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Shyh-Bin Wang, Yi-Lin Chen, and Kwang-Ming Liu

Key words: fishing pressure, northeastern Taiwan, *P. anomala*, reproductive traits.

ABSTRACT

The Japanese butterfish, *Psenopsis anomala*, is one of the most important fish species for trawl fisheries in Taiwan. This species has been intensively exploited in recent decades; however, how the species adapts to this impact by changing its life history traits is poorly known. In this study, we evaluated the change in the reproductive traits of the Japanese butterfish based on samples collected 25 years apart from the waters off northeastern Taiwan. There was a significant change in the mean length of the fish caught between 1984 and 2008. The spawning season was similar for both periods, but energy reserves in the muscle and liver both decreased in 2008, especially prior to the onset of spawning. The sizes at first sexual maturity for both sexes decreased slightly, whereas the total and relative fecundities for females increased substantially. The sex ratio was skewed toward females in the pooled annual samples, as well as in most months of 1984, but this pattern was not found in 2008. It appears that *P. anomala* may compensate for the loss of population biomass by producing numerous smaller eggs and may spawn more egg batches even under lower body mass conditions. These changes are a possible response to the impact of intensive fishing pressure, which has affected not only *P. anomala* but also its prey in the ecosystem. The implications for the management of the demersal fishery resources of this region were further discussed in this study.

I. INTRODUCTION

The assessment of fishing impacts on local marine ecosystems is of great interest to conservation and management practices (Jouffre and Inejih, 2005). Research from many parts of the world (Pauly et al., 1998; Pauly et al., 2000; Kaiser et al., 2002) has indicated that fishing may have multiple effects on an ecosystem through changes in predator-prey interactions, size distributions, or fishery-induced evolution (e.g., smaller size or earlier age-at-maturity). Fishing may also affect populations of non-target species as a result of bycatch or ghost fishing (Kaiser et al., 2002) and lead to a reduction in habitat complexity and changes in community structure.

Substantial reductions in the abundance of commercially important species as well as changes in fish community structure and species composition due to intensive fishing have been documented for many marine ecosystems (Greenstreet and Hall, 1996; Jennings et al., 1999; Blanchard, 2001; Wang et al., 2013). Shin et al. (2005) stated that fishing is always size selective. Removing large fish, which are more valuable, modifies the size structure and functioning of fish assemblages. Greenstreet and Hall (1996) showed that the exploitation of the North Sea groundfish assemblage has led to a decrease in abundance and a shift in size composition from larger to smaller fish. The age and/or size truncation of exploited populations driven by size-selective fishing practices are believed to be a widespread phenomenon in many aquatic ecosystems (Hsieh et al., 2005).

Intensive fishing also leads to changes in the life history traits of exploited populations, such as the growth rate, size at first maturity and fecundity (Jennings et al., 1999; Engelhard and Heino, 2004; Hutchings, 2005; Olsen et al., 2005). Changes in maturation characteristics of Norwegian herring, *Clupea harengus*, and Atlantic cod, *Gadus morhua*, were found to have coincided with a collapse in the stocks (Engelhard and Heino, 2004; Olsen et al., 2005). Hwang et al. (2002) also reported changes in the growth rate and maximum size of the moonfish, *Mene maculate*, in the south-western waters of Taiwan following more than a decade of exploitation.

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The Japanese butterfish, *Psenopsis anomala*, is an economically important demersal fish species that is widely distributed from southern Japan to the East China Sea and is commonly found in trawl catches along the northeastern, northern and western coasts of Taiwan (Wang and Chen, 1995). Although the total catch of this species is not high, averaging approximately 4,700 mt annually between 1999 and 2008 (59% from offshore, 37.5% from far-sea and 3.4% from coastal fisheries) (Anonymous, 1976-2009), the catch from Taiwanese waters is the highest in the world (Hwang, 2006).

The northeastern waters of Taiwan are a traditional and important trawl fishing ground. The catch in this area accounts for 1/6th of the total coastal trawl catch of Taiwan. This region has been intensively fished over the past few decades, resulting in changes in size and composition of the fish species that are captured (Wu, 2002). Catches of several commercially important fish, such as the black croaker (*Atrobucca nibe*), bigeye (*Priacanthus macracanthus*), yellow sea bream (*Dentex tumifrons*), red tilefish (*Branchiostegus japonicus*), lizardfish (*Synodontidae*), and Japanese barracuda (*Sphyraena japonica*) are now dramatically lower than those of 20 years ago (Wang et al., 2007). In addition, a shift in species dominance in the ecosystem has also been reported, as the catch percentage of flatfishes increased substantially in recent years and the total landing decreased (Wang et al., 2013). In a recent study of bycatch fish, Wang et al. (2007) also found an obvious increasing trend in the percentage of trash fish, from 15.8% in 2002 to 28.4% in 2006, with a peak of 50.5% in 2008, suggesting that the economic value of fishing in the region may have decreased. As a result, there has been a call for the protection of fishery resources and the creation of marine protected areas in the coastal regions of Taiwan (Chang and Liao, 2002; Chen, 2006).

The catch statistics of *P. anomala* can be traced back to the 1970s, when the coastal and offshore trawl fisheries targeting butterfish had not yet been well developed. The estimated catch per unit effort (CPUE) of *P. anomala* from these fisheries (Anonymous, 1976-2009) showed significant increases during the early 1980s and reached a peak in the late 80s and early 90s; however, the CPUE fell dramatically thereafter and has remained low in recent years (Fig. 1). The groundfish surveys conducted in 2006 by the Fisheries Research Institute (Taiwan) also showed a significant decline in catches of *P. anomala* in the northern and northeastern waters of Taiwan when compared with data obtained 20 years ago (Chin S.S., pers. comm.).

Despite the economic importance of *P. anomala* and its potential threat due to intensive fishing, little is known about its life history and population dynamics, as well as the changes in these characteristics caused by environmental or human impacts in this region. A preliminary study on the distribution pattern of *P. anomala* in Taiwan waters was conducted by Chen (1959). Further, Wang and Chen (1985) reported the results of a histological study of gonad development. The reproductive biology and seasonal changes in the energy reserves of this species were also described by Wang and Chen (1995) and Wu et al. (2012). However, no additional studies have been conducted to date.

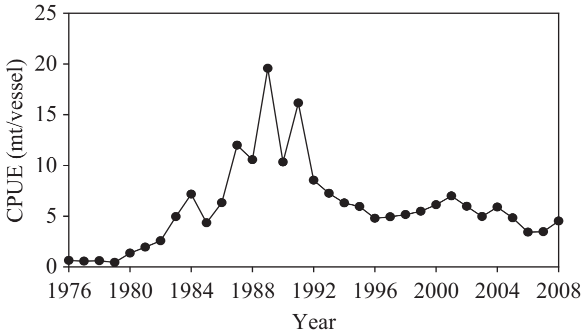

Fig. 1. **Estimated catch-per-unit-effort (CPUE, mt/vessel) of *Psenopsis anomala* from coastal and offshore trawlers operating in the waters around Taiwan between 1976 and 2008.**

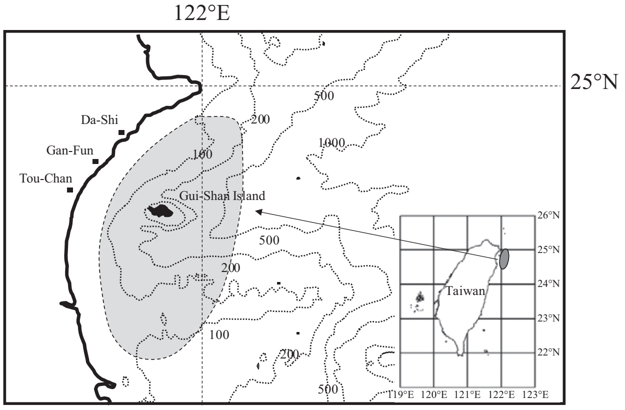

Fig. 2. **Map showing bathymetric contours of the sampling site (shaded area) of the study. Numbers are isobaths in meters.**

By analyzing samples of *P. anomala* collected off the northeastern coast of Taiwan over two time periods separated by 25 years, this study aimed to examine changes in energy reserves and reproductive traits, including spawning season, size at first maturity, sex ratios, and total and relative fecundities, and to explore how these changes may be related to the intensive fishing pressure in the region.

II. MATERIALS AND METHODS

The specimens of *P. anomala* were randomly collected on a bi-weekly basis from the catches of small bottom trawlers operating in the northeastern waters of Taiwan (Fig. 2) from March 2007 to July 2008. Data records from the 1984 sampling, previously published by Wang and Chen (1995), were extracted from the database and used for comparison purposes. The sampling and analytical methodologies were identical for both periods to ensure robust comparison. In total, 670 specimens (270 males and 400 females) were collected in 1984, and 689 specimens (346 males and 343 females) were collected in 2008. In the laboratory, fresh samples were dissected, the sex was identified, and measurements of the fork length (FL, mm, to 0.1 cm), body weight (BW, g, to 0.1 g) and gonad (GW) and liver (LW) weight (to 0.01 g) of each fish were taken. The gonads of mature females during the spawning season were removed and preserved in 10% formalin (Wang and Chen, 1995) for later fecundity estimation.

Because the fork length to body weight relationships (FL-BW) from the earlier sampling event (1984) were only available for January and May (Wang and Chen, 1995), the relationship for 2008 was estimated based on data from January alone for the purpose of comparison. The difference in log-transformed relationships between the two periods was examined using an analysis of covariance (ANCOVA). The Kolmogorov-Smirnov (K-S) test was used to examine the differences in the length frequency distributions of males and females between the two periods. All tests were performed using SAS software (SAS Institute Inc., 2008). In addition, biological indices were calculated to assess possible changes in maturity, energy reserve patterns and fish condition. The gonadosomatic index (GSI) was calculated as $GSI = [GW/(BW-VW)] \times 10^2$. The Fulton-type condition factor was estimated by $CF = [(BW-VW)/FL] \times 10^5$, and the hepatosomatic index (HSI) by $HSI = [LW/(BW-VW)] \times 10^2$, where GW is wet gonad weight (g), BW is wet body weight (g), FL is fork length (mm), VW is wet visceral weight (g) including the liver and gonads, and LW is wet liver weight (g).

Total fecundity, which represented the mean number of eggs possessed by an individual female during the spawning season, was calculated as the (number of eggs > 0.2 mm in 0.05 g gonad tissue) × (total gonad weight/0.05 g gonad weight). The criteria for oocyte development and measurement were described by Wang and Chen (1985). Batch fecundity was estimated by the (number of hydrated eggs in 0.05 g tissue) × (total gonad weight/0.05 g gonad weight) (Wang and Chen, 1995). Relative (i.e., weight-specific) fecundity (per unit body weight) in each month of the spawning season was derived in a similar way. A Chi-squared (χ^2) test was used to examine the homogeneity of sex ratios. Based on these estimates, comparisons between the two sampling periods (1984 *vs*. 2008) were then analyzed.

III. RESULTS

1. Length Frequency Distribution

A comparison of the length frequency distributions of the two sampling events (Fig. 3) revealed that females collected in 1984 were dominated by the 180-195 mm size class, whereas those collected in 2008 were much smaller, predominantly with sizes of 165-185 mm (K-S test, $P < 0.05$). For males, individuals collected in 1984 were dominated by the 165-175 mm size class, whereas those collected in 2008 were smaller, predominantly with sizes of 155-175 mm (K-S test, $P < 0.05$). The difference was more pronounced for females than for males.

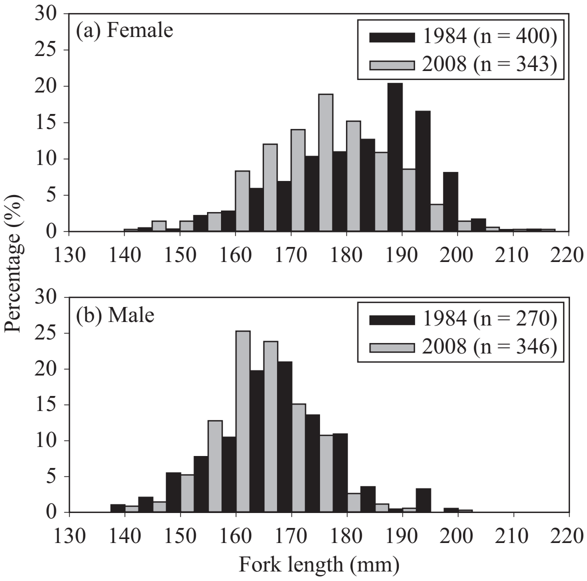

Fig. 3. Comparison of length frequency distribution of (a) female and (b) male *Psenopsis anomala* collected in 1984 and 2008.

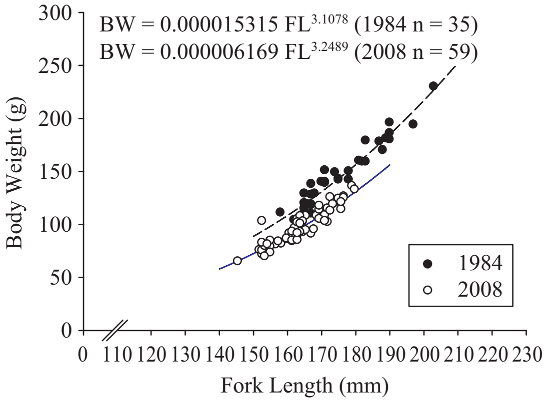

Fig. 4. Comparison of fork length (mm) - body weight (g) relationships for *Psenopsis anomala* collected in winter (January) of 1984 and 2008.

2. FL-BW Relationship in Winter

We found a significant difference ($P < 0.001$) in the log-transformed FL-BW relationship between the samples from January 1984 and January 2008 (Fig. 4). For the same size of fish, the mean body weight of individuals in 2008 (when stock levels were relatively low) was approximately 15% less than that in 1984 (when the fishery was in a rapid development stage, before it reached the highest catch). An unexpected decrease in fish growth appears to have occurred.

3. Sex Ratio

The sex ratios of *P. anomala* in the trawl catches varied seasonally (Fig. 5(a)). In 1984, females dominated during the spawning season from February to October (Wang and Chen, 1995), but males were more abundant at other times of the

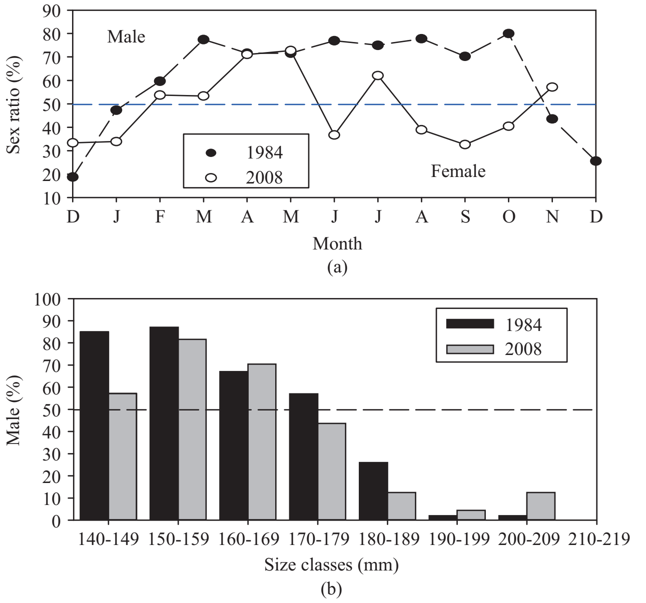

Fig. 5. **Comparison of (a) monthly sex ratio and (b) size-specific sex ratio for *Psenopsis anomala* collected in 1984 and 2008.**

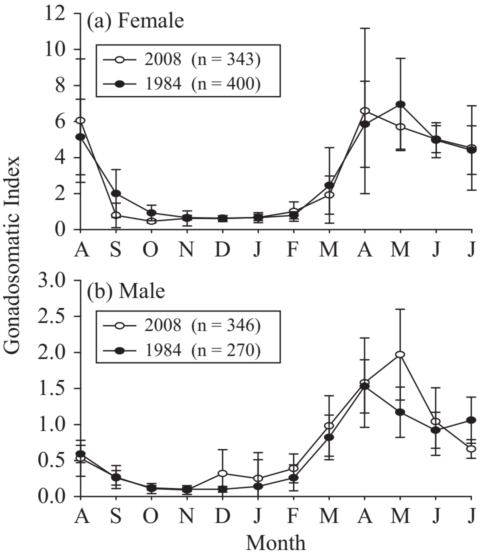

Fig. 6. **Comparison of seasonal changes in gonadosomatic indices for (a) female and (b) male *Psenopsis anomala* collected in 1984 and 2008 (±1 SD are indicated).**

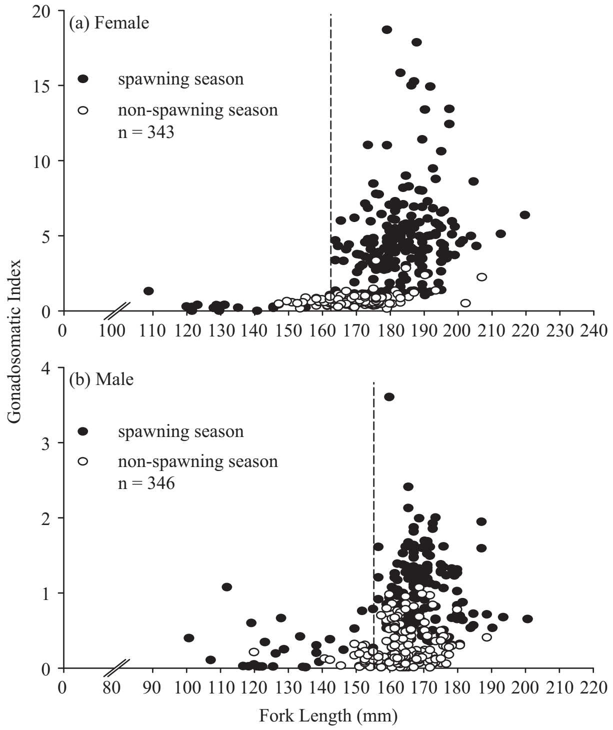

Fig. 7. **Fork length in relation to gonadosomatic index for (a) female and (b) male *Psenopsis anomala* collected in 2008. (dashed line indicates size at first maturity of each sex).**

year. However, the number of females was greater during the peak spawning season from April to May 2008 and was less than that of males in December 2008. When all specimens were pooled, the number of females was significantly more than that of males (χ^2, $P < 0.05$) in 1984, but this pattern was not found in 2008. It is clear that the dominance of female fish in the pooled sample and many of the spawning months in 1984 was no longer apparent in 2008.

In addition, sex ratios by 10 mm size classes (Fig. 5(b)) also showed significant differences. Fish between 140 and 170 mm FL in 1984 and 2008 were mostly males (χ^2, $P < 0.05$), whereas females dominated size classes between 180 and 210 mm in 1984 and between 180 and 200 mm in 2008. The dominance of males in the smaller size classes and of females in the larger size classes was similar in both samples.

4. Spawning Season

Monthly changes in the GSI for both sexes of *P. anomala* (Fig. 6) were nearly identical for the two time periods of this study. Gonad development began in March and peaked in April or May. The GSI decreased rapidly after August and reached the lowest values between October and January, indicating that spawning was essentially completed by the end of the summer.

5. Size at First Maturity

For the 2008 samples, males greater than 155 mm FL and females greater than 162 mm FL exhibited a significant increase in the GSI during the spawning season (Fig. 7). This indicated that size at first maturity was 155 mm for males and 162 mm for females in 2008. These sizes were slightly smaller than those reported in 1984, when the sizes at first maturity were 157 mm and 168 mm for males and females, respectively.

6. Seasonal Conditions and Hepatosomatic Indices (HSI)

The Fulton-type condition indices for both female (Fig. 8(a))

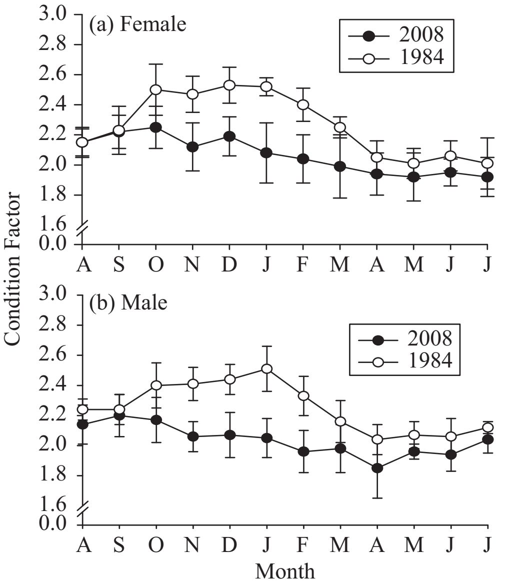

Fig. 8. Comparison of seasonal changes in condition indices of (a) female and (b) male *Psenopsis anomala* collected in 1984 and 2008 (±1 SD are indicated).

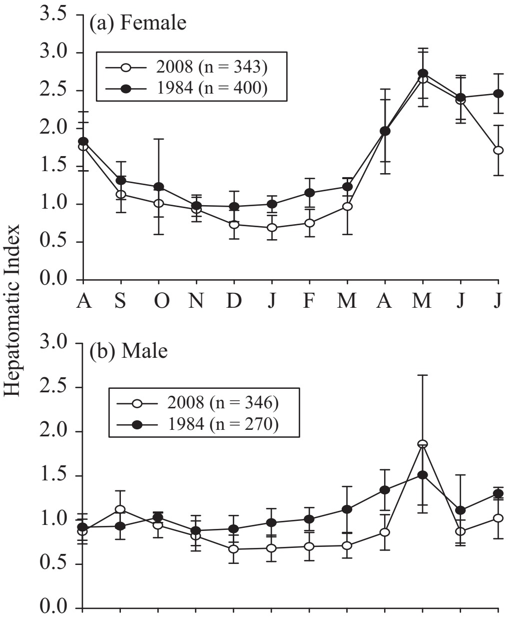

Fig. 9. Comparison of seasonal changes in hepatosomatic indices for (a) female and (b) male *Psenopsis anomala* collected in 1984 and 2008 (±1 SD are indicated).

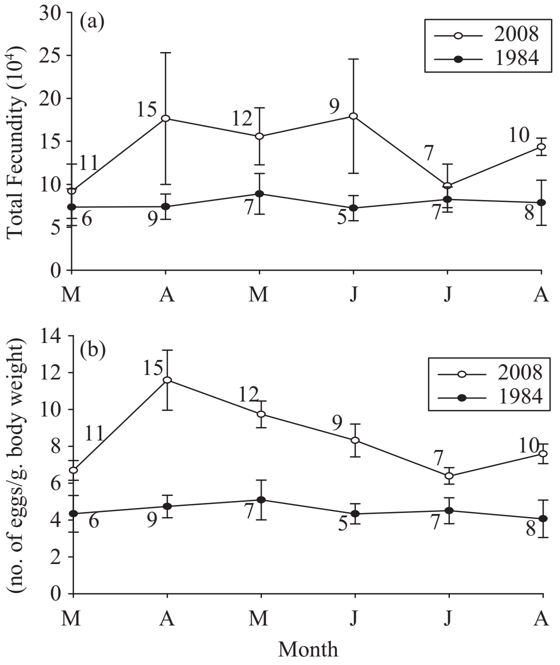

Fig. 10. Comparison of (a) total fecundity and (b) relative fecundity for female *Psenopsis anomala* collected in the spawning season (Mar. to Aug.) of 1984 and 2008 (±1 SD are indicated) (no. represented for the gonad samples examined).

and male (Fig. 8(b)) fish started to decrease after January and reached the lowest values during the major spawning season in 1984. The indices began to increase in August and remained high throughout the fall and winter before decreasing again in January. In 2008, the seasonal patterns were different. Both indices started to decrease right after fall and continued to decline until the end of spawning. It is clear that the overall energy reserves in the muscle for both sexes were lower in 2008 than those in 1984, especially during the fall-winter period when fish began to store the energy required for spawning.

The seasonal pattern of HSI was similar for both sexes (Figs. 9(a) and 9(b)) in both samples, but differed from the pattern shown by the Fulton indices. HSI began to increase in February, when the Fulton indices were at a seasonal low, and was highest for both sexes just before the peak spawning month (May). It decreased sharply immediately after spawning and reached its lowest values between November and February. Comparing the two samplings, for both sexes the HSI was different in the period from December to March, with lower values prior to the spawning season for individuals collected in 2008.

7. Fecundity and Batch Fecundity

Total fecundity, estimated from females with mature ovaries, remained relatively constant from March to August in 1984 (Fig. 10(a)). However, it increased in March, remained high from April to June, and decreased slightly in July and August in 2008. Furthermore, the total fecundity for all spawning months was much higher in 2008 than that in 1984. Fecundity relative to body weight was also higher in 2008 than that in 1984. It increased in March, peaked in April (Fig. 10(b)), and decreased to a low level in July in the 2008 sample; however, it remained relatively constant throughout the spawning months in 1984.

Table 1. Comparisons of GSI, gonad weight (GW), total fecundity (TF), batch fecundity (BF) (no. of hydrated eggs) and its percentage (%) in preovulatory ovaries of *Psenopsis anomala* collected in 1984 and 2008 (range and mean ± 1 SD are indicated).

Year	GSI	GW	TF	BF	%
1984 (N = 18)	7.34-14.57 (10.92 ± 1.93)	11.80-22.40 (16.70 ± 3.33)	67,973-154,560 (104,440 ± 23,659)	27,237-61,824 (40,856 ± 11,315)	33.10-46.30 (38.90 ± 4.48)
2008 (N = 17)	8.02-15.86 (11.20 ± 2.68)	9.30-21.94 (15.01 ± 4.15)	88,183-309,881 (157,533 ± 61,769)	18,748-81,406 (43,532 ± 16,396)	20.10-40.30 (28.40 ± 7.07)

The mean total and batch fecundity (no. of hydrated eggs), estimated from female fish with a similar GSI (i.e., similar developmental stage), were 157,533 ± 61,769 and 43,532 ± 16,396 in 2008, respectively (Table 1), and 104,440 ± 23,659 and 40,856 ± 11,315, respectively, in 1984 (Wang et al., 2008). The total fecundity was significantly different between the two periods. The number of eggs per batch averaged approximately 38.9% of the total fecundity in 1984 but was only 28.4% in 2008 (t-test, $P < 0.01$). The observed higher total fecundity, together with a similar (or even lower) mean gonad weight, and a lower batch fecundity, suggested that female fish in 2008 not only produced a greater number of smaller eggs but may also have produced more batches during the spawning season. Indeed, the most dominant oocyte group (0.45 mm) and the largest oocyte group (0.9 mm) found in pre-ovulatory ovaries were larger in those recorded in 1984 than in those recorded in 2008 (0.3 mm and 0.8 mm, respectively).

IV. DISCUSSION

1. Changes in Size and Sex Compositions

Our study found that after 25 years of exploitation, there has been a significant shift in the dominant size classes of *P. anomala*, from 180-195 to 165-185 mm FL for females and from 165-175 to 155-175 mm FL for males. The mean fork lengths were 186.4 and 170.7 mm in 1984 and 177.6 and 165.3 mm in 2008 for females and males, respectively. It is unlikely that the observed change was the result of sampling error as the sample sizes were large, collected randomly from the same site with similar sampling intervals, and pooled over a 14-month period. The mesh size used by trawlers was also the same for both sampling periods. However, the majority of *P. anomala* caught by trawlers of this region were adults; this was possibly due to stage-specific migration (Wang, 1985). We therefore view this change to be a possible result of the long-term exploitation of adults, which disproportionally removed more females from the population.

Fishing affects demersal fish communities through the selective removal of target species, usually larger species, as well as through non-target species bycatch and habitat modification, thus resulting in changes in the overall biomass, species composition and size structure (Pauly et al., 1998; Jennings et al., 1999). For example, the population structure of Peruvian hake, *Merluccius gayi peruanus*, has changed in response to heavy fishing, with a dramatic reduction in mean size. Large hake dominated landings before the 1980s, but smaller hake represented the bulk of the catches thereafter (Wosnitza-Mendo et al., 2004; Guevara-Carrasco and Lleonart, 2008). In an analysis of data sets from different regions of the world, Bianchi et al. (2000) also found that the size spectra of fish appeared to respond in a consistent way to changes in exploitation levels. In most areas studied, particularly in high-latitude regions, the authors observed a downward slope, reflecting a relative decline in the number of larger fish.

The observed change in size composition of *P. anomala* also affects the monthly and size-specific sex ratios of the species. As females are larger than males and dominate the large size classes, removing large individuals from the population would result in a decrease in the dominant size groups, where males become more abundant. As a result, the sex ratio for the pooled sample, which was significantly different from 1:1 in 1984 and in which females were dominant, showed an equal number of both sexes in 2008. This could also explain why the monthly sex ratio of *P. anomala* differed between 1984 and 2008. In 1984, females overwhelmingly dominated in all spawning months (March to October), but this was not found in 2008 when sex ratios were significantly different, and females were dominant only in April and May. Size-selective fishing that alters the sex ratios of exploited populations and shortens the reproductive life span has been reported for many species (Buxton, 1993; Sadovy, 1996; Jennings et al., 2001). Two grouper species in lightly exploited offshore Jamaican banks had sex ratios (male/female) of 1:0.72 and 1:0.85 compared with 1:5.6 and 1:6.0 at a heavily fished inshore region (Thompson and Munro, 1983).

Significant changes in the sex ratio and size composition, such as those of *P. anomala* reported in our study, should receive great attention as the majority of larger fish are female and larger females also produce more eggs in the population (Wang and Chen, 1995; Trippel, 1998; Macchi et al., 2004; Takasuka et al., 2005; Murua et al., 2006). Intensive fishing that continuously removes large females may result in a reduction in the long-term productivity of the stock.

2. Changes in Body Mass and Energy Reserve

Reductions in population density following harvesting may lead to increased growth and production because lower population abundance is likely to result in an increase in food availability for the remaining individuals. There is also little doubt that fluctuations in the abundance of prey can also affect

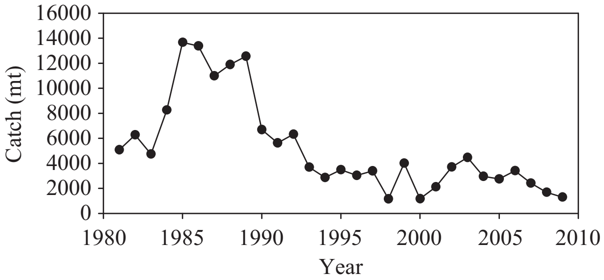

Fig. 11. Historical catch (mt) of small shrimps in Yi-Lan County between 1981 and 2009 (Anonymous, 1976-2009).

the predator population. Any sustained long-term decline or short-term changes in the distribution of prey abundance will eventually translate into a population decline of predator species (Valiela, 1995; Eero et al., 2012).

Our study found no density-dependent effect on the growth of *P. anomala* at low stock levels. Wang and Chen (1995) showed that energy reserves in the liver of *P. anomala* were primarily used to fuel spawning activity. However, because of the much greater mass of somatic tissue relative to the liver, the majority of all energy reserves reside in the somatic tissue. The unusual reductions in energy reserves among individuals from the 2008 sample (as shown by the CF and HSI indices), especially before the onset of spawning, as well as decreases in mean body mass, lead us to contend that prey availability or prey quality may have been reduced in recent years. Such a decrease would most likely be caused by human exploitation (Wang et al., 2007), although changes in environmental productivity might also be possible. However, such an effect is hard to verify at this time without the long-term monitoring of ecosystem changes.

A similar result in the same region was reported by Chang (2008), who reported that a decrease in the mean body weight of black croaker, *A. nibe*, also occurred under low stock conditions. A decrease in prey resources, such as small shrimp (Fig. 11) (mainly *Metapenaeopsis provocatoria longiroitois*), caused by exploitation (as a bycatch of trawl fishing) was suggested to be the most likely reason for such an observation. In another study, a change in the main prey of the bighand thornyhead, *Sebastolobus macrochir*, off the Pacific coast of Northern Honshu, Japan (Hattori et al., 2007) resulted in the change from a high-nutrient diet (many benthic shrimp) in the 1950s, when population biomass was high, to a low-nutrient diet in the 2000s. This has also caused a decrease in the growth of individuals. Close monitoring of ecosystem changes, especially changes in predator-prey interactions, species composition and community structure, will increase our understanding of the complex nature of energy reserve patterns of fish stocks in the region.

3. Changes in Size at First Maturity and Fecundity

The life history parameters of fish are sensitive and plastic in response to environmental changes and food availability. Reproductive output at a given size or age may be compensated for by either a genetic shift (i.e., evolutional change) in the population or phenotypic plasticity. Fishing may lead to a reduction in the mean size of individuals and size or age at maturity (Hutchings, 2005; Swain et al., 2007; Wright, 2007; Chang, 2008; Wang, 2008) because slow growth is favored if small and early maturing individuals are to have a higher probability of reproduction before being caught (Trippel, 1998).

In our study, we observed a decrease in size at first maturity for both sexes, particularly in females in 2007 when compared with 1984. Changes in size or age at first maturity as a result of exploitation are common (Trippel, 1995; Law, 2000; Hutchings, 2005; Chang, 2008; Wang, 2008). In a study of Atlantic cod, *Gadus morhua, Beacham* (1983) found that, after 20 years of exploitation, the age at maturity had decreased by 40-55%, whereas size at first maturity had declined by 30%. A similar finding was reported by Watanabe and Yatsu (2004) in their study of *Scomber japonicus*.

In addition to observing significant changes in size composition and an overall decrease in body mass energy reserves and, thus, mean body weight, our results also showed a significant increase in total fecundity of *P. anomala*. Such increases at low stock levels have been reported for many species. For example, the size-specific fecundity of spiny lobster, *Panulirus marginatus*, increased by approximately 16% after exploitation (De Martini et al., 1992). In another study, the mean fecundity of orange roughy, *Hoplostetbus atlanticus*, increased by approximately 20% when stock abundance declined (by 50%) due to intensive fishing in the east Tasmanian region (Koslow et al., 1995). The authors found that a compensatory increase in individual fecundity coupled with an apparent increase in the percentage of females in the stock limited the decline in egg production to 15%.

While a compensatory response in fecundity at low stock levels is common, an increase in fecundity accompanied by reduced body mass in individuals seems unusual given that, when assuming constant environmental conditions, low stock abundance implies more prey availability for each individual. However, if due to environmental or anthropogenic influences, the available prey resources also decrease, the reproductive effort may still be maintained at the expense of body mass (Lambert and Dutil, 2000) and/or egg size. As a result, a greater number of smaller eggs may be produced. In their study of the life history traits of the eurytopic African cichlid, *Pseudocrenilabrus multicolor victoriae*, Reardon and Chapman (2009) found that egg size was negatively correlated with egg number across field populations; females collected from high-stress environments at sites with low dissolved oxygen generally had a larger number of smaller eggs compared to females at sites with high dissolved oxygen. Fudge and Rose (2008) also showed that reduced survivorship, earlier age at maturity and increased fecundity of Atlantic cod, *Gadus morhus*, resulted in a compensatory level of fecundity that was > 75% of pre-industrial levels. We thus view the observed changes in *P. anomala* at low stock levels, namely, the increased fecundity (even with lower body mass), reduced size at first maturity, and changed sex ratios, as a possible indication of a strong density-dependent response to compensate for the loss of larger (i.e., female) individuals and population biomass due to intensive harvesting in the region.

In conclusion, the key results of our study are the demonstration of important changes in the reproductive traits of *P. anomala* and an apparent shift in the size distribution of the population toward smaller individuals. The size at first maturity for both sexes has also decreased. We observed a change in sex ratios through the selective removal of larger fish, most of which are females. We did not find a compensatory response in fish growth under low stock conditions, perhaps due to a decrease in prey resources in the ecosystem. However, we did find an intriguing strong compensatory response in the fecundity of *P. anomala* even under conditions of reduced mean body weight and energy reserves. The reduced CF and HSI over a long period of time from October to March before the onset of the spawning season indicates a deteriorating habitat for *P. anomala* that deserves further attention.

A decrease in mean body weight at low stock levels has also been reported for black croaker in the same region (Chang, 2008), and the decrease coincided with a dramatic decrease in the catch of small shrimp (mainly *Metapenaeopsis provocatoria longiroitris*) (Fig. 11), the major prey of the black croaker (Hwang and Chen, 1984) and one of the main target species of trawl fishing in the region. In many Asian countries, including Taiwan, most of the trawl bycatch is retained and brought back to port to be used as animal feed in aquaculture (Wang et al., 2007). However, these small fish are also the prey of many commercially important fish species in the region. We believe that the direct, intense fishing of target stocks such as *P. anomala* and black croaker, in conjunction with indirect competition for their prey and/or habitat alternation, may explain our observations. To prevent a continuing decline in *P. anomala* stocks and to conserve the demersal fish resources of the region, we thus advise the implementation of an ecosystem-based fishery management measure that considers the ecosystem as a whole, rather than just single species.

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REFERENCES

Anonymous. (1976-2009). Fisheries Statistical Year Book-Taiwan, Kinmen and Matsu Area. Fisheries Agency, Council of Agriculture, Executive Yuan. (in Chinese with English abstract).

Beacham, T. D. (1983). Variability in median size and age at sexual maturity of Atlantic cod (*Gadus morhua*) on the Scotian Shelf in the Northwest Atlantic Ocean. Fishery Bulletin 81, 303-321.

Bianchi, G., H. Gislason, K. Graham, L. Hill, X. Jin, K. Koranteng, S. Manickchand-Heileman, I. Payá, K. Sainsbury, F. Sanchez and K. Zwanenburg (2000). Impact of fishing on size composition and diversity of demersal fish communities. ICES Journal of Marine Science 57, 558-571.

Blanchard, F. (2001). The effect of fishing on demersal fish community dynamics: an hypothesis. ICES Journal of Marine Science 58, 711-718.

Buxton, C. D. (1993). Life-history changes in exploited reef fishes on the east coast of South Africa. Environmental Biology of Fishes 36, 47-63.

Chang, J. J. (2008). Effects of fishing on demersal fish resources: a case study using *Atrobucca nibe* from surrounding waters of Guei-Shan Island, Northeastern Taiwan. M.S. Thesis, Institute of Marine Affairs and Resource Management, National Taiwan Ocean University, Taiwan, Republic of China. (in Chinese with English abstract).

Chang, L. S. and M. L. Liao (2002). Ecological Conservation: world trend in development of protective areas. National Policy Foundation. December, 2002. Taipei, Taiwan.

Chen, C. I. (2006). What shall we do for setting up marine protective areas in Taiwan. Fountain Youth Bimonthly 5, 48-56.

Chen, G. C. (1959). Preliminary investigations on Hand-brailer fishery and its resources in Taiwan Strait. III. Fishing ground, fishing seasons and migrations of major species. China Fishery Monthly 74, 4-11.

De Martini, E. E., D. M. Ellis and V. A. Honda (1992). Comparisons of spiny lobster *Panilirus marginatus* fecundity, egg size and spawning frequency before and after exploitation. Fishery Bulletin 91, 1-7.

Eero, M., M. Vinther, H. Haslob, B. Huwer, M. Casini, M. Storr-Paulsen and F. W. Köster (2012). Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. Conservation Letters 5, 486-492.

Engelhard, G. H. and M. Heino (2004). Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. Fisheries Research 66, 299-310.

Fudge, S. B. and G. A. Rose (2008). Life history co-variation in a fishery depleted Atlantic cod stock. Fisheries Research 92, 107-113.

Greenstreet, S. P. R. and S. J. Hall (1996). Fishing and the ground-fish assemblage structure in the north-western North Sea: and analysis of long-term and spatial trends. Journal of Animal Ecology 65, 577-598.

Greenstreet, S. P. R., F. E. Spence and J. A. McMillan (1999). Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish species assemblage between 1925 and 1996. Fisheries Research 40, 153-183.

Guevara-Carrasco, R. and J. Lleonart (2008). Dynamics and Fishery of the Peruvian hake: between the nature and the man. Journal of Marine Systems 71, 249-259.

Hattori, T., Y. Narimatsu, M. Ito, Y. Ueda, K. Fujiwara and D. Kitagawa (2007). Growth changes in Bighand thornyhead *Sebastolobus macrochir* off the Pacific coast of northern Honshu, Japan. Fisheries Science 73, 341-347.

Hsieh, C. H., S. M. Glaser, A. J. Lucas and G. Sugihara (2005). Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435, 336-340.

Hutchings, J. A. (2005). Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhus*). Canadian Journal of Fisheries and Aquatic Sciences 62, 824-832.

Hwang, K. M. and C. T. Chen (1984). Studies on the fishery biology of black croaker, *Atrobucca nibe* in surrounding waters of Guei Shan Island, Taiwan. Journal of Fisheries Society of Taiwan 11, 35-52.

Hwang, S. Y., C. T. Chen and K. M. Liu (2002). Age and growth of the moon fish (*Mene maculate*), before and after heavy exploitation in Southwestern Taiwan waters. Journal of Fisheries Society of Taiwan 29, 299-311.

Hwang, S. Z. (2006). The top one catch of the fish around the world from Taiwan: the Japanese Butterfish *Psenopsis anomala*. The Fisheries Research Institute Newsletter 15, 42.

Jennings, S., S. P. R. Greenstreet and J. D. Reynolds (1999). Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. Journal of Animal Ecology

68, 617-627.

Jennings, S., M. J. Kaiser and J. D. Reynolds (2001). Marine Fisheries Ecology. Blackwell Science Ltd, London.

Jouffre, D. and C. A. Inejih (2005). Assessing the impact of fisheries on demersal fish assemblages of the Mauritanian continental shelf, 1987-1999 using dominance curves. ICES Journal of Marine Science 62, 380-383.

Kaiser, M. J., J. S. Collie, S. J. Hall and I. R. Poiner (2002). Modification of marine habitats by trawling activities: prognosis and solutions. Fish and Fisheries 3, 114-136.

Koslow, J. A., J. Bell, P. Virtue and D. C. Smith (1995). Fecundity and its variability in orange roughy - effects of population density, condition, egg size and senescence. Journal of Fish Biology 47, 1063-1080.

Lambert, Y. and J. D. Dutil (2000). Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Science 57, 815-825.

Law, R. (2000). Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57, 659-668.

Macchi, G. J., M. Pajaro and M. Ehrlich (2004). Seasonal egg production pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). Fisheries Research 67, 25-38.

Murua, H., P. Lucio, M. Santurtun and L. Motos (2006). Seasonal variation in egg production and batch fecundity of European hake *Merluccius merluccius* (L.) in the Bay of Biscay. Journal of Fish Biology 69, 1304-1316.

Olsen, E. M., G. R. Lilly, M. Heino, M. J. Morgan, J. Brattey and U. Dieckmann (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Science 62, 811-823.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and J. F. Torres (1998). Fishing down marine food webs. Science 279, 860-863.

Pauly, D., V. Christensen and C. Walters (2000). Ecopath, Ecosim and Ecospace as tools for evaluating ecosystems impact of fisheries. ICES Journal of Marine Science 57, 697-706.

Reardon, E. E. and L. J. Chapman (2009). Hypoxia and life-history traits in a eurytopic African cichlid. Journal of Fish Biology 75, 1795-1815.

Sadovy, Y. J. (1996). Reproduction of reef fishery species. In: Reef fisheries, edited by Polunin, N. V. C. and C. Ms Roberts. Chapman & Hall, London. 15-59.

SAS Institute Inc. (2008). SAS/STAT user's guide. SAS Institute Inc., Cary, NC, USA.

Shin, Y. J., M. J. Rochet, S. Jennings, J. G. Field and H. Gislason (2005). Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science 62, 384-396.

Swain, D. P., A. F. Sinclair and J. M. Hanson (2007). Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B 274, 1015-1022.

Takasuka, A., Y. Oozeki, H. Kubota, Y. Tsuruta and T. Funamoto (2005). Temperature impacts on reproductive parameters for Japanese anchovy: comparison between inshore and offshore waters. Fisheries Research 76, 475-482.

Thompson, R. and J. L. Munro (1983). The biology, ecology and bioeconomics of the hinds and groupers, Serranidae. ICLARM Studies and Review 7, 59-81.

Trippel, E. A. (1995). Age at maturity as a stress indicator in fisheries. BioScience 45, 759-771.

Trippel, E. A. (1998). Egg size and viability and seasonal offspring production of young Atlantic Cod. Transactions of the American Fisheries Society 127, 339-359.

Valiela, I. (1995). Marine Ecological Processes. 2nd Edition. Springer-Verlag, New York, USA.

Wang, S. B. (1985). Studies on the morphometric and reproductive biology of *P. anomala* (T. & S.) from the surrounding waters of Gui-Shan Island, Taiwan. M.S. Thesis, Department of Fisheries, National Taiwan Ocean University, Taiwan, Republic of China. (in Chinese with English abstract).

Wang, S. B. and C. T. Chen (1985). Reproductive periodicity and gonad development of the Japanese butterfish *Psenopsis anomala*. Bulletin of the Institute of Zoology, Academia Sinica 28, 225-235.

Wang, S. B. and C. T. Chen (1995). Reproductive biology of Japanese butterfish *Psenopsis anomala* (Stromateidas) from coastal waters of Northeastern Taiwan. Fisheries Research 23, 127-141.

Wang, S. B., W. K. Chen and S. J. Joung (2013). Seasonal dynamics of flatfish assemblage in coastal waters off northeastern Taiwan: with implications for shift in species dominance of the ecosystem. Journal of Marine Science and Technology 21 (Suppl.), 23-30.

Wang, S. B., W. K. Chen and K. M. Liu (2008). Reproductive biology and seasonal condition cycle of five spot flounder *Pseudorhombus pentophthalmus* in surrounding waters of Gui-Shan Island, northeastern Taiwan. Journal of Fisheries Society of Taiwan 35, 45-59.

Wang, S. B., J. C. Ou, J. J. Chang and K. M. Liu (2007). Characteristics of the trash fish generated by bottom trawling in surrounding waters of Guei-Shan Island, northeastern Taiwan. Journal of Fisheries Society of Taiwan 34, 379-395.

Wang, W. C. (2008). Fishing impact on reproduction and growth of the bigeye, *Priacanthus macracanthus* in waters off northeastern Taiwan. MS Thesis, Institute of Marine Affairs and Resource Management, National Taiwan Ocean University, Taiwan, Republic of China. (in Chinese with English abstract).

Watanabe, C. and A. Yatsu (2004). Effects of density-dependence and sea surface temperature on inter-annual variation in length-at-age of chub mackerel (*Scomber japonicus*) in the Kuroshio-Oyashio area during 1970-1997. Fishery Bulletin 102, 196-206.

Wosnitza-Mendo, C., R. Guevara-Carrasco and M. Ballón (2004). Possible causes of the drastic decline in mean length of Peruvian hake in 1992. Boletin Instituto del Mar del Perú 21, 1-26.

Wright, P. J. (2007). Understanding the maturation process for field investigations of fisheries-induced evolution. Marine Ecology Progress Series 333, 279-283.

Wu, C. C., W. C. Su, K. M. Liu, J. S. Weng and L. J. Wu (2012). Reproductive biology of the Japanese butterfish, *Psenopsis anomala*, in the waters off southwestern Taiwan. Journal of Applied Ichthyology 28(2), 209-216.

Wu, Z. H. (2002). Studies on the structure of demersal fish community in north and northeast coast of Taiwan. MS Thesis, Department of Environmental Biology and Fishery Sciences, National Taiwan Ocean University, Taiwan, Republic of China. (in Chinese with English abstract).