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Roles of fishing and climate change in long-term fish species succession and population dynamics in the outer Beibu Gulf, South China Sea

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Abstract

A prevailing, controversial hypothesis is that fishing pressure has played a greater role than climatic and environmental drivers, in changing fish species succession and biomass fluctuation in the South China Sea (SCS). Based on otter trawl survey data from 1959 to 2010 in the outer Beibu Gulf (OBG), northern SCS, large seasonal and interannual variation is reported for fish species composition, the proportional abundances of dominant taxa, and fish biomass. Generalized additive models are developed to quantify relationships between fish biomass and the external factors of fishing pressure and climate change. Fishing pressure proved to be the main driver of sharp declines in demersal fish stocks, with high-value species being replaced by low-value ones over time. Abrupt decreases in fish biomass during the years of 1993 and 1998 correspond to El Niño events, with climate change possibly the main driver of proportional representation of pelagic species in fisheries trawl catch. The need to differentiate impacts of fishing and environmental drivers on fish species with different life history strategies is stressed to better understand fish community dynamics.

Key words: fish species succession, biomass fluctuation, fishing effect, climate influence, Beibu Gulf, northern South China Sea

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1 Introduction

In marine ecosystems, external factors that cause fishery stocks to fluctuate include changes in environmental conditions and human exploitation. While fishing activity may have occurred for many decades or longer in coastal waters, the global exploitation of fishery stocks occurred around 1990 (Brander, 2013), with increased fishing intensity leading to rapid declines in fish stock abundances (Vincent and Hall, 1996; Pauly et al., 1998; Hutchings, 2000; Jackson et al., 2001; Kuparinen and Merilä, 2007). Whereas overexploitation can affect the life history of target fish species (Kuparinen and Merilä, 2007) and impact marine ecosystems (Chen et al., 2008), climate change can impact the physical, biological and biochemical features of the ocean (IPCC, 2007). Studies have demonstrated climate change to impact both the distribution and community structure of fish species, and their biomass in global marine ecosystems (Tian et al., 2004, 2008, 2011; Hobday, 2010; Nye et al., 2010; Cheung et al., 2011; Last et al., 2011).

There is no doubt that fisheries have declined globally, but the major driver in many cases remains controversial. In offshore and oceanic fisheries, studies have revealed fluctuations in fishery production to be driven by climate change rather than human activity (Chavez et al., 2003; Tian et al., 2006; Qiu, 2015). Conversely, it is held that human activity drives declines in fishery stocks, leading to “fishing down the food web” (Pauly et al., 1998; Chen et al., 2008). As high-productivity areas, coastal waters sustain many fish species during stages of their life history (Seitz et al., 2014), but these waters are becoming increasingly

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*Corresponding author, E-mail: wxhscs@163.com stressed (Snickars et al., 2015). Human activity and climate change are recognized as two major drivers altering coastal ecosystems (Harley et al., 2006).

The outer waters of the Beibu Gulf (OBG; Fig. 1) is located south of the Beibu Gulf. Its northwest border is the boundary of the Beibu Gulf delimited by China and Vietnam with line drawing from the Yinggehai of southwest Hainan Island to Con Co Island of Vietnam, and the southeast part is adjacent to the Xisha Islands. The region is surrounded by the Hainan Island, Xisha Islands and Vietnam.

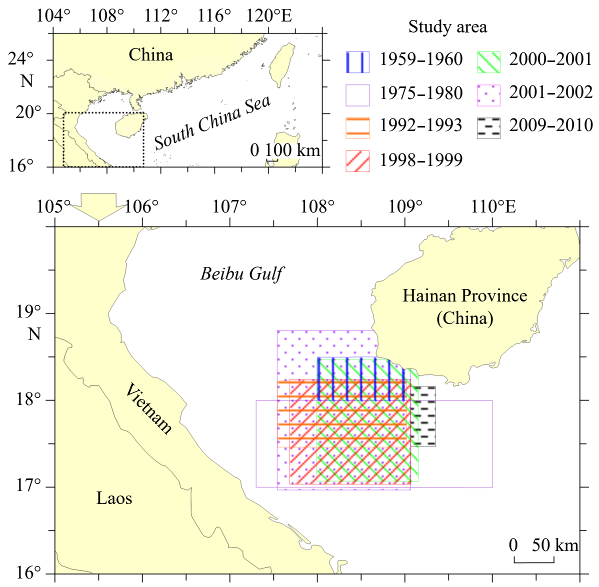

Fig. 1. Study area, outer Beibu Gulf (OBG).

Because of long-term over-exploitation of fishery resources in the Beibu Gulf, the biomass of major commercial fish species has decreased (Yuan, 1995). However, the information on the status of fisheries resources in the OBG is limited. Few studies have focused on biological analysis of commercial fish species in this region (Wang et al., 2008; Li et al., 2009). Large changes were observed in fish species compositions and dominant species after 50 years of exploitation in the OBG. The roles fishing pressure or environmental change played in these changes were unclear.

Based on data collected in fishery-independent otter trawl surveys in the OBG from 1959–1960, 1992–1993, 1998–1999, 2000–2001, 2001–2002 and 2009–2010, we evaluate the effects of fishing and climate in changes in fish-stock population dynamics. Nonlinear regression models were developed to fit the seasonal and interannual trends in total stock density, to reveal fluctuations in OBG fish stocks over the past 50 years. Factors that drive trends and fluctuations are evaluated using a Generalized Additive Model (GAM). This research provides insights into the relative effects of fishing pressure and the environment on fish populations within the OBG.

2 Materials and methods

2.1 *Survey data*

We use data from fishery-independent otter trawl surveys conducted by the South China Sea Fisheries Research Institute in the OBG from 1959–1960, 1992–1993, 1998–1999, 2000–2001, 2001–2002 and 2009–2010. As areas covered in surveys varied, this study only includes areas that overlap. The geographical range and frequency of sampling are reported in Table 1 and Fig. 1.

2.2 *Climate index and SST*

Studies have shown the El Niño-Southern Oscillation (ENSO) to signal major physicochemical environmental conditions in the SCS, like rainfall, monsoon circulation and coastal upwelling (Zhao and Tang, 2007; Tan and Shi, 2009; Zhou et al., 2010). Physicochemical conditions impact fish community structure and stock abundances (Tian et al., 2004, 2011, 2014; Qiu et al., 2010). We use an ENSO index, with data from https://www.esrl.noaa.gov/psd/data/correlation/oni.data, sea surface temperature (SST) data from NOAA OceanWatch (http://oceanwatch.pifsc.noaa.gov) for the central Pacific region, and weekly averaged SST data on a 1° grid (latitude × longitude) over 17°–19°N and 107.5°–109.5°E. Given an absence of fishery data from 1961 to 1974 and 1979 to 1991, relationships between fishery fluctuations and climate factors using 1992–2010 data are discussed.

2.3 *Fishing pressure index*

The price of crude oil (PCO) and motorized fishing boat horsepower (HFB) are used to indicate anthropogenic influence; both indices have been previously related to levels of fishing intensity (Qiu et al., 2010; Wang et al., 2012b). Crude oil price data were obtained from http://www.opec.org/opec_web/en/data_graphs/40.htm, while data for fishing boat horsepower were taken from Qiu et al. (2010).

2.4 *Stock density*

Fish abundance at a sampling station is indicated by stock density (D, kg/km^2) within an otter trawl, calculated as

$$D = C/\left[v \cdot t \cdot L \cdot X_2 \cdot (1 - X_1)\right], \qquad (1)$$

where C is the catch biomass (kg) in a trawl haul; v is the ground-speed trawling velocity (km/h); t is the trawling duration (h) at a sampling station; L is the head rope length (km) of an otter trawl net; X_2 is the fraction of head rope length of a trawlnet and we used 0.66 in this study (Sparre and Venema, 1998); and X_1 is a ratio of escape, which for trawlers in southeast Asia a value of X_1 =

Table 1. Geographical ranges and frequency of otter trawl sampling in different years

Years	North latitude	East longitude	Frequency of sampling	Sample size
1959–1960	18°00.00′–18°30.00′	108°00.00′–109°00.00′	monthly, from Oct. 1959 to Sep. 1960	2 stations × 12 months
1975–1978*	17°00.00′–18°00.00′	107°30.00′–110°00.00′	Jan. 1975; Mar. 1976; Apr. 1977; Aug. 1978	survey months’ averages
1992–1993	17°27.78′–18°13.50′	107°32.52′–109°00.94′	Sep. 1992 and May 1993	6 stations × 2 months
1998–1999	17°01.98′–18°14.22′	107°40.98′–109°04.17′	Feb., Sep. and Dec. 1998; Jan. and Apr. 1999	7 stations × 5 months
2000–2001	17°04.00′–18°28.00′	107°59.60′–109°09.17′	quarterly, Jul. and Oct. 2000, and Feb. and May 2001	6 stations × 4 months
2001–2002	16°57.91′–18°48.26′	107°32.43′–109°03.78′	Nov. 2001 and Jan. 2002	9 stations × 2 months
2009–2010	17°27.86′–18°09.61′	107°58.83′–109°20.97′	quarterly, Nov. 2009 and Feb., May and Sep. 2010	10 stations × 4 months

Note: * Data from Li (1985).

0.5 is commonly used (Sparre and Venema, 1998). Because variable trawl velocities and sampling gear produced inconsistent swept-areas in surveys, fish stock density was calculated using Eq. (1).

2.5 *Data analysis*

We used a GAM to fit the relationship between stock density (D_i) and the impacts of climate and anthropogenic factors (Jensen et al., 2005; Chang et al., 2010; Li et al., 2015):

$$\mathrm{lg}D_i = s(\mathrm{SST}) + s(\mathrm{ENSO}) + s(\mathrm{PCO}) + s(\mathrm{HFB}) + s(t_i) + \varepsilon, \tag{2}$$

where $\mathrm{lg}D_i$ is the log-transformed fish stock density of the sampling site in year i; SST is sea surface temperature (°C); ENSO is an index of El Niño-Southern Oscillation; PCO is price of crude oil (US$/t); HFB is motorized fishing boat horsepower (10^6 kW); t_i is the time of year i (expressed in days); s is a spline smoother; and ε is a random error term.

A nonlinear regression model was developed to simulate seasonal and interannual trends in total stock density (Legendre and Legendre, 2012):

$$Y_i = a + b \cdot t_i + c \cdot \cos[(2\pi/T) \cdot (t_i + d)], \tag{3}$$

where Y_i is log-transformed fish stock density; a and d are constants; b and c are partial regression coefficients corresponding to t_i; and T is the number of days in one year, averaged as 365.25 d. Values of a, b, c and d are estimated by iterating the nonlinear regression. The regression model comprises two parts: $a + b \cdot t_i$, which fits a linear interannual trend in fish stock density, and $c \cdot \cos[(2\pi/T) \cdot (t_i + d)]$, which models periodic (seasonal) fluctuations.

The trend in fish stock density from 1959–2010 was simulated using GAM. The sampling date was set as an independent variable (t_i), log-transformed values of stock density as a dependent variable (Y_i), with the regression parameters estimated through nonlinear iterative regression analysis according to Eq. (3).

3 Results

3.1 *Species succession*

Fish species composition over the past five decades is presented in Table 2. Dominant large-sized species of high-value have decreased in proportional representation in catch over time. From 1959–1960 and 1975–1978, the dominant species was the demersal red snapper *Lutjanus erythropterus*, with a biomass of 18.6% and 20.9% of the total catch, respectively; the dominant standard length group (40–50 cm) accounted for 40% of total biomass (Li, 1985). Red snapper was no longer dominant in subsequent surveys, wherein only sporadic catches of juveniles were reported. Instead, smaller-sized, lower-valued species have increased in proportional representation in catch. For example, from 1959–1960 and 1975–1978, none of the smaller, lower-value glowbelly (*Acropoma japonicum*) or apogonid, or leiognathid taxa were dominant species, but these taxa did become dominant in surveys after the 1990s. Proportional catches of small pelagic fishes, like jack mackerel *Trachurus japonicus* and round scad *Decapterus maruadsi*, also increased, with these taxa coming to dominate trawl catch. As such, after 50 years exploitation, once-dominant large-sized, long-lived, high trophic level taxa have been succeeded by shorter-lived, smaller-sized taxa of lower trophic level; additionally, species compositions are less stable, with the proportional representation of dominant taxa in trawl catches varying from year to year.

Demersal fish represented the majority of fishes in OBG communities, accounting for 90%, 86%, 85% and 84% of taxa retained in trawls from 1992–1993, 1998–1999, 2001–2002 and 2009–2010, respectively. For these same survey periods cephalopods, represented 6%, 0.6%, 7% and 8% of catch, respectively (Fig. 2). Crustaceans were only sporadically represented in catch. The greatest proportion of demersal commercial fish taxa (57%) was caught in 2001–2002, followed by 43% in 1992–1993, and 32% in 2009–2010. The proportion of other demersal fish taxa (52%) in 2009–2010 was highest, followed by 47% in 1992–1993, and 28% in 2001–2002. The proportional representation of pelagic fish in catch increased abruptly in 1998–1999 with 8.9%, but progress-

Table 2. Decadal changes in dominant fishes in the OBG: species or species groups with biomass >1% of otter trawl survey catch

Years	Dominant species and their biomass percentage/%
1959–1960	*Lutjanus erythropterus* (18.6), *Argyrosomus* spp. (5.2), *Sphyraena* spp. (5.1), *Upeneus moluccensis* (5.1), *U. sulphureus* (5.0), other Sciaenid species except *Argyrosomus* spp. (4.7), *Priacanthus macracanthus* (4.3), *Therapon* spp. (3.3), *Pomadasys hasta* (3.2), *Synodus* spp. (3.2), *Caranx* spp. (2.4), *Nemipterus* spp. (2.3), *Arius* spp. (2.0)
1975–1978*	*L. erythropterus* (20.9), *Navodon* spp. (11.1), *Priacanthus* spp. (5.3), *Trichiurus haumela* (3.8), *Otolithes* spp. (2.0), *Nemipterus virgatus* (1.7), *Therapon theraps* (1.2), *Epinephelus* spp. (1.2), *Saurida* spp. (1)
1992–1993	*Acropoma japonicum* (24.3), *Argyrosomus argentatus* (11.9), *U. moluccensis* (5.7), *Plotosus angillaris* (5.5), *Navodon xanthopterus* (5.2), *Loligo chinensis* (3.6), *Upeneus bensasi* (2.7), *T. haumela* (2.6), *Raja hollandi* (2.0), *Alutera monoceros* (2.0), *Decapterus maruadsi* (1.9), *Saurida undosquamis* (1.7), *P. macracanthus* (1.4), *L. erythropterus* (1.4), *Gastrophysus spadiceus* (1.3), *Gastrophysus lunaris* (1.3), *Champsodon* spp. (1.1), *Lagocephalus inermis* (1.0)
1998–1999	other demersal fish (26.9), *Trichiurus* spp. (9.0), *A. japonicum* (6.6), Apogonids (4.6), Leiognathids (4.3), Pelagic Carangids (*Trachurus japonicus*, *D. maruadsi*, etc.) (3.6), other pelagic fish (3.6), Sciaenids (3.4), Crustacea (3.3), *G. lunaris* (3.2), Mullids (2.9), *Champsodon atridorsalis* (2.6), *Lepidotrigla* spp. (2.1), *Fistularia petimba* (1.5), *Nemipterus* spp. (1.4), Chondrichthyes (1.2), Rajiformes (1.2), *Epinephelus* spp. (1.1), *Caranx mate* (1.0)
2001–2002	*Parargyrops edita* (13.2), *P. macracanthus* (11.2), *A. japonicum* (8.3), *Argyrosomus macrocephalus* (7.6), *G. lunaris* (4.7), *T. haumela* (4.5), *A. monoceros* (3.2), *Dasyatis zugei* (3.1), *Scomberomorus commersoni* (3.0), *T. japonicus* (2.2), *Nemipterus virgatus* (2.0), *Sepia latimanus* (1.9), *Muraenesox cinereus* (1.7), *Epinephelus diacanthus* (1.6), *Formio niger* (1.4), *Apogonichthys carinatus* (1.4), *U. sulphureus* (1.4), *Loligo chinensis* (1.3), *Sepia esculenta* (1.1), *Saurida tumbil* (1.0)
2009–2010	*A. japonicum* (35.9), *A. macrocephalus* (7.5), *A. monoceros* (4.4), *Loligo edulis* (3.6), *T. japonicus* (2.5), *Psenopsis anomala* (2.3), *G. spadiceus* (2.2), *D. maruadsi* (2.1), *D. zugei* (2.0), *Johnius belengeri* (1.5), *T. haumela* (1.2), *Lutjanus russellii* (1.2), *Raja hollandi* (1.2), *Priacanthus tayenus* (1.1), *L. erythropterus* (1.1)

Note: * Data from Li (1985).

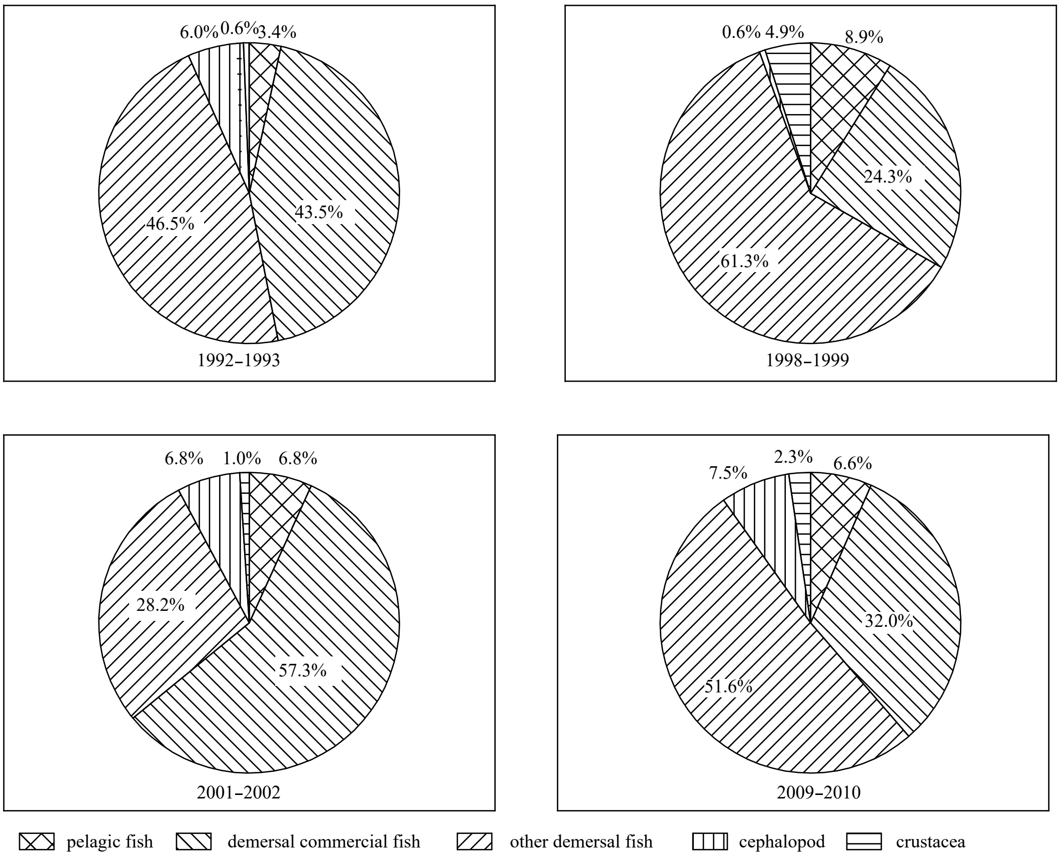

Fig. 2. Percentage of major finfish, cephalopod and crustacean catch in trawls over time.

ively declined to 6.8% in 2001–2002, and 6.6% in 2009–2010.

3.2 *Seasonal and interannual trends of stock density*

Parameters in the nonlinear regression models using Eq. (3) were estimated by iteration (Table 3). Seasonal variations and interannual trends in total fish stock density are depicted in Fig. 3. To study fluctuations in stock density we divided fishing data for periods between 1959 and 2010 into the time blocks of: 1959–1978, 1975–1993, 1992–1999, 1998–2001 and 2001–2010. From 1959–1978, total stock density trended upward, with a slope of

Table 3. Parameters estimated from the nonlinear regression models of fish stock density

Years	Parameters	Estimated	Std. error	*t* value	Pr (>|*t*|)
1959–1978	*a*	1.073	4.754×10^{-1}	2.257	3.429×10^{-2} *
	b	7.994×10^{-5}	2.064×10^{-5}	3.872	8.230×10^{-4} ***
	c	-1.178×10^{-1}	6.815×10^{-2}	−1.729	9.791×10^{-2} •
	d	9.338×10^{3}	2.965×10^{1}	314.922	$<2\times10^{-16}$ ***
1975–1993	*a*	4.752	9.067×10^{-1}	5.240	2.080×10^{4} ***
	b	-4.923×10^{-5}	2.889×10^{-5}	−1.704	1.141×10^{1}
	c	-2.318×10^{-1}	6.791×10^{-2}	−3.412	5.150×10^{3} **
	d	4.116×10^{4}	3.790×10^{1}	1 086.121	$<2\times10^{-16}$ ***
1992–1999	*a*	1.160×10^{1}	2.650	4.379	7.52×10^{-5} ***
	b	-2.525×10^{-4}	7.462×10^{-5}	−3.384	1.54×10^{-3} **
	c	8.430×10^{-2}	1.019×10^{-1}	0.827	4.127×10^{-1}
	d	9.645×10^{3}	5.873×10^{1}	164.232	$<2\times10^{-16}$ ***
1998–2001	*a*	-1.300×10^{1}	3.550	−3.661	5.05×10^{-4} ***
	b	4.293×10^{-4}	9.714×10^{-5}	4.419	3.84×10^{-5} ***
	c	-1.305×10^{-1}	6.545×10^{-2}	−1.994	5.029×10^{-2} •
	d	1.895×10^{4}	2.742×10^{1}	690.933	$<2\times10^{-16}$ ***
2001–2010	*a*	3.852×10^{-1}	1.004	0.384	0.702 6
	b	6.456×10^{-5}	2.561×10^{-5}	2.521	0.014 1 *
	c	-1.036×10^{-1}	6.107×10^{-2}	−1.697	0.094 4 •
	d	-5.678×10^{3}	2.676×10^{1}	−212.208	$<2\times10^{-16}$ ***

Note: *** $p<0.001$, ** $0.001<p<0.01$, * $0.01<p<0.05$, and • $0.05<p<0.1$. The unit of b is a^{-1}.

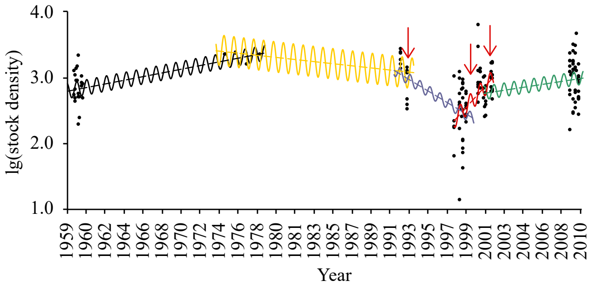

Fig. 3. Seasonal and interannual trends in log-transformed fish stock density in the OBG. Red arrows indicate El Niño events in 1992–1993, 1998–1999 and 2002.

7.994×10^{-5} a^{-1}. Trends in stock density decreased from 1975–1993 and 1992–1999, with slopes of -4.923×10^{-5} a^{-1} and -2.525×10^{-4} a^{-1}, respectively, before greatly increasing from 1998–2001, and to a lesser extent from 2001 to 2010. The amplitude in stock density seasonal variation from 1975 to 1993 (-2.318×10^{-1}) was greatest among the five time periods.

3.3 *Effects of fishing and climate on stock density*

The GAM explains 33.8% of variance in log-transformed fish stock density in the OBG, with an adjusted R^2 of 0.31. The response curve (Fig. 4) increases, decreases and increases between 1959 and 2010. Based on the GAM, the effect of fishing explains 36.7% of variance, with both the HFB in South China provinces and PCO having highly significant effects on stock density (Fig. 5). Stock density declined with increasing HFB, but increased with increasing PCO. Stock density response curves to climate influences are presented in Fig. 6. Climate explains 39% of variance in stock density. Stock density first decreased, then increased with increasing SST, being negatively influenced by SST between 21.5°C and 26.6°C, and positively influenced over 26.6°C. Stock density increased with increasing ENSO indices, but declined during an El Niño event (Figs 4 and 6).

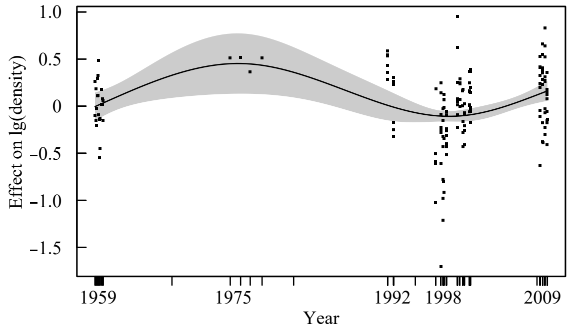

Fig. 4. Trend curve in log-transformed fish stock density in the OBG from 1959 to 2010 based on generalized additive model (GAM).

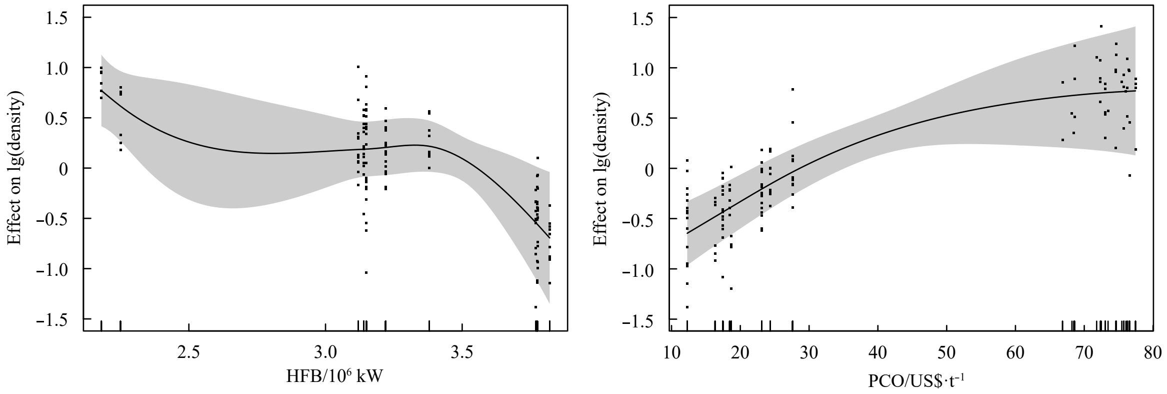

Fig. 5. Partial GAM plots showing effects of motorized fishing boat horsepower (HFB) (a) and crude oil price (PCO) (b) on log-transformed fish stock density data from 1992 to 2010. Both univariate explanatory variables are highly significant (p<0.001).

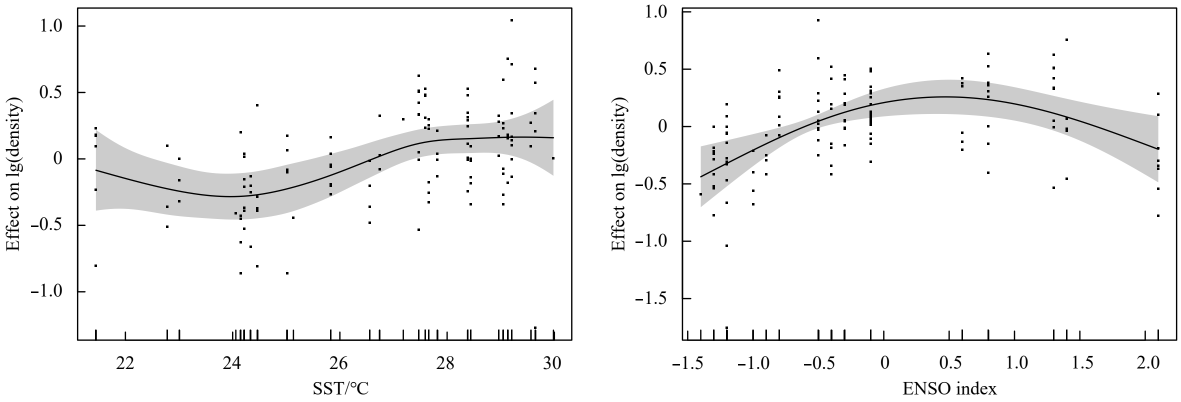

Fig. 6. Partial GAM plots showing effects of SST (a) and the ENSO index (b) on log-transformed fish stock density data from 1992 to 2010. Both univariate explanatory variables are highly significant (p<0.01).

4 Discussion

Over five decades, long-lived, large-sized fish species at high trophic levels have decreased in proportional abundance in trawl catches through the OBG, succeeded by short-lived, smaller-sized fish species at lower trophic levels. Additionally, the proportion of pelagic fishes in catch has also trended upward.

4.1 *Effects of fishing*

Red snapper is a demersal species of warm waters in and adjacent to the OBG. It was once mainly caught in longline and otter trawl fisheries (1950s and 1960s), during which time the catch was relatively stable (Table 2). With the increase in motorized fishing boats in and adjacent to the OBG since the 1960s, this species has been overfished and its habitat damaged (Sun and Lin, 2004). Since the early 1970s in particular, bottom gillnets were introduced into the fishery, and catch increased at the first then declined drastically as the area covered by bottom gillnets was greater and the fishing efficiency higher than either previous trawl or longline fisheries. Consequently, red snapper stocks were nearly depleted within several years (Table 2), with their proportional representation in catch decreasing from 20.9% in 1975–1978 to 1.4% in 1992–1993, 1.1% in 2009–2010, and disappearing altogether in 2001–2002 surveys. Although fishing for red snapper using bottom gillnets was subsequently prohibited later on, this species has shown no sign of recovery (Chen and Kong, 1991; Wang et al., 2012a).

Succession of dominant species may be an expression of the “top-down control” theory of marine food-webs. Red snapper fed mainly on other fishes, which accounted for 24.5% (in biomass) of their prey (Chen and Liu, 1982). Any decrease in higher trophic level carnivorous fish (like red snapper) could lead to an increase in lower-trophic prey fishes in the community (Parsons, 1992). Accordingly, an increase in the proportion of small-size fishes, like the seabass *A. japonicum*, in catch could be attributed to removal of predators. Additionally, removal of top predators could lead to fish assemblage structure being more variable, and with reduced temporal stability of dominant taxa.

The number of motorized fishing vessels and their horsepower have increased rapidly in southern China since 1960. In 1953 there were only four motorized fishing vessels of combined horsepower about 595 kW (Qiu et al., 2008). From 1960 to 1980 this increased steadily to 9.3×10^3 boats of combined horsepower of 0.55×10^6 kW in 1980. By 1990 this had increased to 67.95×10^3 motorized fishing boats (7.3 times that of 1980) of combined horsepower 1.86×10^6 kW (3.4 times that of 1980), and by 2010 to 80.88×10^3 vessels of combined horsepower 4.67×10^6 kW.

The increase in number of motorized fishing boats, growth in fishery labor, and transfer of non-fishery labor to the fishing industry, have steadily increased fishing capacity in both the SCS, and throughout China’s seas. Since the early 1980s, these changes have also correlated with sharp declines in fishery resources.

Commercial fish resources in the Beibu Gulf from 1992 to 1993 were significantly lower than those in the early 1960s (Yuan et al., 1995; Qiu, 1995). To control fishing effort, fisheries in the SCS have been seasonally closed since 1999. Though this closure has slowed the decline in fisheries resources, and recoveries have been reported in recent years in the Beibu Gulf, the timing of these recoveries also correlates with the rising price of international crude oil (Fig. 5), which by increasing the costs of fishing may have reduced fishing effort (Wang et al., 2012b).

4.2 *Climate influences*

SST may reflect nutrient conditions in the waters of the SCS, as an inverse correlation between primary production and SST is here apparent, with high primary production related to low SST and vice versa (Tan and Shi, 2009). Anomalously high SST values during El Niño events in 1992–1993 and 1997–1998 correlated with low primary production in SCS (Zhao and Tang, 2007). As low primary production lowers zooplankton abundance, and plankton are at the base of food chains, OBG fish stock densities declined abruptly during the 1993, 1998 and 2002 El Niño events (Figs 3 and 7).

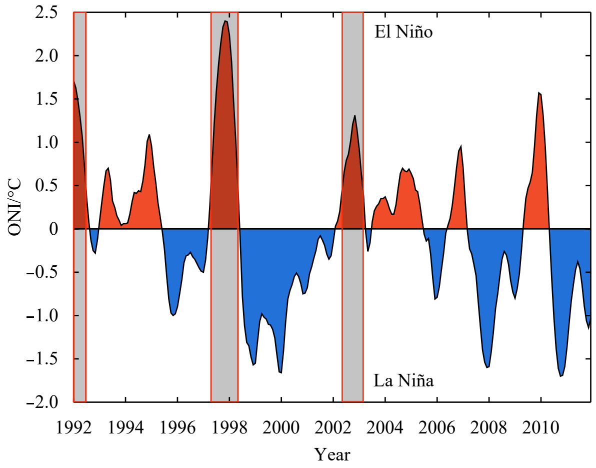

Fig. 7. Time series of Oceanic Niño index (ONI) from 1992–2011. The ONI is the primary indicator of El Niño (warm) and La Niña (cool) events in the tropical Pacific used by NOAA. The red panel indicates extreme El Niño-Southern Oscillation events.

Tropical cyclones are frequent in the SCS, increasing nutrient levels through wind-induced mixing and upwelling, contributing to enhanced primary production (Zheng and Tang, 2007; Zhao et al., 2008; Qiu et al., 2010). A positive correlation between fish production and tropical cyclones (with time lags of 0–5 years) has been reported for the northern SCS (Qiu et al., 2010). While climate was relatively stable from 1958 to 1959, with a low index of tropical cyclone influence (TCI), TCI was high from 1971 to 1973 (Qiu et al., 2010). With time lag effects, relatively low stock densities were experienced from 1959 to 1960, while high densities occurred from 1975 to 1978 (Figs 3 and 4).

Seasonal monsoon circulation is strongly modulated by El Niño events (Xie et al., 2003; Liu et al., 2004; Zhao and Tang, 2007), with the winter monsoon weakened due to El Niño effects in the SCS for the 1997–1998 period (Zhao and Tang, 2007). A positive correlation between fish production and the winter monsoon was reported for the northern SCS (Qiu et al. (2010). We report low fish stock densities to coincide with El Niño events in 1992–1993, 1997–1998 and 2002 (Figs 3 and 7).

Variations in the density and distribution of the migratory jack mackerel are related to various abiotic and biotic factors (Arcos et al., 2001; Bertrand et al., 2004). Jack mackerel can exploit a large range of oceanographic conditions and adapt to environmental change by moving to more favorable areas (Bertrand et al., 2004). Although total density of this species declined sharply in 1993, 1998 and 2002, the biomass of pelagic fish remained relatively stable, comprising 3.4%, 8.9% and 6.79% of the total catch from 1992 to 1993, 1998 to 1999 and 2001 to 2002, respectively (Figs 2 and 3).

5 Conclusions

External factors contributing to species succession and fish biomass fluctuation include fishing pressure and the natural environment. Unsustainable levels of fishing have depleted fisheries stocks, especially those of demersal species, with assemblages once characterized by high-value species now replaced with lower-value species. Abrupt decreases in fish density occurred in 1993, 1998 and 2002, corresponding to El Niño events. While the biomass of pelagic fish remained relatively stable, the proportion of pelagic species (round scad (*D. maruadsi*) and jack mackerel (*T. japonicus*)) in total catch increased.

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