-0218, USA.

<sup>C</sup>Corresponding author. Email: tschiu@ntu.edu.tw

Abstract. Seasonal variation in hydrographic conditions in Taiwan Strait is strongly influenced by the monsoonal system. During northern winter, the China Coastal Current, pushed by the north-east (NE) monsoon, moves southwards into Taiwan Strait and during northern summer, the South China Sea Surface Current, driven by the south-west (SW) monsoon, invades the strait until the NE monsoon again prevails. As the SW monsoon wanes (in northern autumn), the Kuroshio Branch Current enters from the southern part of the strait, but stagnates in the middle because of interference by the China Coastal Current. As the NW monsoon wanes (in northern spring), the stagnation ceases and the SW monsoon begins. We characterised zooplankton (including copepods and ichthyoplankton) communities during a period when the SW monsoon was prevalent (in August), at the onset of the NE monsoon (in November) and as the NE monsoon waned (in March). Multivariate analyses of zooplankton composition and species abundances demonstrated that the structures of communities are closely related to oceanic variables (such as temperature, salinity and upwelling), which, in turn, are heavily influenced by the monsoons. The zooplankton faunas in Taiwan Strait are a mixture of local species and intruding species, the latter introduced from along the China coast during northern winter and from the South China Sea during northern summer. Our findings are fundamental to practical ecosystem management and an effective long-term monitoring programme.

Extra keywords: coastal current, indicator species, Kuroshio, species composition, upwelling.

# Introduction

Continuous censusing of zooplankton communities and species abundances is an effective way of monitoring aquatic ecosystems (Rebstock 2001; Beaugrand et al. 2002; Lindley and Reid 2002). In order to use biological indicators as a proxy for changes in marine environmental conditions, the interrelationships between oceanographic conditions and zooplankton communities need first to be established, because zooplankton community structure is profoundly influenced by environmental factors (Mallin 1991; Roman et al. 1993). Copepods are a main component of mesozooplankton and a major food source for ichthyoplankton (Poulet and Williams 1991). Food availability, as well as the physical environment, is an important factor influencing the survivorship of young fishes (Brian et al. 1996; Werner et al. 1996) and subsequent recruitment success. Understanding how copeped and ichthyoplankton communities are coupled with hydrographic conditions is thus essential for monitoring ecosystems and achieving sustainable fisheries.

Taiwan Strait serves as an important conduit for the exchange of biota between the East and South China Seas

in the western North Pacific. The marine environment of the strait is influenced by monsoon systems and is further affected by the bottom topography and the circulation of currents (Jan et al. 2002). When the north-east (NE) monsoon begins in early northern winter (November), the China Coastal Current (CC) moves southwards into the northern part of the strait and the Kuroshio Branch Current (KB) moves northward into the Penghu Channel, reaching to the southeastern part of the strait (Wang and Chern 1988). However, the KB is confined south of the Changyun Ridge (CyR) because CC water dominates the strait in northern winter when NE winds prevail. The NE monsoon begins to wane in northern spring (March) and then the KB reaches the northern strait (Jan et al. 1998). When the south-west (SW) monsoon begins during early northern summer (June), the South China Sea Current (SCS) moves as a wedge northwards into the southern part of the strait, displacing the KB water. The SCS water dominates the strait in northern summer and early northern autumn while the SW winds prevail (Fang 1982).

Physical processes influencing plankton distributions and abundances have been elucidated in various marine

© CSIRO 2005 10.1071/MF04058 1323-1650/05/020153

ecosystems (Boucher et al. 1987; Gowen et al. 1998; Sanchez-Velasco and Shirasago 1999; Gómez et al. 2000). However, very few studies have focused on a marine environment in which circulation patterns are strongly influenced by monsoon systems, except for the Arabian Sea (Kidwai and Amjad 2000; Kidwai and Amjad 2001). Taiwan Strait is an ideal system in which to study the effect of monsoons on the marine ecosystem owing to its suitable geographic location and well-known circulation patterns and fauna. Although seasonal variability in marine conditions in Taiwan Strait have been comprehensively studied (Jan et al. 2002), the coupling of variations in zooplankton communities to the physical environment requires further investigation. The aim of this study was to examine copepod and ichthyoplankton distributions and abundances in relation to the prevailing environmental conditions.

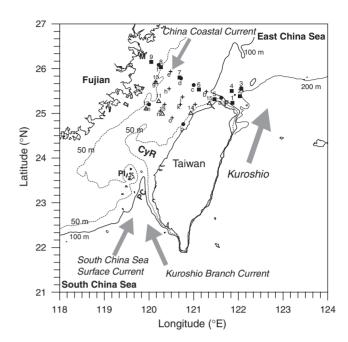
#### Materials and methods

#### Samples

Three cruises in the northern Taiwan Strait and adjacent waters north of Taiwan were carried out during August and November 1999 and March 2000 (Fig. 1). In March 2000, 16 stations (stations 'a' to 'p') in the northern strait were surveyed; however, plankton samples were collected at only six stations (a, c, d, f, m, and p). For convenience, cruises in August, November and March are named summer, winter and spring samplings respectively. Zooplankton samples were collected using circular nets with a mouth diameter of 45 cm and a mesh size of 150 µm for copepods and with a mouth diameter of 130 cm and a mesh size of 1 mm for ichthyoplankton. A flowmeter (Hydro-Bios, Kiel-Holtenau, Germany) was mounted at the centre of each net mouth to measure the filtered volume. The two nets were fastened to a wire and towed obliquely from the bottom of the water column to the surface. Temperature, salinity, dissolved oxygen and fluorescence were recorded using a conductivity-temperature-depth (CTD) profiler (Sea-Bird Electronics Inc., Bellevue, WA). The fluorescence values were used as an index of phytoplankton biomass; however, dissolved oxygen measurements could not be used for further analyses because of constant saturation of values with reference to the water temperature. To obtain a large-scale pattern of the marine environment, images of sea-surface temperatures (SSTs) on 16 August 1999, 24 November 1999 and 21 March 2000 from the advanced very-high-resolution radiometer (AVHRR) satellite of the National Oceanic and Atmospheric Administration (NOAA) were used. In the laboratory, copepods were subsampled using a Folsom splitter to a size of 300~400 individuals. Subsampled copepods and all larval fishes were identified to species wherever possible. Species densities were estimated from the number of individuals recovered from subsampling and the filtered water volume, and relative abundances (%) were calculated from species densities, accordingly.

#### Data analysis

To examine variations in copepod and ichthyoplankton compositions among stations, we use a statistical visualisation method to picture their associations. The species composition data, using four environmental variables (temperature, salinity, bottom depth and fluorescence) as covariates, were subjected to a constrained canonical correspondence analysis (CCA). The first two CCA axes were selected to illustrate the scatter pattern of stations and environmental variables if seasonal variations were exhibited. The 15 most-abundant species of copepods and ichthyoplankton at each station were defined as dominant species. A two-way indicator species analysis (TWINSPAN) (Hill *et al.* 1975), based on



**Fig. 1.** Map showing sampling stations, currents, and isobaths of Taiwan Strait. The sampling stations in August 1999 (hollow triangles), November 1999 (solid squares), and March 2000 (solid circles), and the stations with only conductivity–temperature–depth (CTD) data in March 2000 (crosses) were shown. CyR, Changyun Ridge; F, Cape Fuguei; M, Matsu; PC, Penghu Channel; PI, Penghu Island.

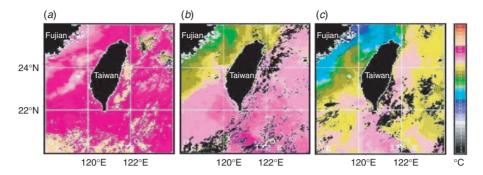
the presence/absence of the dominant species at each station, was applied to verify seasonal variation (station clusters) and to simultaneously determine cluster-associated indicator species. Finally, the distinctiveness of the seasonal compositions was confirmed by Spearman's rank correlation. To detect differences in abundances among seasons, the categorised total copepod and ichthyoplankton values were examined by bootstrapping analysis of variance (Manly 1997) and multiple pairwise comparisons were performed using bootstrapping tests. The same approach was applied to the four species of copepod and one species of ichthyoplankton that occurred in all seasons. Relationships between the zooplankton abundances (copepods and ichthyoplankton) and hydrographic conditions (depth, sea-surface water temperature, salinity and fluorescence) were examined using a canonical correlation analysis.

## Results

## Marine conditions

The satellite images of sea-surface temperatures (SSTs) show two typical patterns of summer and winter conditions: the strait is covered by South China Sea water (>26°C, Fig. 2a) in summer; and by the China Coastal Current (<22°C) in the north and by the Kuroshio Branch Current (c. 26°C) in the south (Fig. 2b) in early winter. However, in the transitional phase in spring, the warm Kuroshio Branch Current begins to penetrate into the northern strait (c. 23°C, Fig. 2c).

Through analysis of the vertical profiles of temperature and salinity in the northern transect (from Matsu to Cape Fuguei, Fig. 1), a local upwelling site was located in the western strait  $\sim$ 40 km off the south-eastern China coast,



**Fig. 2.** Satellite images showing sea surface temperature (SST, °C) around Taiwan on (a) 16 August 1999, (b) 24 November 1999 and (c) 24 March 2000. (From the data bank of National Center for Ocean Research (NCOR), Taiwan website.)

where there were relatively low temperatures and high salinity (Fig. 3a,b). Water with very low salinity was also found close to the shore, indicating freshwater runoff. In winter, the water was mixed well vertically in the eastern strait, and a cline of salinity and temperature decreased to the west (Fig. 3c,d). The occurrence of low temperatures and salinities in the western strait lasted until spring, but a high temperature and salinity lens formed in the deeper water layer (40–60 m) in the middle region of the strait (Fig. 3e, f).

## Copepod and ichthyoplankton compositions

In total, 146 species of copepods in 50 genera and 28 families and 99 fish species in 82 genera and 50 families were identified in this study. The CCA diagram derived from the copepod species compositions indicates clear seasonal structures in which data from stations of the same season clustered together (Fig. 4a). The first two-dimensional (2-D) configuration, in which temperature and salinity are heavily loaded on the first axis and fluorescence on the second, explains 77.3% of variations. The copepod species composition was highly associated with environmental factors with canonical correlations of 0.955 and 0.844 respectively. The summer stations of s8, s9, s10 and s12 were found to be distinctively correlated with high fluorescence values. For ichthyoplankton, the scatterplots of the first two CCA scores show seasonal patterns in which summer stations are distinctively clustered together, whereas the winter and spring stations are extensively spread out (Fig. 4b). The first 2-D configuration, with temperature and salinity almost equally loaded on the first axis, accounts for 65.0% of the variation. The ichthyoplankton composition is also highly correlated with the environment variables, with canonical coefficients of 0.980 and 0.917 respectively.

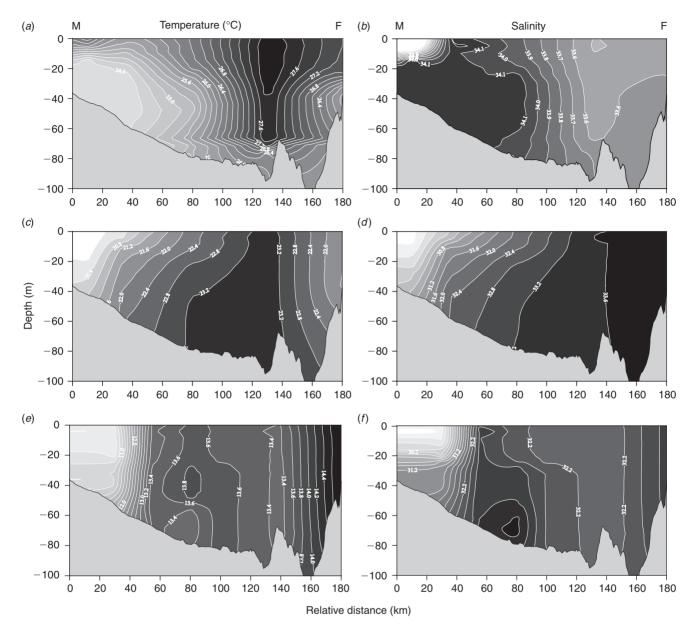
Results of two-way indicator species analysis (TWINSPAN) confirmed the characteristics of seasonal compositions, i.e. 93% (28/30) of the stations were precisely assigned back to the seasonal categories, except that spring stations 'm' and 'p' were inconsistently joined to the 'summer' and 'winter' clusters respectively (Fig. 5). Using relative probability, TWINSPAN also simultaneously assigned the

corresponding indicator species back to the cluster (season). It turned out that 15 species of copepods and 15 species of ichthyoplankton were shown to be indicators of the seasonal clusters: four copepod species and four ichthyoplankton species for 'spring', eight and nine for 'summer', and three and two for 'winter' respectively.

Species compositions of copepods and ichthyoplankton in each season are ranked in Tables 1 and 2. Four species of copepods, Acrocalanus gibber, Clausocalanus furcatus, Oncaea venusta and Paracalanus parvus, occurred abundantly in all three seasons. Four species, Acartia pacifica, Canthocalanus pauper, Oithona plumifera and Temora turbinata, occurred in both summer and winter; three species, Calanus sinicus, Clausocalanus minor and Paracalanus aculeatus, in both winter and spring; and only one species, Parvocalanus crassirostris, in both spring and summer. Only one ichthyoplankton species, *Trichiurus lepturus*, showed in all three seasons. Five species, Auxis rochei, Diaphus theta, Encrasicholina heteroloba, Engyprosopon multisquama and Saurida elongate, were recorded in both summer and winter; Benthosema pterotum in both winter and spring; and Bregmaceros arabicus in both spring and summer. It is worth noting that some species occurred uniquely in a specific season with a significant abundance (>5%), for instance: the copepods E. acutifrons (5.37%) in summer, C. affinis (17.53%) and O. similis (10.51%) in spring; and the ichthyoplankton B. nectabanus (22.97%) in winter and B. pectinirostris (8.33%), S. japonicus (7.76%) and P. indicus (6.90%) in spring. The distinctiveness of seasonal compositions was also illustrated by the fact that no significant relationships were found among seasonal groups at the 5% level of Spearman's rank tests (copepod:  $r_{s(summer, winter)} = 0.15$ ,  $r_{\text{s(winter, spring)}} = 0.12$  and  $r_{\text{s(summer, spring)}} = -0.11$ ; ichthyoplankton:  $r_{\text{s(summer, winter)}} = 0.04$ ,  $r_{\text{s(winter, spring)}} = -0.20$ and  $r_{\text{s(summer, spring)}} = -0.44$ ).

### Copepod and ichthyoplankton abundance

Seasonal variations in abundances of copepods and ichthyoplankton were confirmed by bootstrapping analysis

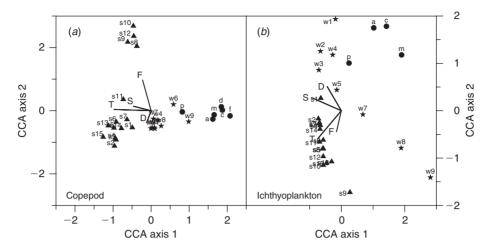


**Fig. 3.** Vertical sections of (a) temperature and (b) salinity in the north transect (From Matsu (M) to Cape Fuguei (F)) in summer, (c) temperature and (d) salinity in winter, and (e) temperature and (f) salinity in spring.

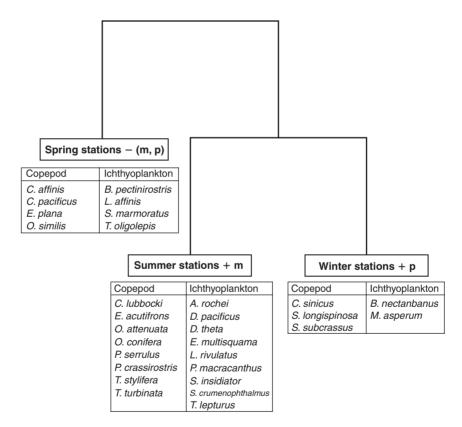
of variance (both P < 0.001); they followed a trend of reaching a peak in abundance in summer, decreasing in winter and increasing in spring. The results of multiple pair-wise comparisons indicated that the abundances of copepods and ichthyoplankton were significantly higher in summer compared to winter and spring. Specifically, for species recorded year-round, *Acrocalanus gibber* was higher in summer than in winter and spring (P = 0.003), *Clausocalanus furcatus* showed no significant differences among the three seasons (P = 0.628), *Oncaea venusta* was higher in summer than in winter and spring (P = 0.004), *Paracalanus parvus* was higher in spring than in summer and winter (P < 0.001), and

*Trichiurus lepturus* showed no differences among the three seasons (P = 0.410).

A significant correlation (r = 0.779, P = 0.005) was found to support the relationship between zooplankton abundances and environmental factors according to the canonical correlation analysis. Both copepods and ichthyoplankton were significantly loaded on the zooplankton dataset, whereas ichthyoplankton were loaded with a score higher than that for copepods (0.984 v. 0.834). For environmental factors, the loadings concentrated on the temperature, indicating temperature was the most significant environmental factor to influence copepod and ichthyoplankton abundances.



**Fig. 4.** Ordination diagram of canonical correspondence analysis (CCA) based on the species compositions of (a) copepods and (b) larval fishes. Triangles, stars and circles indicate stations in summer, winter and spring respectively.



**Fig. 5.** Diagram of two-way (station and species) indicator species analysis based on presence/absence of the dominant species, showing station clusters depicting season categories with significant corresponding indicator species.

# Discussion

The first objective of this study was to document seasonal variations of the marine conditions in Taiwan Strait. From the physical data, we produced vertical sections of temperature and salinity for the northern transect (Fig. 3) and found

that the water masses in the strait were seasonally structured. We also observed an upwelling event triggered by Ekman transport in the western strait (Fig. 3a) where surface water was driven north-easterly offshore by the prevailing winds during the SW monsoon. This recurring upwelling event was

Table 1. Dominant species of copepods in each season, the average relative abundance (%) also shown

Summer		Winter		Spring					
Copepod									
Parvocalanus crassirostris <sup>C</sup>	15.11	Paracalanus parvus <sup>D</sup>	16.07	Paracalanus parvus <sup>D</sup>	53.64				
Paracalanus parvus <sup>D</sup>	12.68	Paracalanus aculeatus <sup>B</sup>	10.56	Corycaeus affinis	17.53				
Oncaea venusta <sup>D</sup>	8.90	Calanus sinicus <sup>B</sup>	9.64	Oithona similis	10.51				
Temora turbinata <sup>A</sup>	6.56	Acartia pacifica <sup>A</sup>	9.51	Calanus sinicus <sup>B</sup>	6.66				
Euterpina acutifrons	5.37	Scolecithricella longispinosa	3.34	Oncaea venusta <sup>D</sup>	1.97				
Canthocalanus pauper <sup>A</sup>	5.20	Oncaea venusta <sup>D</sup>	3.00	Paracalanus aculeatus <sup>B</sup>	1.74				
Acrocalanus gibber <sup>D</sup>	4.28	Temora turbinata <sup>A</sup>	2.76	Clausocalanus furcatus <sup>D</sup>	0.54				
Oithona attenuata	4.20	Canthocalanus pauper <sup>A</sup>	2.34	Clausocalanus minor <sup>B</sup>	0.44				
Oncaea conifera	3.03	Clausocalanus furcatus <sup>D</sup>	2.18	Acrocalanus gibber <sup>D</sup>	0.38				
Oithona plumifera <sup>A</sup>	2.51	Clausocalanus minor <sup>B</sup>	1.98	Temora stylifera	0.30				
Paracalanus serrulus	2.48	Acrocalanus gibber <sup>D</sup>	1.86	Parvocalanus crassirostris <sup>C</sup>	0.25				
Corycaeus lubbocki	2.37	Subeucalanus subcrassus	1.55	Corycaeus pacificus	0.20				
Clausocalanus furcatus <sup>D</sup>	1.92	Oithona plumifera <sup>A</sup>	1.53	Oncaea mediterranea	0.20				
Oithona brevicornis	1.74	Subeucalanus pileatus	1.46	Lucicutia flavicornis	0.18				
Acartia pacifica <sup>A</sup>	1.58	Oithona fallax	1.18	Euchaeta plana	0.17				
Total	77.93		68.96		94.71				

<sup>&</sup>lt;sup>A</sup> Species occurring both in summer and winter; <sup>B</sup> species occurring both in winter and spring; <sup>C</sup> species occurring both in spring and summer; <sup>D</sup> species occurring in all three seasons.

Table 2. Dominant species of larval fishes in each season, the average relative abundance (%) also shown

Summer		Winter		Spring					
Larval fish									
Trichiurus lepturus <sup>D</sup>	13.60	Bregmaceros nectabanus	22.97	Sebastiscus marmoratus <sup>B</sup>	15.48				
Encrasicholina heteroloba <sup>A</sup>	7.44	Myctophum asperum	12.50	Benthosema pterotum <sup>B</sup>	9.09				
Saurida elongata <sup>A</sup>	4.32	Trichiurus lepturus <sup>D</sup>	11.46	Boleophthalmus pectinirostris	8.33				
Priacanthus macracanthus	3.43	Benthosema pterotum <sup>B</sup>	8.96	Scomber japonicus	7.76				
Leiognathus rivulatus	3.19	Encrasicholina heteroloba <sup>A</sup>	8.53	Platycephalus indicus	6.90				
Apogon endekataenia	2.68	Sebastiscus marmoratus <sup>B</sup>	6.25	Bregmaceros arabicus <sup>C</sup>	4.17				
Auxis rochei <sup>A</sup>	2.65	Auxis rochei <sup>A</sup>	3.13	Myctophum nitidulum	4.17				
Secutor insidiator	2.28	Pseudolabrus japonicus	3.13	Trichiurus lepturus <sup>D</sup>	2.01				
Diaphus theta	1.81	Saurida elongata <sup>A</sup>	2.30	Liza affinis	0.94				
Diaphus pacificus <sup>A</sup>	1.72	Diaphus pacificus <sup>A</sup>	2.08	Decapterus maruadsi	0.86				
Bregmaceros arabicus <sup>C</sup>	1.64	Engyprosopon multisquama <sup>A</sup>	2.08	Decapterus russellii	0.57				
Ceratoscopelus warmingi	1.54	Hyperoglyphe japonica	2.08	Hygophum proximum	0.57				
Symphurus orientalis	1.46	Lampanyctus ritteri	2.08	Pagrus major	0.57				
Engyprosopon multisquama <sup>A</sup>	1.44	Limnichthys fasciatus	2.08	Scomber australasicus	0.57				
Selar crumenophthalmus	1.43	Pterycombus petersii	2.08	Tarphops oligolepis	0.47				
Total	50.63		91.71		62.46				

A Species occurring both in summer and winter; B species occurring both in winter and spring; C species occurring both in spring and summer; D species occurring in all three seasons.

also documented by Jan *et al.* (1994) and it was found to be a site with high levels of nutrients (Chung *et al.* 2001). The joint effect of high nutrients and strong sunlight during the summer could result in high fluorescence as recorded in this study (Fig. 4). In winter and spring, temperatures and salinities showed decreasing trends from east to west in the strait (Fig. 3c,d,e,f), where low temperatures and salinities were correlated with the influence of the China Coastal Current. In spring, a core of high temperature and salinity was also observed in deep water (Fig. 3e,f) indicating an intrusion of

the Kuroshio Branch Current into the northern strait. From satellite images of surface temperature (Fig. 2), we determined the seasonal changes of the marine conditions in the strait, and this pattern conforms well to the circulation model proposed by Jan *et al.* (2002).

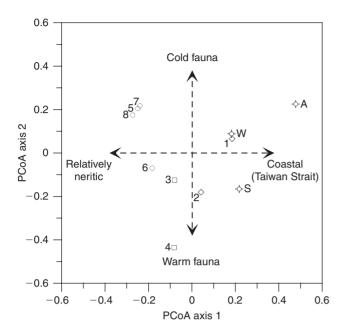
The second objective of this study was to understand seasonal successions of copepods and ichthyoplankton in Taiwan Strait. The results of TWINSPAN analysis not only characterised the seasonal changes in the communities but also showed the corresponding indicator species of each (Fig. 5).

Nonetheless, spring station 'm' was grouped with the 'summer' stations because it was the first station that encountered the effects of the Kuroshio Branch Current (Figs 1 and 2c) immediately before the marine system changed to the prevailing SW monsoon. Spring station 'p' was grouped with the 'winter' stations because it was the last station to be influenced by the China Coastal Current as the prevailing NE monsoon began to retreat. In the 'summer' group, the copepod species were basically unique except for some species of T. stylifera contributed by spring station 'm', whereas P. crassirostris co-occurred in summer and spring, and T. turbinata in summer and winter. However, ichthyoplankton species A. rochei, D. pacificus and E. multisquama occurred extensively from summer to winter and T. lepturus was even found year-round. Although some species were found yearround (Tables 1 and 2), their contributions to the seasonal compositions differed greatly. For instance, A. gibber and O. venusta were abundant in summer and decreased in winter and spring, which confirmed the record of Chen and Zhang (1965). Paracalanus parvus was the most abundant species in spring but decreased in summer and winter. This species even contributed more than half to the total numerical abundance of copepods in spring. We also found that C. furcatus was representative of a warm-water environment influenced by the Kuroshio or South China Sea currents; i.e. it was commonly found in all summer stations, it was also confined to the north of Taiwan during winter (stations 1 to 4, see Fig. 1) and occurred only at station 'm' in spring (Fig. 5). During winter, the sea north of Taiwan is influenced by the intrusion of the Kuroshio proper (Liu et al. 1992), which forms a seasonal eddy to house warm-water species. In spring, the area around station 'm' is the first place that encounters the Kuroshio Branch Current (Fig. 2c). This current flows north along a 50-m-deep trough located left of the Changyun Ridge (CyR) (Fig. 1). Our results display a complex strait fauna influenced by seasonal community successions.

The third objective of this study was to analyse how the zooplankton is linked to the changing marine conditions. As shown by the temperature and salinity profiles, the local fauna is established in summer when strait water is stratified (Fig. 3) and its primary productivity (fluorescence) may be high (s8, s9, s10 and s12; see Fig. 4a). Subsequently, energy cascades are established within this brief summer stratification, on which high copepod and ichthyoplankton abundances are based. However, during other seasons the sea is relatively unstable because the strait waters are vertically mixed (Fig. 3). In this situation, even though the China Coastal Current potentially can bring in high levels of nutrients, the energy is not sufficiently transferred into biological productivity. The correspondence of copepod species with seasonal marine conditions can be discerned using canonical correspondence analysis (CCA) (Fig. 4a). The analysis exhibited a configuration of an ordination system highly loaded by temperature and salinity on the first CCA axis and by fluorescence on the second. The CCA diagram derived from the ichthyoplankton data revealed a seasonal variation that was not as obvious as that of the copepods (Fig. 4b). However, we could still separate a cluster of summer stations from winter and spring stations. The more widely scattered pattern of the winter and spring stations implied that ichthyoplankton secondarily respond to seasonal hydrographic events. Since the CCA illustrated that the two basic water-mass parameters of temperature (T) and salinity (S) were almost equally loaded on the first axis, this possibly indicates that the ichthyoplankton composition is significantly determined by variations in the water masses.

A water mass can be characterised by its temperature and salinity properties. In general, in a TS-diagram drawn from the western North Pacific, a curve of relatively high temperatures and salinities is attributed to the water of Kuroshio proper or its branch currents, which with high temperatures and median salinities represents water from the South China Sea and with low temperatures and low salinities corresponds to the China Coastal Current (Wang and Chern 1988; Fig. 1). In order to establish the mechanisms that link zooplankton variations to hydrographic conditions, we compiled results of several copepod studies in the vicinity of Taiwan Strait (Shih and Chiu 1998; Hsieh and Chiu 2002; Lan et al. 2004; Lo et al. 2004a, 2004b). Relative abundances of dominant species were extracted when available. We computed a pair-wise percentage similarity index (psi) for all groups (Whittaker 1952) and used its compliment (1 - psi) as a distance measure to apply a principal coordinate analysis (Pielou 1984). As can be seen in Fig. 6, the first axis exhibited a contrast between coastal (Taiwan Strait) and oceanic areas and the second axis exhibited a contrast between northern (cold) and southern (warm) water origins. Our data are shown on the right-hand side with cold and warm distinctions. As a whole, we postulated that local faunas of Taiwan Strait are mixed with exotic species. Depending on seasonality, exotic species intrude to the strait either from the north along with the China Coastal Current, or from the south accompanying the South China Sea Current or the Kuroshio Branch Current.

Taiwan Strait has a distinctive oceanographic feature: the major currents are basically controlled by the timing and strength of the monsoons. This circulation pattern, in turn, determines the variation in community structures of copepods and ichthyoplankton. As climate change might influence the monsoon systems of the south-east Asia, the circulations and therefore the zooplankton communities of the strait might change significantly as a consequence. On the other hand, the world's largest dam, the Three Gorges Dam, on the Yangtze River is currently being constructed (Shen and Xie 2003). It is estimated that the productivity of the East China Sea will be significantly reduced after the dam is complete owing to a reduction in the volume, and changes in composition, of the river runoff (Chen 2000). This reduction of river runoff could also influence the productivity and strength of the China



**Fig. 6.** Ordination diagram of principal coordinate analysis (PCoA) based on relative abundances of dominant copepod species extracted from four extant materials. Diamonds from Lan *et al.* (2004): 1 – China Coastal Current and 2 – Kuroshio Branch Current; square from Lo *et al.* (2004*a*, 2004*b*): 3 – upwelling and 4 – SW Taiwan Strait; circle from Shih and Chiu (1998): 5 – East China Sea, 6 – Kuroshio proper, 7 – mixing water of East China Sea and Kuroshio proper, 8 – north coast of Taiwan; and starred circle from this study: A – spring, S – summer, W – winter.

Coastal Current, which will have dramatic impacts on the ecosystems of Taiwan Strait. This study contributes basic ecological information on Taiwan Strait. To achieve sustainable ecosystem management, it is necessary to establish a long-term monitoring programme in the strait to help deal with future natural as well as anthropogenic events.

## Acknowledgments

160

We thank Dr S. Jan of the Institute of Hydrological Sciences, National Central University for providing insightful advices on circulation of Taiwan Strait. We also thank the crews of *Ocean Research I & II* for their help when sampling at sea. Identification of ichthyoplankton species was provided by Ms K. Z. Chang and Ms C. C. Chen in the Economic Fish Laboratory, Institute of Zoology, National Taiwan University. Reconfirmation of copepod species discussed with Dr C.-t. Shih. The images of SST are provided by the National Center for Ocean Research, National Taiwan University. This experiment was supported by National Science Council under grant No. NSC89-2611-M002-049-OP4, and complies with the current laws of the Republic of China.

#### References

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. Science **296**, 1692–1694. doi:10.1126/SCIENCE.1071329

Boucher, M., Ibanez, F., and Prieur, L. (1987). Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front. *Journal of Marine Research* **45**, 133–173.

Brian, M., St. John, M., and Wieland, K. (1996). Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. *Marine Ecology Progress Series* 134, 265–281.

Chen, C. T. A. (2000). The Three Gorges Dam: reducing the upwelling and thus productivity in the East China Sea. *Geophysical Research Letters* **27**, 381–383. doi:10.1029/1999GL002373

Chen, Q. C., and Zhang, S. Z. (1965). The planktonic copepods of the Yellow Sea and the East China Sea. 1. Calanoida. *Studia Marina Sinica* 7, 20–133 [In Chinese with English abstract].

Chung, S. W., Jan, S., and Liu, K. K. (2001). Nutrient fluxes through the Taiwan Strait in spring and summer 1999. *Journal of Oceanography* 57, 47–53. doi:10.1023/A:1011122703552

Fang, K. L. (1982). A study of water masses in Taiwan Strait. Acta Oceanographica Taiwanica 13, 140–153.

Gómez, F., Echevarría, F., García, C. M., Prieto, L., Ruiz, J., Reul, A., Jiménez-Gómez, F., and Varela, M. (2000). Microplankton distribution in the Strait of Gibraltar: coupling between organisms and hydrodynamic structures. *Journal of Plankton Research* 22, 603–617. doi:10.1093/PLANKT/22.4.603

Gowen, R. J., Raine, R., Dickey-Collas, M., and White, M. (1998).
Plankton distributions in relation to physical oceanographic features on the southern Malin Shelf, August 1996. ICES Journal of Marine Science 55, 1095–1111. doi:10.1006/JMSC.1998.0418

Hill, M. O., Bunce, R. G. H., and Shaw, M. W. (1975). Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *Journal of Ecology* 63, 597–613.

Hsieh, C. H., and Chiu, T. S. (2002). Summer spatial distribution of copepods and fish larvae in relation to hydrography in the northern Taiwan Strait. *Zoological Studies* 41, 85–98.

Jan, S., Chern, C. S., and Wang, J. (1994). Influences of sea surface wind stress on summertime flow pattern in the Taiwan Strait. *Acta Oceanographica Taiwanica* 33, 63–80 [In Chinese with English abstract].

Jan, S., Chern, C. S., and Wang, J. (1998). A numerical study of currents in the Taiwan Strait during winter. *Journal of Terrestrial, Atmospheric and Oceanic Sciences* 9, 615–642.

Jan, S., Wang, J., Chern, C. S., and Chao, S. Y. (2002). Seasonal variation of the circulation in the Taiwan Strait. *Journal of Marine Systems* 35, 249–268. doi:10.1016/S0924-7963(02)00130-6

Kidwai, S., and Amjad, S. (2000). Zooplankton: pre-southwest and northeast monsoons of 1993 to 1994, from the North Arabian Sea. *Marine Biology* **136**, 561–571. doi:10.1007/S002270050716

Kidwai, S., and Amjad, S. (2001). Abundance and distribution of ichthyolarvae from upper pelagic waters of the northwestern Arabian Sea during different monsoon periods, 1992–1994. ICES Journal of Marine Science 58, 719–724. doi:10.1006/JMSC.2000.1057

Lan, Y. C., Shih, C.-t., Lee, M. A., and Shieh, H. Z. (2004). Spring distribution of copepods in relation to water masses in the northern Taiwan Strait. *Zoological Studies* 43, 332–343.

Lindley, J. A., and Reid, P. C. (2002). Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Marine Biology* **141**, 153–165. doi:10.1007/S00227-002-0803-Z

Liu, K. K., Gong, G. C., Pai, C. Z., Wei, C. L., and Chao, S. Y. (1992). Response of Kuroshio upwelling to the onset of the northeast monsoon in the sea north of Taiwan: observations and a numerical simulation. *Journal of Geophysical Research* 97, 12 511–12 526.

- Lo, W. T., Shih, C.-t., and Huang, J. S. (2004a). Diel vertical migration of the planktonic copepods at an upwelling station north of Taiwan, western North Pacific. *Journal of Plankton Research* 26, 89–97. doi:10.1093/PLANKT/FBH004
- Lo, W. T., Huang, J. S., and Chen, Q. C. (2004b). Spatial distribution of copepods in surface waters of the southeastern Taiwan Strait. *Zoological Studies* 43, 218–228.
- Mallin, M. A. (1991). Zooplankton abundance and community structure in a mesohaline North Carolina estuary. *Estuaries* 14, 481–488.
- Manly, B. F. J. (1997). 'Randomization, Bootstrap and Monte Carlo Methods in Biology.' (Chapman & Hall: London.)
- Pielou, E. C. (1984). 'The Interpretation of Ecological Data.' (John Wiley & Sons: New York.)
- Poulet, S. A., and Williams, R. (1991). Characteristics and properties of copepods affecting the recruitment of fish larvae. In 'Proceedings of the Fourth International Conference on Copepoda'. (Eds S. Uye, S. Nishida and J.-S. Ho.) pp. 271–290. Bulletin of the Plankton Society of Japan Spec. Vol.
- Rebstock, G. A. (2001). Long-term stability of species composition in calanoid copepods off southern California. *Marine Ecology Progress Series* 215, 213–224.
- Roman, M. R., Gauzens, A. L., Rhinehart, W. K., and White, J. R. (1993). Effects of low oxygen waters on Cheasepeak Bay zooplankton. *Limnology and Oceanography* **38**, 1603–1614.

- Sanchez-Velasco, L., and Shirasago, B. (1999). Spatial distribution of some groups of microzooplankton in relation to oceanographic process in the vicinity of a submarine canyon in the north-western Mediterranean Sea. *ICES Journal of Marine Science* **56**, 1–14. doi:10.1006/JMSC.1998.0413
- Shen, G. Z., and Xie, Z. Q. (2003). Three Gorges project: chance and challenge. *Nature* **304**, 681.
- Shih, C.-t., and Chiu, T. S. (1998). Copepod diversity in the water masses of the southern East China Sea north of Taiwan. *Journal of Marine Systems* **15**, 533–542. doi:10.1016/S0924-7963(97)00053-5
- Wang, J., and Chern, C.-S. (1988). On the Kuroshio branch in the Taiwan Strait during wintertime. *Progress in Oceanography* **21**, 469–491. doi:10.1016/0079-6611(88)90022-5
- Werner, F. E., Perry, R. I., Lough, G., and Naimie, C. E. (1996). Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep-Sea Research II* 43, 1793–1822. doi:10.1016/S0967-0645(96)00042-2
- Whittaker, R. H. (1952). A study of summer foliage insect communities in the Great Smoky Mountains. *Ecological Monographs* 22, 1–44.

Manuscript received 28 March 2004; revised 10 January 2005; and accepted 17 January 2005.