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Regional and Seasonal Differences in Species Composition and Trophic Groups for Tidepool Fishes of a Western Pacific Island – Taiwan

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Abstract

Spatial and temporal variations in the species composition of assemblages are common in many marine organisms, including fishes. Variations in the fish species composition of subtidal coral reefs have been well documented, however much less is known about such differences for intertidal fish assemblages. This is surprising, given that intertidal fishes are more vulnerable to terrestrial human disturbances. It is critical to evaluate the ecology and biology of intertidal fishes before they are severely impacted by coastal development, especially in developing countries such as those in the tropical western Pacific region where coastal development is rapidly increasing. In this study, we investigated the species composition, abundance, biomass and species number (richness) for intertidal fish assemblages in subtropical (northern) and tropical (southern) Taiwan across four seasons by collecting fishes from tidepools using clove oil. We also examined the gut contents of collected fishes to identify their trophic functional groups in order to investigate regional and seasonal variations for different trophic groups. We found significant differences in the species composition of tidepool fish assemblages between subtropical and tropical Taiwan. Bathygobius fuscus, Abudefduf vaigiensis and Istiblennius dussumieri were dominant species in subtropical Taiwan, whereas Bathygobius coalitus, Abudefduf septemfasciatus and Istiblennius lineatus were dominant in tropical Taiwan. Other species such as Bathygobius cocosensis, Abudefduf sordidus and Istiblennius edentulus were common in both regions. For trophic groups, omnivores and detritivores had or showed trends towards higher species numbers and abundances in the subtropical region, whereas herbivores, planktivores and general carnivores had or showed trends towards higher species numbers and biomass in the tropical region. Overall, many intertidal fish species and trophic groups showed differences in abundance, biomass and species number between subtropical and tropical Taiwan. Further studies on large scale geographical gradients in trophic groups and species compositions in the Indo-west Pacific region are encouraged to assist with ecosystem monitoring and assessment.

Keywords*: Intertidal fishes, spatio-temporal pattern, feeding guild, diet*

Introduction

Both terrestrial and marine organisms often display spatial and temporal patterns in abundance and diversity, which are strongly related to environmental variations. For example, a warmer climate and a higher variety of habitats and prey types in the tropics result in higher abundances or diversity of animals and plants at the equator with a steady decline towards the poles (reviews in Hillebrand, 2004a). Compared to terrestrial ecosystems, marine ecosystems tend to show much clearer spatial and temporal patterns in abundance and diversity due to a more consistent gradient of environmental factors (Hillebrand, 2004b; Dawson and Hamner, 2008). In marine environments, reef-associated organisms show a strong correlation between space/seasons and abundance/diversity (Mora *et al*., 2003; Bellwood *et al*., 2005). The species compositions of fish assemblages in particular have been found to show clear spatial and temporal patterns which are linked to fish migratory and reproductive behavior (Hyndes *et al*., 1999; Jaureguizar *et al*., 2004). Other factors can also explain spatial and temporal patterns of reef organisms, including higher food or habitat availability in the warmer climate closer to the equator (Bellwood and Hughes, 2001), higher productivity and energy in the tropics (Gaston, 2000) and more suitable temperature ranges in the tropics (Harriott and Banks, 2002; Munday, 2002). While fishes of reef ecosystems are well-studied, spatial

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and temporal patterns in species abundances and diversity for other marine ecosystems are not so clear (but see Ysebaert and Herman, 2002; Zabin *et al*., 2013; Arakaki *et al*., 2014; Okada *et al*., 2015).

Geographical or latitudinal patterns are also observed in the abundance and diversity of many trophic groups, such as herbivores, omnivores and carnivores (Hillebrand, 2004a). These trophic groups generally increase in abundance and diversity with proximity to the equator, and such geographical trends might be due to the availability of their food sources (Carnicer and Díaz-Delgado, 2008). The abundance and diversity of many different herbivores for example, has been shown to be determined by the geographical distribution of the algae or plants they consume (Floeter *et al*., 2005; Novotny *et al*., 2006; Kissling *et al*., 2007). Although the food sources of omnivores and carnivores are abundant closer to the equator, many studies suggest that diverse habitats and the environmental conditions are what drive high omnivore and carnivore diversity in the tropics (Worm *et al*., 2005; Bojarska and Selva, 2012; Díaz-Ruiz *et al*., 2013). However, most broad geographical patterns in the abundance and diversity of trophic groups have been examined through meta-analyses conducted on large studies of species composition and diet (González-Bergonzoni *et al*., 2012). The limited information available on trophic structures in the marine environment makes it difficult to examine geographical patterns of abundance and diversity for each trophic group in marine ecosystems. In addition, seasonal variation in food sources also affects the diet of predators which can complicate investigations of geographical patterns in trophic groups (Afeworki *et al*., 2013). Comprehensive studies on the diet of organisms and species compositions in marine ecosystems across seasons and regions are necessary in order to understand how space and time interact to influence patterns of abundance and diversity for marine trophic groups. This is particularly so for marine ecosystems other than reefs, such as intertidal zones which have received relatively little attention (Wen *et al*., 2005; Pennings *et al*., 2009; Feller *et al*., 2013).

Intertidal zones are defined as areas between the high tide line and the low tide line. This may include different habitats such as salt marsh, mangrove, sandy beach and rocky/reef tidepool (Horn *et al*., 1999). These areas are subjected to large daily fluctuations in many environmental parameters (*e.g.* temperature and salinity) due to the change of water level with the tides (Underwood and Chapman, 2000). Marine organisms, including vertebrates (*i.e.* fish), living in intertidal zones have adapted to this harsh environment (Gibson and Yoshiyama, 1999; Plaut, 1999). Intertidal fishes have physiological adaptations that allow them to cope with a harsh daily environment, and consequently they tend to be more resistant to acute environmental damage or pollution than other fishes (Ellis and Bell, 2013). Despite this, species within these intertidal marine ecosystems are vulnerable to human disturbance, especially on the coasts of many developing countries in the tropical Pacific region (Horn *et al*., 1999; Wen *et al*., 2010; Gillet, 2011). Intertidal areas have been heavily impacted by human activities, particularly urbanization and development in coastal areas (Kennish, 2001; Bulleri, 2005). In addition, artificial structures have extended into natural coastal habitats (Bulleri and Chapman, 2010), affecting many marine organisms and greatly altering the ecosystems (Burt *et al*., 2009; Wen *et al*., 2010). Currently, a limited understanding of intertidal species composition in some areas, such as Taiwan, makes it impossible to examine broad differences in abundance and diversity in the tropical western Pacific region and how these may change over time with increasing human disturbances (Prochazka *et al*., 1999).

The island of Taiwan is located at the northern point of a marine biodiversity hotspot in the western Pacific Ocean (Chen and Shashank, 2009) and is divided into tropical and subtropical climatic regions (south and north). Subtidal reefs in northern and southern Taiwan have distinctly different species compositions (Shao *et al*., 2002; Hsiao *et al*., 2011), and these differences extend beyond Taiwan to other nearby countries (*i.e.* Japan and the Philippines, Liu *et al*., 2008; Chen and Shashank, 2009). The subtidal fish, coral and algal assemblages in Taiwan exhibit seasonal/temporal patterns due to the climatic and oceanic conditions they experience (Kuo *et al*., 2001; Tsai *et al*., 2004; Kuo *et al*., 2012). Whether the species composition and trophic groups of intertidal fish assemblages in northern and southern Taiwan show the same spatial and seasonal patterns as subtidal fish assemblages is yet to be determined. Species composition studies of intertidal fishes around the western Pacific Ocean have been conducted in Japan (Arakaki and Tokeshi, 2006; Murase, 2013, 2015) and Korea (Kwun *et al*., 2016). While some studies in Taiwan have provided a list of intertidal fish species (Lee, 1980), these studies lack quantified abundance data and information about fish diets. Quantified data on the number of individuals and species of tidepool fishes in Taiwan is critical in order to establish a baseline for evaluating the impact of human disturbances in the near future. Therefore, this study aims to establish spatial and temporal patterns in species composition and trophic groups for intertidal fish assemblages in Taiwan, and to compare these with surrounding regions in the western Pacfic Ocean.

Materials and Methods

Sampling sites and fish collection

From 2001 to 2002, intertidal fishes were collected from three sites in northern Taiwan and three sites in southern Taiwan, to represent subtropical and tropical regions respectively based on their temperature records (additional Figure 1.). The intertidal zones between these two regions along the Taiwanese coast were sandy beach (western) or coastal cliff (eastern), where tidepools were not available to examine intertidal fishes. Tidepools with similar topography and environmental conditions were only found in Badouzih, Yeliou and Aodi of northern Taiwan, and Checheng, Siangjiaowan and Jioupeng of southern Taiwan (Figure 1..). Tidepools from northern Taiwan were limestone rocky tidepools with smooth surfaces and those from southern Taiwan were coral reef tidepools with rough surfaces and higher rugosity. We carefully choose tidepools with similar diameter and depth (approximately 2 m^3) and elevation (mid-tide zone and 2-3 m above waterline during low tide) to reduce possible confounding factors on fish composition (Cox *et al*., 2011). However, only one tidepool at each site was examined due to rare replicates being found at these sites.

In order to accommodate limited replication, which is common in the natural environment (Legendre *et al*., 2010), we planned repeated sampling instead of pseudoreplication and rather than having no replication at all (Davies and Gray, 2015). As such, we sampled the same sites five times, three months apart so as to encompass all seasons, except in Siangjiaowan (where sampling was done four times). We sampled in January, April, August and October of 2001, and January of 2002. Sampling was conducted between 1100 and 1600 hours during low tide to help ensure stomach fullness of the collected fishes (Munoz and Ojeda, 1997). Fishes from tidepools were used to represent resident intertidal fishes, because daily migratory intertidal fishes would rarely stay within tidepools during low tide (Griffiths, 2003; Arakaki and Tokeshi, 2006). Clove oil and hand nets were used to collect tidepool fishes following Wen *et al*. (2005). We used clove oil (anaesthesia) rather than rotenone (fish poison) to collect tidepool fishes, because clove oil is just as effective for catching hardy intertidal fishes but is less damaging to the surrounding environment (Wen *et al*., 2005). In addition, most cryptic fishes (such as hole dwellers like Blenniidae) tend to vacate their holes or crevices before becoming paralyzed when clove oil is used, making collection easier. After being euthanized with clove oil, all collected fishes were injected with 10% seawater buffered formalin then transported to the laboratory in an icebox for identification and processing (Chen and Shao, 2010; Shao, 2017).

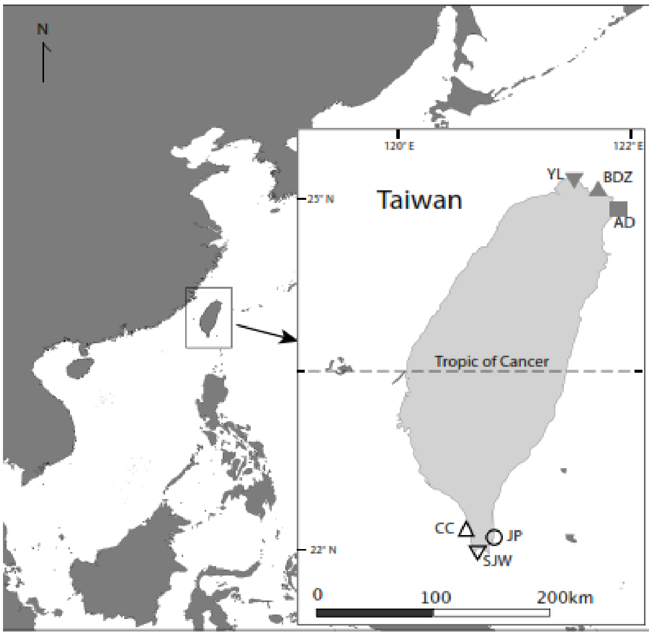

Figure 1. Map of Taiwan showing the locations of the six study sites. The three northern sites are Badouzih (BDZ, 25°08’33”N, 121°48’12”E), Yeliou (YL, 25°11’58”N, 121°41’31”E), and Aodi (AD, 25°03’12”N, 121°55’50”E); and the three southern sites are Checheng (CC, 22°05’59”N, 120°43’00”E), Siangjiaowan (SJW, 21°55’28”N, 120°49’58”E), and Jioupeng (JP, 22°08’25”N, 120°53’40”E).

Gut contents analysis

The total length and wet body-weight of each collected individual were measured to the nearest millimetre and milligram respectively. The gut contents from each individual was removed and stored in a 10% seawater buffered formalin solution to preserve the food items. Food items from the gut contents were identified visually using a dissecting microscope (10X) and an optical microscope (50X) when food items were small (*i.e.* filamentous algae and detritus). Taxonomic identifications of prey were made using two standard field guides (Gosliner *et al*., 1996; Allen *et al*., 2003). The proportion of each food item in the gut contents was estimated using the point-contact method (Jones, 1968; German and Horn, 2006), because the major trophic group in this study was herbivores. This method approximated the volume or coverage of each item in the gut contents using a 10 x 10 net reticle with 0.5 cm x 0.5 cm cells. The number of intersections on the reticle occupied by a gut item compared to all gut items represented its percentage in the individual fish. Although the volume, weight and frequency of food items in stomach contents analyses have commonly been evaluated using IRI (index of relative importance; Hyslop, 1980), this is not practical for fragmented and small food items commonly found in the gut contents of intertidal fishes (e.g. Blenniidae and Gobiidae). Food items were identified to the finest level possible, and then grouped at Class or Order level. The categories for gut contents were: Filamentous algae, Sheet algae, Corticated algae, Sand, Detritus, Foraminifera, Cyanobacteria, Gastropoda, Diatom, Medusa, Polychaeta, Insecta, Copepoda, Amphipoda, Isopoda, Ostracoda, Decapoda crab, Decapoda shrimp, Nauplius, Arthropoda, Heteropoda, Cirripedia, Bivalvia, Mysidae, Hydroida, Cladocera, Fish, Fish eggs, and Fish scales. Unidentifiable fragments of crustacean or other prey were defined as “unidentified crustacean” and “unidentified item” respectively.

Trophic groups

The dietary information collected for each species (Additional Table 1) was used to categorize all of the species into different trophic functional groups. These were: 1) herbivore, 2) detritivore, 3) planktivore, 4) omnivore, 5) general carnivore 6) benthic invertebrate feeder. In the scientific literature, no universal or concrete definition of trophic functional groups has been provided that incorporates the actual proportion of prey consumed by organisms (Gerking 1994). Herbivores and carnivores are generally thought of as solely consuming plant/algae and animals respectively (Horn and Ojeda, 1999; Norton and Cook, 1999). However, both herbivorous and carnivorous fishes can have other items in their stomachs that may not conform to such strict perceptions. Therefore, in this study, trophic functional groups were defined according to the predominant (>90%) food category found in their gut contents. For example, herbivores were defined as organisms with >90% algae in their gut contents, and carnivores defined as having >90% animal prey. Fishes with both algae and animal prey in their gut but not more than 90% of any one category were defined as omnivores. At a finer scale, carnivores were divided into the further categories of: planktivore, benthic invertebrate feeder and general carnivore. Planktivores fed on predominantly (>90%) zooplankton, benthic invertebrate feeders fed on >90% small benthic invertebrates and amphipods (<5 mm), and general carnivores on >90% fish and large decapoda crustaceans (>5 mm) such as shrimp and crabs. Although both biomass and abundance were chosen to examine trophic groups, biomass represents the trophic relationship better than abundance (Velasco *et al*., 2010). We differentiated between “resident” and “transient” species within functional groups, to distinguish between species occasionally trapped in tidepools or that occurred seasonally in a large group (transient), and those that stayed in the tidepools as permanent occupiers (resident). For example, Mugilidae and Atherinidae, which were categorised as transient fishes, were only caught once or twice throughout the whole study. Due to only a few transient species being collected on limited occasions, only resident trophic groups were compared between subtropical and tropical Taiwan. Resident and transient species were defined from both our own data and behavioral information from the literature (Horn *et al*., 1999; Griffiths, 2003; Arakaki and Tokeshi, 2006).

Statistical analyses

The number of individuals and the measured biomass for each tidepool were standardized according to the size of each tidepool prior to statistical analyses. The species richness of tidepool fishes was compared between subtropical and tropical Taiwan with rarefaction curves with repeated sampling (four seasons) sample-based Poisson model (Colwell *et al*., 2012). Rarefaction curves used an asymptote analysis based on Hill number and can estimate species diversity/richness from uneven sampling efforts and uneven sizes of sampling areas such as the uneven number of tidepool samples and tidepool sizes in this study (Work *et al*., 2010; Chao *et al*., 2014).

The influence of region, season and site (nested within region) on abundance, species number (richness) and biomass of total tidepool fishes and each trophic group were investigated

Table 1. Full list of species collected and the number of individuals from each of the six study sites.

Family	Species	Badouzih	Yeliou	Aodi	Checheng	Siangjiaowan	Jioupeng	Species total
Pomacentridae	*Abudefduf bengalensis*	3	0	2	0	0	0	5
Pomacentridae	*Abudefduf notatus*	4	3	0	0	1	0	8
Pomacentridae	*Abudefduf septemfasciatus*	0	0	1	2	11	17	31
Pomacentridae	*Abudefduf sordidus*	36	32	9	20	7	14	118
Pomacentridae	*Abudefduf vaigiensis*	55	90	7	4	20	0	176
Acanthuridae	*Acanthurus triostegus*	0	0	0	2	6	4	12
Gobiidae	*Asterropteryx semipunctata*	0	0	2	0	0	0	2
Gobiidae	*Bathygobius coalitus*	1	0	1	8	10	80	100
Gobiidae	*Bathygobius cocosensis*	23	10	31	7	10	18	99
Gobiidae	*Bathygobius cotticeps*	8	0	2	0	7	0	17
Gobiidae	*Bathygobius cyclopterus*	10	5	0	0	1	0	16
Gobiidae	*Bathygobius fuscus*	49	27	68	0	0	0	144
Blenniidae	*Blenniella bilitonensis*	2	0	10	0	0	0	12
Blenniidae	*Blenniella chrysospilos*	0	0	11	0	0	0	11
Blenniidae	*Blenniella periophthalmus*	0	1	1	2	0	0	4
Pomacentridae	*Chrysiptera brownriggii*	0	0	0	1	0	0	1
Pomacentridae	*Chrysiptera glauca*	0	0	2	1	9	8	20
Pomacentridae	*Chrysiptera unimaculata*	0	0	0	6	17	1	24
Muraenidae	*Echidna nebulosa*	0	0	0	0	16	0	16
Muraenidae	*Echidna polyzona*	0	0	1	0	1	0	2
Tripterygiidae	*Enneapterygius etheostomus*	11	1	4	0	0	0	16
Blenniidae	*Entomacrodus decussatus*	3	0	0	0	0	2	5
Blenniidae	*Entomacrodus striatus*	26	4	0	0	0	2	32
Serranidae	*Epinephelus corallicola*	0	0	1	0	0	0	1
Kyphosidae	*Girella mezina*	0	1	0	2	0	0	3
Serranidae	*Grammistes sexlineatus*	0	0	0	3	1	0	4
Muraenidae	*Gymnothorax favagineus*	0	0	1	0	1	0	2
Labridae	*Halichoeres marginatus*	0	0	0	1	6	0	7
Atherinidae	*Hypoatherina tsurugae*	0	0	0	0	653	0	653
Blenniidae	*Istiblennius dussumieri*	7	10	96	0	4	0	117
Blenniidae	*Istiblennius edentulus*	39	30	11	23	44	25	172
Blenniidae	*Istiblennius lineatus*	5	1	49	24	18	27	124
Gobiidae	*Istigobius ornatus*	0	0	0	0	12	0	12
Kuhliidae	*Kuhlia mugil*	48	0	0	13	0	18	79
Mugilidae	*Chelon macrolepis*	227	0	74	0	13	0	314
Lutjanidae	*Lutjanus gibbus*	0	0	1	0	0	0	1
Kyphosidae	*Microcanthus strigatus*	0	0	1	0	0	0	1
Blenniidae	*Omobranchus germaini*	1	0	14	0	0	0	15
Apogonidae	*Ostorhinchus cookii*	0	0	0	2	16	0	18
Gobiidae	*Parioglossus formosus*	0	0	0	1	0	0	1
Blenniidae	*Petroscirtes breviceps*	1	0	0	0	0	0	1
Blenniidae	*Praealticus margaritarius*	1	1	0	0	0	4	6
Blenniidae	*Praealticus striatus*	10	3	15	0	0	52	80
Blenniidae	*Praealticus tanegasimae*	70	9	3	0	0	5	87
Gobiidae	*Priolepis semidoliata*	0	0	1	0	0	0	1
Scorpaenidae	*Scorpaenodes guamensis*	0	0	0	0	25	2	27
Clinidae	*Springeratus xanthosoma*	1	0	0	0	0	0	1
Labridae	*Stethojulis interrupta*	1	0	0	0	0	0	1
Labridae	*Stethojulis terina*	0	0	1	0	0	0	1
Labridae	*Stethojulis trilineata*	6	0	0	0	23	0	29
Terapontidae	*Terapon jarbua*	1	0	0	0	0	0	1
Labridae	*Thalassoma hardwicke*	0	0	0	1	1	1	3
Labridae	*Thalassoma purpureum*	0	0	0	1	7	6	14
Mugilidae	*Moolgarda cunnesius*	1	0	0	0	0	0	1
	Site total	650	228	420	124	940	286	2648

using Generalized Linear Mixed Models (GLMMs) and Generalized Linear Models (GLMs) as no prior assumption of homogeneity is required. A null model (no factor) and alternative models with a combination of two fixed factors (region and season) and a random factor (site nested within region) were compared with Akaike's information criterion (AIC; Symonds and Moussalli, 2011). AIC corrected (AICc) was used in this study due to the small sample size. The Akaike weights of each model were calculated from their AICc, and the model with the highest Akaike weight was selected as the best goodness-of-fit model to explain the effect of these three factors on tidepool fishes. The abundance, species number and biomass of each trophic group was analysed using a zero-inflated model with Poisson and negative binomial distribution due to many zeros in the data for a few trophic groups. Analyses were conducted in R with *MASS, pscl, glmmADMB* package (3.2.4; R Development Core Team, 2016) and also in PAST software (Hammer *et al*., 2001).

The species composition of intertidal fish assemblages was analysed using PERMANOVA (permutational multivariate analysis of variance). We examined differences in species composition between subtropical and tropical regions as well as among seasons (Anderson, 2001) using three factors: 1) region (subtropical vs. tropical), 2) site (nested within region), and 3) season. Homogeneity of the multivariate variance was verified for all three model terms using PERMDISP (permutational analysis of multivariate dispersions, Anderson, 2001). Conformation to normality is not required for this non-parametric multivariate analysis (Anderson and Millar, 2004).

The abundance data was log (x+1) transformed and a similarity matrix was constructed using the modified Gower coefficient (Anderson *et al*., 2006). Type I (sequential) sums of squares was used to meet the assumptions of PERMANOVA due to the unbalanced sampling design. Monte Carlo randomization was used to generate a probability distribution for calculating a *p* value (p(MC)) for each factor due to a limited sample size at each site for each season (one tidepool). A similarity percentage (SIMPER) analysis was used to evaluate the contributions of fish species to variations between subtropical and tropical Taiwan. Patterns of variation in intertidal fishes between subtropical and tropical regions were visualized using Principal Coordinates Analysis (PCO) to show the differences based on the PERMANOVA results (Anderson and Willis, 2003). In addition, Pearson's correlation analysis was used to show the most correlated variables (fish species) on the PCO plot. Multivariate analysis and plotting were conducted in Primer-E v.7 (Anderson *et al*., 2008)

Results and Discussion

Tidepool fishes overall

A total of 2648 individuals from 54 species and 17 families were collected from the six sites during the five sampling periods spanning all seasons (Table 1.). Of these, 1298 individuals from 39 species and 13 families were from northern Taiwan and 1350 individuals from 37 species and 12 families were from southern Taiwan. There was no clear difference in species number (richness) between northern and southern Taiwan from rarefaction curves (Figure 2.). Fishes that were abundant in most samples of this study were: Gobiidae (*Bathygobius fuscus*, *Bathygobius cocosensis*, *Bathygobius coalitus*), Blenniidae (*Praealticus striatus*, *Praealticus tanegasimae*, *Istiblennius dussumieri*, *Istiblennius lineatus*, *Istiblennius edentulus*) and Pomacentridae (*Abudefduf sordidus*, *Abudefduf vaigiensis*). Of the 2648 fishes collected, resident species made up 68% while transient species, which consisted of only three species (*Hypoatherina tsurugae*, *Chelon macrolepis*, *Moolgarda cunnesius*), made up 32%. However, these three transient species only occurred in large numbers in one or two tidepools once or twice throughout the whole study. We excluded them from our analyses to focus on resident species only. Surprisingly, the overall abundance and biomass of tidepool fishes was not associated with any given factor (region, season or site, GLMM, Table 2.), even though the average abundance and biomass of fishes were quite different between subtropical (northern) and tropical (southern) Taiwan (Table 3.). Species number was influenced by site only (GLMM, Table 2.). The number of species at both subtropical and tropical sites was around ten for each sampling period (Table 3.).

Species composition

The species composition of intertidal fish assemblages was significantly different between regions and sites, but not across seasons (PERMANOVA, Table 4.). The difference in species composition between subtropical and tropical areas was driven by higher abundances of *Abudefduf notatus, A. vaigiensis* and *B. fuscus* in the subtropical region (Pearson's correlation analysis, Figure 3). Higher abundances of *B. coalitus* at two of the tropical sites (Checheng and Jioupeng) also contributed to the difference between subtropical and tropical regions. A range of other fishes also contributed to the difference in species composition between subtropical and tropical Taiwan (SIMPER, Table 5). *B. fuscus*, *Blenniella bilitonensis, Blenniella chrysospilos, Enneapterygius etheostomus* and

Omobranchus germaini were collected in subtropical (northern) but not in tropical (southern) Taiwan. Other species like *Acanthurus triostegus*, *Chrysiptera unimaculata*, *Echidna nebulosa, Ostorhinchus cookii, Scorpaenodes guamensis* and *Thalassoma purpureum* were only collected in tropical Taiwan. These results suggest that some tidepool fish species may have a limited distribution within Taiwan.

While no significant difference was found among sites within subtropical (northern) Taiwan, tropical (southern) Taiwan showed a significant difference in species composition according to site, which was because the species found in one site (Siangjiaowan) were different to those from the other two southern sites (Figure 3.). Siangjiaowan was characterized by many species which were considered to be more subtidal reef species than intertidal species such as *Abudefduf septemfasciatus, Chrysiptera glauca*, *C. unimaculata*, *E. nebulosa*, *Halichoeres marginatus, H. tsurugae, O. cookii, S. guamensis*, *Stethojulis trilineata* and *T. purpureum*.

Trophic functional groups

The different trophic groups did not share a consistent regional pattern (Figure 4). Herbivores, omnivores and detritivores were found to be the dominant trophic groups in tidepools across Taiwan, being two to three times more abundant than the pooled carnivores. These dominant trophic groups had or showed trends towards higher abundances in subtropical compared to tropical Taiwan, while most carnivores, which included planktivores, benthic invertebrate feeders and general carnivores had or showed trends towards higher abundances in southern, tropical Taiwan (Figure 4a.). Only detritivores and general carnivores showed statistically significant differences in abundances between subtropical and tropical Taiwan. The biomass of the three dominant trophic groups did not vary between regions, while all carnivores either had or showed trends towards higher biomass in tropical compared to subtropical Taiwan (Figure 4b.). Herbivores, planktivores and general carnivores had or showed trends towards higher species numbers in the tropical region compared to the subtropical region (Figure 4c.), but only the planktivores showed statistically significant differences (Table 6). Besides regional differences, only herbivores of tidepool fishes also showed seasonal variations in abundance, biomass and species number (Table 6.), which might relate to seasonal patterns in the availability of their algal food sources (Tsai *et al*., 2004). In addition, differences according to site (nested within region) were common for herbivores, planktivores, benthic invertebrate feeders and general carnivores for most, if not all, of the measured dependant variables (abundance, biomass and species number). This might suggest that there are different microhabitats which support finer scale variation within intertidal fish communities.

Table 2. Results from the Generalized Linear Mixed Model (GLMM) for total tidepool fishes. The GLMM examined associations of regional, seasonal and site(region) factors on abundance, species number (richness) and biomass of total tidepool fishes.

Formula	df	AICc	Akaike weight
Abundance~1	1	311.579	0.699
Richness~ Site(Region)	2	155.246	0.512
Biomass~1	1	389.365	0.653

Table 3. Differences in intertidal fish assemblages between subtropical (northern) and tropical (southern) Taiwan. Data presented are the average (±SE) abundances, species numbers (richness) and biomass of tidepool fishes per tidepool for the subtropical and tropical regions. (The numbers for abundance and biomass have been standardized).

	Subtropical	Tropical
Abundance	66.4±15.5	30.9 ± 8.3
Richness	10.5±1.0	10.9±1.0
Biomass	205.1±53.4	118.6 ± 25.2

Table 4. PERMANOVA results showing the effects of three factors on species composition of intertidal fish assemblages**.** The three factors were Region (subtropical and tropical), Season (January, April, August and October) and Site (nested within region). Star (*) indicates statistical significance where α = 0.05.

Source	df	SS	MS	Pseudo-F	p(MC)
Region	1	2.050	2.0500	3.0812	0.03*
Season	3	1.034	0.3447	1.2934	0.14
Site(Region)	4	2.642	0.6605	2.242	0.01*
Region x Season	3	1.005	0.3350	1.2647	0.18
Site(region) x Season	12	3.174	0.2645	0.89791	0.72
Residual	5	1.473	0.2946		
Total	28	11.379			

Table 5. SIMPER results showing the species that contributed the most to regional differences in species composition.

Species	Subtropical average abundance	Tropical average abundance	Average dissimilarity	Contribution (%)	Cumulative (%)
Bathygobius fuscus	1.74	0	5.5	7.38	7.38
Istiblennius lineatus	0.82	1.46	4.17	5.6	12.98
Chelon macrolepis	1.31	0.26	4.07	5.46	18.44
Bathygobius coalitus	0.09	1.24	3.86	5.19	23.62
Abudefduf vaigiensis	1.34	0.62	3.83	5.14	28.77
Istiblennius dussumieri	1.23	0.11	3.77	5.06	33.83
Istiblennius edentulus	1.51	1.64	3.62	4.85	38.68
Kuhlia mugil	0.73	0.72	3.26	4.38	43.06
Abudefduf sordidus	1.34	1.15	3.17	4.26	47.32
Praealticus striatus	0.64	0.6	3.04	4.08	51.4
Bathygobius cocosensis	1.27	1.06	2.99	4.02	55.41
Praealticus tanegasimae	0.9	0.16	2.84	3.8	59.22
Abudefduf septemfasciatus	0.05	0.76	2.49	3.35	62.56
Chrysiptera unimaculata	0	0.7	2.11	2.83	65.4
Chrysiptera glauca	0.07	0.61	1.92	2.58	67.97
Scorpaenodes guamensis	0	0.61	1.67	2.24	70.22
Ostorhinchus cookii	0	0.54	1.53	2.05	72.26
Thalassoma purpureum	0	0.49	1.44	1.93	74.2
Entomacrodus striatus	0.43	0.1	1.33	1.78	75.98
Enneapterygius etheostomus	0.45	0	1.27	1.7	77.68
Acanthurus triostegus	0	0.44	1.25	1.68	79.36
Stethojulis trilineata	0.18	0.35	1.23	1.64	81
Omobranchus germaini	0.39	0	1.1	1.48	82.48
Bathygobius cotticeps	0.3	0.24	1.06	1.43	83.91
Echidna nebulosa	0	0.4	0.97	1.3	85.21
Bathygobius cyclopterus	0.28	0.05	0.9	1.21	86.42
Blenniella chrysospilos	0.23	0	0.84	1.13	87.54
Abudefduf notatus	0.26	0.05	0.8	1.08	88.62
Blenniella bilitonensis	0.23	0	0.76	1.02	89.64
Praealticus margaritarius	0.09	0.11	0.7	0.94	90.58

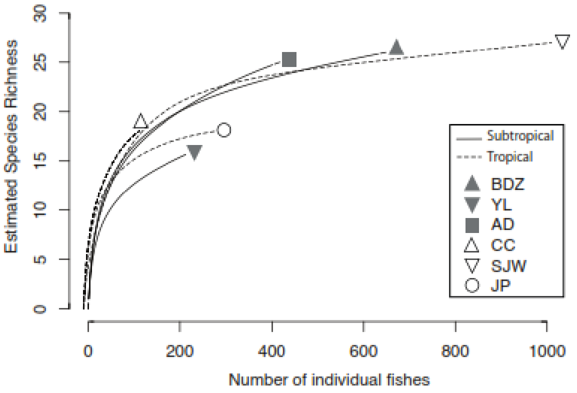

Figure 2. Rarefaction curves of tidepool fish species richness in subtropical (solid lines) and tropical (dotted lines) Taiwan.

This study is a spatial and temporal survey of intertidal fishes from northern and southern Taiwan, spanning subtropical and tropical zones of the western Pacific Ocean. Our quantitative data on intertidal fishes and their trophic groups (from dietary analysis) serves as a baseline record of species composition, abundance, biomass and species numbers for subtropical and tropical coasts in the western Pacific.

We did not find statistically significant differences in regional and seasonal patterns of abundance, biomass or species richness overall for resident tidepool fishes in Taiwan, despite the fact that the averages were quite different between the two regions. This may be due to differences in microhabitats across each site, which support different fish communities. Our analysis of the species composition of tidepool fish assemblages in Taiwan supports this, as we found significant differences in species compositions between subtropical and tropical Taiwan and differences between a couple of sampling sites.

The regional differences in the species composition of tidepool fish assemblages are consistent with other studies on shallow water and subtidal fishes (*e.g.* Shao *et al*., 2002; Hsiao *et al*., 2011). Interestingly, pairs of species within the same genera were occurring in parallel in subtropical and tropical Taiwan. For example, *Bathygobius fuscus* (Gobiidae) was abundant in northern (subtropical) Taiwan but was not found in the south whereas *B. coalitus* was abundant in the south but very rare in the north. Other examples of this also occurred in Blenniidae (*Istiblennius dussumieri* in the north vs. *I. lineatus* in the south) and Pomacentridae (*Abudefduf vaigiensis* in the north vs. *A. septemfasciatus* in the south). These sister species are also very similar in appearance. These species pairs may be good models for investigating sympatric speciation in rocky intertidal ecosystems in the Indo-Pacific region. However, more molecular evidence is needed for an informed discussion about sympatric evolutionary patterns in these species (*e.g*. Horne and van Herwerden, 2013).

By synthesizing our findings with the existing literature on intertidal fishes in the Pacific (Table 7.), we paint a more comprehensive picture of broader regional patterns in intertidal fishes. We only examine the spatial patterns for Pacific tidepool/intertidal fishes here (Table 7.) because the species compositions of rocky intertidal fish assemblages are quite different between oceanographic regions (Prochazka *et al*., 1999). Our study found that Blenniidae, Gobiidae and Pomacentridae were the dominant families of intertidal fishes in Taiwan. These findings complement those of other studies on intertidal fishes that have been done in subtropical (Japan, Arakaki and Tokeshi, 2006; Arakaki *et al*., 2014; Murase, 2015; Okada *et al*., 2015) and tropical (Hawai'i, Cox *et al*., 2011) areas of the Pacific. Our synthesis of the available information shows that Blenniidae and Gobiidae are the two most dominant families among rocky intertidal fishes across different latitudes on Pacific coasts and islands (Table 7.). In addition, Pomacentridae is an abundant family in tropical/subtropical tidepools (Taiwan, Hawai'i and Colombia), but its abundance decreases towards higher latitudes (Japan and Australia). At higher latitudes, Tripterygiidae becomes more abundant on coasts in the western Pacific and Cottidae becomes more abundant on coasts in the eastern Pacific.

We compared our data with the literature on intertidal fishes around the Pacific Ocean (Table 7.) to examine the theory from Hillebrand (2004a) that biodiversity will increase with proximity to the equator. Comparisons between studies should be treated with caution however, due to potentially different interpretations of resident and transient

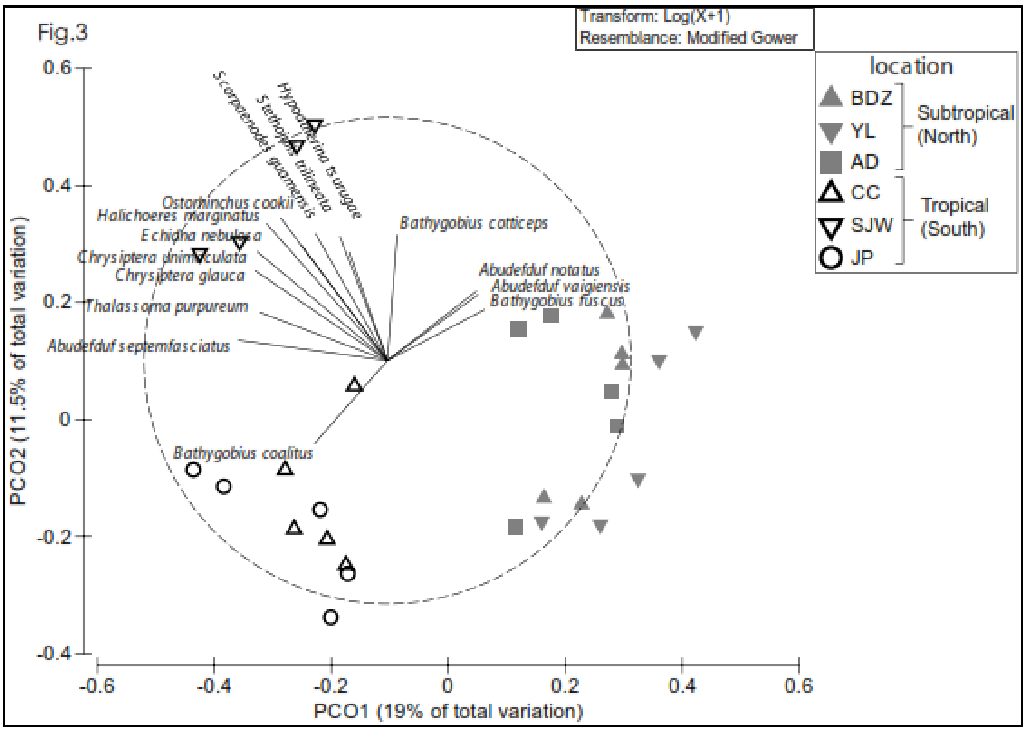

Figure 3. Principal Coordinates Analysis (PCO) plot showing variation in intertidal fishes between subtropical and tropical Taiwan.

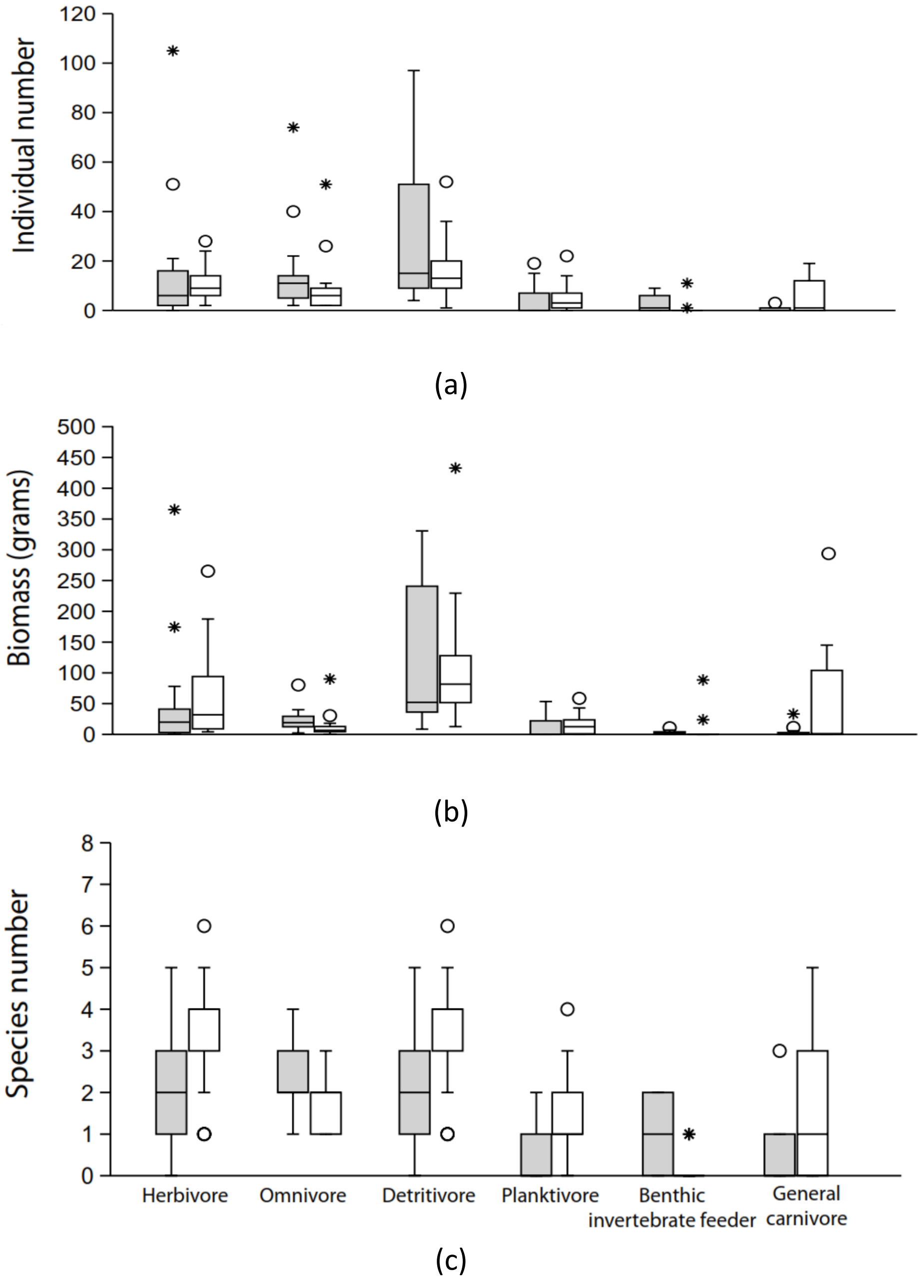

Figure 4. Boxplots of (a) abundance, (b) biomass and (c) species number for the trophic groups of intertidal fishes in both subtropical (northern) and tropical (southern) Taiwan. Lines within the boxes represent medians, and the upper and lower boundaries of the boxes represent 25th and 75th percentiles. Whiskers outside the boxes indicate the largest data point less than 1.5 times the box height. Circle symbols ° on the boxplots represent outliers outside the inner fence of box, star symbol * represent the value more than 3 times the box height.

species, sampling of tidepools at different vertical heights from the low tide line, and some tidepool volumes having to be approximated based on the data available in the literature. Species richness of resident tidepool fishes in the tropics/subtropics of the western Pacific (around 2.9/3.1 species per m^3, this study; around 0.69 species per m^3, Murase, 2015) is higher than in the tropical eastern Pacific (0.63 species per m^3, Castellanos-Galindo *et al*. 2005), the tropical central Pacific (around 0.39 species per m^3, Cox *et al*., 2011), and the temperate Pacific (around 0.17 species per m^3 Griffiths 2002; Griffiths *et al*., 2003). A similar pattern arises if all collected samples are considered, including resident, transient and rare species, with subtropical tidepools having the highest species number (3.25 species per m^3, this study; 3.56 species per m^3, Murase, 2015), followed by tropical tidepools (3.1 species per m^3, this study; 2.9 species per m^3, Castellanos-Galindo *et al*. 2005; 0.83 species per m^3, Cox *et al*., 2011), and temperate rocky tidepools having the lowest species number of all studies (0.71 species per m^3, Griffiths, 2002; Griffiths *et al*., 2003). For intertidal fishes in the Pacific, it therefore appears that there is not a clear gradient of increasing biodiversity towards the equator, and that region, rather than latitude, may be a better predictor of species richness. The western Pacific appears to have the highest number of intertidal fish species of all the Pacific regions.

In this study, we found a higher abundance and biomass of carnivores (with the exception of benthic invertebrate feeders) in the tropics

Table 6. Results from the Generalized Linear Mixed Models (GLMMs) for trophic groups. Models with poisson, negative binomial, and zero-inflation assumptions were used to examine associations of regional and seasonal factors on abundance, biomass and species number for each trophic group of tidepool fishes.

Trophic group	Best fit model	Model family	AICc	Akaike weight
Abundance				
Herbivore	Season	GLNB	215.114	0.392
Omnivore	NULL	GLNB	212.764	0.305
Detritivore	Region	GLNB	242.217	0.370
Planktivore	Site(Region)	ZINB	148.557	0.563
Benthic invertebrate feeder	NULL	ZINB	95.067	0.329
General carnivore	Region+Site(Region)	GLMM.ZIP	90.524	0.640
Biomass				
Herbivore	Season+Site(Region)	GLMM.NB	291.060	0.485
Omnivore	NULL	GLNB	233.363	0.318
Detritivore	NULL	GLNB	337.600	0.574
Planktivore	Region+Site(Region)	GLMM.ZINB	117.550	0.966
Benthic invertebrate feeder	Site(Region)	GLMM.ZINB	113.561	0.690
General carnivore	Site(Region)	GLMM.ZINB	92.911	0.540
Species number				
Herbivore	Season+Site(Region)	GLMM.NB	291.060	0.485
Omnivore	NULL	GLNB	233.363	0.318
Detritivore	NULL	GLNB	337.257	0.570
Planktivore	Region+Site(Region)	GLMM.ZLNB	177.773	0.964
Benthic invertebrate feeder	Site(Region)	GLMM.ZINB	115.868	0.894
General carnivore	Site(Region)	GLMM.ZIP	75.848	0.343

Table 7. Dominant families of rocky tidepool fishes in three broad Pacific regions. Dominant families were determined from this study and the scientific literature. The numbers in brackets represent abundances as a percentage of all tidepool fishes in that location. (NA= percentage not available).

Region	Location	Dominant families	Reference
Tropical (western Pacific)	Taiwan	Blenniidae (34%), Gobiidae (21%), Pomacentridae (20%)	This study
Tropical (central Pacific)	Hawai'i	Gobiidae (34%), Blenniidae (19%), Pomacentridae (16%)	(Cox *et al*., 2011)
Tropical (eastern Pacific)	Colombia	Gobiidae (55%), Pomacentridae (21%)	(Castellanos-Galindo *et al*., 2005)
Subtropical (western Pacific)	Taiwan	Blenniidae (42%), Gobiidae (24%), Pomacentridae (24%)	This study
Subtropical (western Pacific)	Shikizaki, Japan	Gobiidae (94%)	(Arakaki and Tokeshi, 2006)
Subtropical (western Pacific)	Yaku-shima, Japan	Blenniidae (49%), Gobiidae (32%)	(Murase, 2015)
Subtropical/temperate (eastern Pacific)	California, United States of America	Cottidae (60%)	(Yoshiyama *et al.,* 1986)
Temperate (eastern Pacific)	California, United States of America	Cottidae (NA), Stichaeldae (NA), Gobiesocidae (NA)	(Boyle and Horn, 2006)
Temperate (eastern Pacific)	Chile	Blenniidae, Tripterygiidae, Larisomidae, Kyphosidae (~20% for each)	(Munoz and Ojeda, 1997)
Temperate (western Pacific)	Australia	Gobiidae (45%), Tripterygiidae (27%)	(Griffiths *et al.,* 2003)

compared to the subtropics. This regional trend of tidepool carnivorous fishes is consistent with latitudinal patterns that have been found for trophic groups in other ecosystems (Hillebrand, 2004a). Conversely, we found that there were less herbivores, omnivores and detritivores in the tropics. These findings suggest that the principle of increasing abundance with proximity to the equator does not hold for all trophic groups of tidepool fishes in Taiwan, and this could potentially be the case more broadly across the western Pacific. However, the inaccessibility of non-English records, and limited studies examining intertidal fish trophic groups in this region may introduce a bias to this observation.

Based on biomass and abundance, detritivores are the major trophic functional group in the intertidal zone of subtropical and tropical Taiwan as well as in other regions (Hundt *et al*., 2014). Despite the relatively small size of most detritivorous species, they have a large biomass overall compared to other trophic groups because of their high numbers. Notably, Blenniidae which are generally small in size were very numerous in our survey data. Detritus and filamentous algae were the two most common food items in the gut contents of Blenniidae, which is in line with findings from other studies on intertidal blennies (Wilson, 2000; Castellanos-Galindo and Giraldo, 2008). Detritus is often found in the diet of benthic fishes, but may be consumed incidentally while they are feeding on infauna (Gerking, 1994). However, Wilson (2000) and Wilson *et al*. (2001) suggest that detritus is a rich nitrogen and lipid resource for subtidal coral blennies (*Salarias patzneri*). Given the likely nutritional benefit of detritus for Blenniidae, and that we found the gut contents of tidepool blennies on average consisted of twice as much detritus as algae, we categorized them as detritivores. Other methods for identifying diet, such as stable isotope analysis, could be employed to ascertain Blenniidae's trophic group in future (e.g. Ho *et al*., 2007). Detritivorous fishes play an important role in transferring nutrients from detritus into higher trophic levels within reef ecosystems (Wilson *et al*. 2003). The predominance of detritivorous blennies within tidepools around Taiwan means this family is likely a strong contributor to nutrient transfer, and plays an important role in the trophodynamics of intertidal assemblages.

Herbivores, mainly Pomacentridae and Acanthuridae, were second to detritivores as the most dominant trophic functional group in terms of abundance, biomass and species number. This is in contrast to other studies of trophic structures in intertidal fishes, which have tended to show carnivorous species as being the most numerous (Munoz and Ojeda, 1997; Velasco *et al*., 2010). These studies examined fishes in temperate regions however, where herbivory is expected to be less common (Gibson and Yoshiyama, 1999). We found that the abundance of herbivores in subtropical Taiwan was higher than in tropical Taiwan, but the species number was higher in tropical Taiwan. One explanation for the higher abundance of herbivores in the subtropical region could be higher algal abundance. Algal abundance and coverage was not surveyed in this study, but Wen *et al*. (2013) showed that macroalgae occurs in higher abundance in subtropical compared to tropical shallow reefs. The most common macroalgae that we found in the gut contents of herbivores (i.e. *Cladophora* spp., *Centroceras* spp., *Sphacelaria* spp., *Chaetomopha* spp., *Hypnea* spp., *Gelidium* spp., *Ulva* spp. and *Enteromorpha* spp.) are also more abundant in subtropical Taiwan lending support to this explanation (Tsai *et al*., 2004). In contrast to our findings, herbivores on coral reefs have been shown to be more abundant as well as account for higher biomass in tropical regions compared to subtropical and temperate regions, despite there being less macroalgae in the tropics (Meekan and Choat, 1997). Many rational explanations have been suggested for this, for example, macroalgae in tropical regions can be easier to digest and have a higher energy content (reviews in Horn, 1989). Yet, no solid conclusions from studies on the interaction between intertidal herbivores and algae have been made. This may be because coastal eutrophication from human activities has changed the abundance and biomass of coastal algae globally, which makes it difficult to examine the relationship between herbivores and algae in intertidal areas without biases (Burkepile and Hay, 2006).

We detected minimal significant seasonal variations in species composition, abundance, biomass and species number for intertidal fishes and their trophic functional groups in subtropical and tropical Taiwan. This is in contrast to many studies on coral reef fishes which have indicated seasonal variations in movement, composition and recruitment of fishes due to seasonal fluctuations in environmental parameters or food availability (Abesamis and Russ, 2010; Bijoux *et al*., 2013; Okazaki *et al*., 2012). With respect to intertidal fishes however, overall our results are in line with other studies which show stable species diversity in subtropical and tropical tidepool fish assemblages across seasons (Castellanos-Galindo *et al*., 2005; Murase, 2013). We observed some transient species in large numbers in one or two of our samples, suggesting seasonal variation. However, these species did not appear in other sites in the same region, hence there is no conclusive evidence of seasonal variation in these species. It may be that the species composition of intertidal fish assemblages can remain stable across seasons because the diet of these fishes might shift as food (macroalgae and invertebrate) availability changes. Such dietary shifts could explain why seasonal stability in species diversity has also been found for tidepool fishes in other parts of the Pacific (e.g. Castellanos-Galindo *et al*., 2005; Murase, 2013). Indeed, benthic macroalgae and other invertebrates which are food sources for fishes show significant seasonal variation in subtropical and tropical Taiwan (Tsai *et al*. 2004; Shieh and Chi 2010). A closer examination of the diets of intertidal fishes across time may reflect these seasonal patterns.

Due to the temporary and patchy nature of tidepools, it was a challenge to quantify fish abundance and diversity, as uncontrollable factors may introduce bias. The fishes we collected from tidepools were used to represent the abundance and diversity of intertidal fish assemblages. Although Arakaki and Tokeshi (2006) did not find significant differences between captured samples and underwater visual census (UVC) data on temperate-subtropical intertidal fishes, the possibility that we missed some resident species during fish collection cannot be ignored. For instance, in an exploratory survey using UVC during high tide, we saw more mobile fishes such as Pomacentridae and Labridae in the intertidal zone, but much fewer resident species like Gobiidae and Blenniidae (Wen pers. obs.). This suggests that mobile species will migrate with the tides and resident species are too cryptic to be observed by UVC. Collection of tidepool fishes was chosen for our purpose because these cryptic fishes are less studied as compared to the mobile species commonly surveyed in other subtidal studies. In addition, the size of the tidepool may affect species composition. For example, the site Siangjiaowan, where the tidepool was unavoidably twice the size of those at other sites, had more carnivores and larger individuals. However, the difference between northern (subtropical) and southern (tropical) Taiwan was consistent across all sites.

Many logistical and physical obstacles inherent in the study of intertidal fishes have made this an under-studied area of research. This is problematic, because with increasing coastal development and human activity, the impacts on intertidal fish assemblages are dramatically increasing. Very limited impact assessments can be done on intertidal fishes due to the lack of long-term studies and baseline data. For example, one site used in this study (Aodi) is only 50 m from breakwaters (Wen *et al*., 2010), and even though the tidepool we chose seems to be in a natural, unaffected condition, the potential influence from nearby human activities were unknown. The intertidal habitat examined in Wen *et al*. (2010) has since disappeared but the lack of historical data for a comprehensive before-after-control-impact study makes it difficult to illustrate the loss. Likewise, only a few studies have been published on the Indo-western Pacific Ocean biodiversity hotspot. Little is known about the geographical (latitudinal or longitudinal) patterns of intertidal fishes in the Indo-western Pacific region compared to the eastern Pacific. While the present study makes headway in this regard, more studies on intertidal fishes are encouraged to build up a baseline of data, which will assist in measuring and understanding potential future impacts from human disturbance.

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