## Deriving Recruitment and Spawning Patterns from a Survey of Juvenile Grouper (Pisces: Serranidae) Occurrences in the Philippines

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## ABSTRACT

Preliminary data on the patterns of occurrence of juvenile groupers in the Philippines was examined. Survey questionnaires were randomly distributed to respondents (i.e., fishers and traders of juvenile groupers). Patterns of presence/absence of the juveniles were examined and recruitment and spawning patterns were inferred from survey results. Results showed that patterns of recruitment of juvenile groupers in the Philippines varied greatly with each area/region. The large variability in the recruitment patterns precluded a "general pattern". Upon closer examination, however, some emergent signals were noted, albeit not very strong. Spatio-temporal patterns for recruitment of juvenile groupers seemed to be influenced by change in seasons (summer and wet) and monsoons (northeasterlies and southwesterlies). Inferred spawning patterns likewise varied with area/region and an inter-specific variation in spawning behaviour may be possible.

Although results are preliminary due to lack of intensive data verification, a more rigorous type of sampling protocol is worth pursuing in the future. The results of this preliminary examination provided insights on the recruitment of the commercially important epinepheline serranids in the Philippines.

Key words: groupers, lapu-lapu, fish recruitment, spawning patterns

### **INTRODUCTION**

Fish resources are currently being fully-exploited on a global scale (Hilborn & Walters, 1992; Alverson & Larkin, 1992). Increasing evidence of over-exploitation of fish stocks has been documented (e.g., Munro &

Williams, 1985; Russ, 1991; Hilborn & Walters, 1992; Alverson & Larkin, 1992) and management schemes are often either lacking or ineffective (Longhurst & Pauly, 1987). Biological information such as stock size, age, growth, mortality, and recruitment provide the building blocks of population dynamics models which are essential to the development of sound management schemes for these exploited resources.

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The Family Serranidae (Subfamily Epinephelinae), commonly known as groupers (Heemstra & Randall, 1993), is an important group among the marine fish species that are highly exploited. Local names for groupers include lapu-lapu, pugapo, and suno, among others (Rau & Rau, 1980; Schroeder, 1980) Groupers are generally long-lived, slow growing species with low rates of natural mortality (Ralston, 1987). These characteristics make them highly vulnerable to overfishing Groupers are generally a high-priced food fish in most parts of the tropics and it has been reported that these are often heavily exploited (Ralston, 1987). The coastal fisheries of the tropical seas which are often characterized by large artisanal and subsistence fisheries of the developing countries, recorded more than 97,000 tons of groupers captured worldwide in 1990 (Heemstra & Randall, 1993).

Coral reef fish have complex life cycles (Roughgarden et al., 1988). Almost all coral reef fish have two distinct life history stages occurring in two different environments (i.e., a sedentary reef-associated phase and a more mobile pelagic phase) (Doherty, 1991; Leis, 1991). It has been observed that recruitment (transition from the larval phase to a settled existence closely associated with the coral reef structure) may considerably influence the abundance of fish stock (Doherty, 1987 & 1991; Doherty & Fowler, 1994). Large variations in the abundance of recruits with time are likely to have a strong "forcing function" on the population dynamics of fish stocks on coral reefs (Williams, 1980; Victor, 1983 & 1986; Doherty, 1987; Doherty & Fowler, 1994). Local changes in the abundance and demography of a few reef fish families have been shown to be driven by historical patterns of recruitment (interacting with density-independent mortalities) (Sale & Ferrell, 1988). Information on recruitment patterns will greatly assist management strategies for these important fish resources (Doherty, 1987; Roberts, 1996). Theoretical models in fisheries, such as stock-recruitment relationships developed by Ricker (1954) and Beverton & Holt (1957) have been utilized to estimate fish stock sizes which are dependent on the replenishment of populations through larval recruitment (Roberts, 1996).

Difficulty in the identification of the juveniles and the scarcity of the newly settled larvae in the field complicate recruitment studies in groupers (Leis, 1987). In the subfamily Epinephelinae, available information deal mostly on their larval biology. In general, the distribution of grouper larvae has been found to be similar to that of the adults' distribution over continental shelves (Powles, 1977; Young et al., 1986). Doherty et al. (1994) elucidated well the dynamics of fish recruitment through field surveys of spatio-temporal settlement of Plectropomus larvae on the northern reefs of the Great Barrier Reef in Australia. In the Philippines, there is a paucity of published literature on larval biology, much less spatiotemporal variations of recruited juveniles, of groupers.

The aim of this study was to carry out a cursory examination of the recruitment patterns of the commercially important epinepheline serranids in the Philippines. Specific objectives were the following:

- (a) To determine species of epinepheline serranids that are observed or captured as juveniles;
- (b) To determine temporal and spatial patterns of recruitment of juveniles of epinepheline serranids based on survey questionnaires; and
- (c) To obtain information on the spawning seasonality of groupers inferred from the timing of occurrences of settled juveniles

This study was an initial assessment of data from a survey of local fishers and traders of juvenile groupers in selected regions in the Philippines. No actual sampling of reef fish recruits was carried out. It should also be noted that the assessment was restricted to presence or absence data from the questionnaires because upon review of the data, the investigators observed that there were unreliable estimates of absolute abundance of settled groupers. Thus, all abundance data from surveys were not included.

#### METHODOLOGY

An extensive survey in 1990-1991 to determine the seasonal occurrence and relative abundance of juvenile groupers in the Philippines was carried out by the research staff of the Bureau of Fisheries and Aquatic Resources (BFAR) under the helm of L. Penolio Survey sheets (Annex A) were distributed to regional offices of BFAR nationwide. Support staff handed out these questionnaires in various fishing localities in each region (Fig. 1) where artisanal fishery has been known The questionnaires were handed out randomly to respondents, mainly fishers, and were then retrieved More questionnaires were distributed in areas where fisher population was big, like the areas adjacent to Manila Bay, while fewer questionnaires were given in areas with smaller fisher population, like those within



Fig. 1. Map of the Philippines showing the regional divisions with important fishing localities

Region X. A total of 200 questionnaires were distributed. The survey focused mainly on the seasonality of occurrences of juvenile groupers, but it also asked for estimates of catch rates of fingerlings and the types of artisanal fishery gears used although these were not analyzed due to the need for proper verification or validation of the abundance estimates The distribution of questionnaires was biased by prevailing weather conditions. Approximately 50% of the questionnaires were returned and analyzed.

A similar but less extensive survey was carried out in the period August 1993-February 1994 by S. Mamauag. Survey questionnaires (Annex B; modified from a format of the Lobster Project of the Marine Science Institute under Dr. Annette Juinio-Meñez) were distributed to several areas in the Philippines, viz., Pangasinan area, Palawan area, Samar area, Cebu area, Bohol area and Misamis Occidental-Lanao del Norte area (Fig. 1). Randomly chosen fishers and traders in juvenile groupers from each region were given questionnaires Around 28 questionnaires were variably distributed to all areas depending on the population of fishers (Table 1). The questionnaires initially asked the respondents to provide a list of species of juvenile groupers captured with an adequate description of each species. Some respondents were shown photographs of grouper species in color to verify species identification A total of 17 questionnaires were returned and analyzed.

Additional sources of information on the presence/ absence of juvenile groupers (mostly taken from the traders' activities) in a few areas in the Philippines were

Table 1. Number of questionnaires distributed in a separate survey for selected areas and number returned for analysis

Area	# distributed	# returned
Pangasinan	6	4
Palawan	8	5
Samar	8	5
Cebu/Bohol	3	2
Misamis	3	1
Total	28	17

utilized to help verify the reliability of the results. For example, results of the Resource Ecological Assessment (REA) funded by the Philippine Department of Agriculture, which aimed to evaluate the grouper fry industry in Calauag, Quezon, in 1991 were used Data from the Southeast Asian Fisheries Development Center's (SEAFDEC) Grouper Research on the survey of finfish fry in Iloilo (Fig. 1) were also used.

#### RESULTS

#### **Juvenile groupers**

Based on the survey data compiled, only a few species of groupers in their juvenile forms were observed (Table 2). Comparison with previous but unpublished data on species of groupers occurring in some areas in the Philippines showed a disparity in the species composition (Table 2).

# Temporal and spatial recruitment patterns of juvenile serranids in the Philippines

Based on the survey results, the peak occurrence of juvenile groupers within the year was highly variable across several regions (Fig. 2). The occurrence of juveniles peaked in 12 of 16 areas (i.e., regions), generally around the summer months, although this pattern was not particularly strong (Fig. 2) Relatively fewer records were noted during the rainy season and some overlapped through summer-rainy months Yearround occurrence of juveniles was also observed but peak months fell on the summer months (April-June), as in the case of juveniles found off the coast west of Samar. Year-round occurrence was specifically noted in Davao Gulf (Fig. 2).

Although not very consistent, recruitment may follow a monsoonal pattern. Peak in abundance occurred generally during the northeast monsoon (October-March) in areas like Babuyan Channel (Cagayan Valley: Region II), Lamon Bay (Quezon: Region IV), south of Sibuyan Sea (Northern Panay: Region VI), and Iligan Bay (Lanao del Norte: Region X) (Fig. 2). During the southwest monsoon (April-September), the abundance of juveniles peaked in areas such as Lingayen Gulf Table 2. Juvenile groupers observed in the survey and list of grouper species reported in previous studies

Present study (=juveniles)	Aragones & Mamauag (1992, unpublished) (=adults)	Pagdilao et al. (1992, unpublished) (=adults)
Cromileptes	Aethaloperca rogaa	A. leucogrammicus
altiveles	Anyperodon	C. argus
Epinephelus	leucogrammicus	C. boenack
fuscoguttatus	Cephalopholis argus	C. urodeta
E. coioides	C. boenack	C. altivelis
E. guttatus	C. cyanostigma	E. areolatus
E. macrospilos	C. microprion	E. fasciatus
E. merra	C. miniata	E. fuscoguttatus
E. ongus	C. sexmaculata	E. macrospilos
E. fasciatus	C. sonerrati	E. merra
E. sexfasciatus	C. urodeta	E. microdon
Cephalopholis	C. altiveles	E. ryncholepis
cyanostigma	Epinephelus	E. ongus
Cephalopholis	areolatus	E. coioides
urodeta	E. fasciatus	E. sexfasciatus
Cephalopholis	E. fuscoguttatus	P. leopardus
boenack	E. haxagonatus	P. melanoleucus
Plectropomus	E. macrospilos	P. oligacanthus
leopardus	E. malabaricus	P. truncatus
P. laevis	E. merra	
Variola louti	E. ongus	
	E. quoyanus	
	E. sexfasciatus	
	E. coioides	
	P. laevis	
	P. leopardus	
	P. oligacanthus	
	P. maculatus	
	P. areolatus	
	Variola albimarginata	
	V. louti	

(Pangasinan: Region I), off the western coast of Luzon including Manila Bay (Region III), Ragay Gulf (Camarines Provinces: Region V), and off the western coast of Samar (Region VIII) (Fig. 2).

#### Spawning patterns

Seasonality of spawning was inferred mainly from related patterns of recruitment in the survey, as spawning seasonality was not addressed directly in the survey Similar to recruitment pattern, the inferred



Fig. 2. Peak occurrences of juvenile groupers in the Philippines

seasonality of spawning of groupers in the Philippines was highly variable (Fig. 3) Spawning patterns varied among the various areas/regions in the Philippines Some areas had annual periodicity while others showed biannual patterns.

## DISCUSSION

## Juvenile groupers in the Philippines

Few species of juvenile groupers were more frequently noted than the others in the survey. Many respondents from Bolinao, Pangasinan, recounted that juveniles of E. merra, E. fasciatus, and E. summana were the most commonly observed. In an earlier separate cursory visual assessment made by Mamauag in 1989, the three aforementioned species comprised the bulk of the caged juvenile groupers. In the Cebu-Bohol area (Fig.



Fig. 3. Inferred spawning patterns of groupers in the Philippines

1), E. tauvina (=E. coioides) has been the main target species in the commercial fishery, and its juveniles became popular among the traders (Silapan, pers. comm.). In Iloilo (Fig. 1), the SEAFDEC's finfish fry project staff reported that although juvenile groupers were scarce, E. suillus and E. sexfasciatus were collected during their sampling activities. Both species were present in the fishery, but no data on species composition in the fishery was available for comparison

Variation in the species composition may be due in part to the different levels of intensity of sampling for each study Identification of species depended largely on the traditional knowledge of fishers and traders which resulted in the absence of some species of groupers known to occur in the Philippines (e.g., Schroeder, 1980; Rau & Rau, 1980; Aragones & Mamauag, 1992; Pagdilao et al., 1992; Randall et al., 1990; Heemstra & Randall, 1993). This problem was exacerbated further by the difficulty in identifying juveniles. Also, except for some juvenile grouper species that were commonly caught (e.g., *E. merra* in Bolinao), it has been the general consensus among the fishers and traders that juveniles of groupers were generally scarce. This is true for the epinepheline serranids in general. A review of the early life history of tropical groupers revealed the relative rarity of their larvae over continental shelves compared to other equally important coral reef fish species (e.g., snappers) (Leis, 1987) Juvenile groupers are generally cryptic, thus, reducing their ease in detection in the benthic environment (Sale, 1991).

Although it remains to be established, the observed dominance of some species of juvenile groupers is key to prediction of established adult populations. The predominance of juveniles of E. merra, E. fasciatus, and E. summana, observed in fish ponds in Bolinao, Pangasinan during the 1989 cursory survey correlates well with the observed dominant species in the local fishery. Aragones & Mamauag (1992, unpublished data) found E. merra, E. fasciatus, and E. summana to be among the most abundant groupers in Bolinao (Table 3, Column 2) based on a two-year fishery catch data carried out to provide biological information and some aspects of the fishery of Bolinao groupers In Guiuan, Samar, the presence of young P. leopardus (about 10 cm TL) in relatively large quantities in several fish cages was noted by Mamauag during a cursory survey made in 1993. Pagdilao et al. (1992) reported that P. leopardus was the most abundant among the groupers (Table 3) in catch records at the fish landing sites in Guiuan collected during the period 1985-1986. These reports seem to imply that the presence of juveniles in an area can be roughly indicative of the presence of adults in the same area, assuming that other important factors (e.g., postrecruitment processes [see Jones, 1991]) do not significantly alter abundance and composition of species.

However, due to the limited number of juvenile grouper species observed and the absence of abundance estimates, as compared to the magnitude of the size of the adult populations recorded from the fishery, further conclusions regarding their potential relationship require further investigation. The findings of this study are promising and heuristic, as these results can be utilized as proxy estimator for recruitment processes (e.g., Victor, 1983 & 1986; Doherty, 1987).

Alternatively, the occurrence and distribution of adults in their habitats (i.e., fishing locality) provide keys in lieu of the problem in taxonomy, rarity, and absence of juveniles in the study There were similarities in the spatial occurrence of dominant species of juvenile groupers in the present study and conspecific adults in previous studies. The presence of the adults may give clues to the availability of potential juvenile recruits Although recruitment is highly variable in time and space (Sale, 1981; Victor, 1986; Doherty, 1987 & 1991; Doherty & Fowler, 1994) and pre-settlement fish larvae go through a hazardous pelagic phase (Leis, 1991) before these settle into preferred areas (see Victor, 1991), groupers, nonetheless, show similar adult and larvae distributions even over large continental shelves (Powles, 1977; Young et al., 1986; Leis, 1987). Although the data gathered in this study are preliminary, it is likely that patterns of adult distribution reflect the presence and/ or absence of juveniles.

### Spatio-temporal recruitment patterns

The relatively large spatio-temporal variability patterns in juvenile peak occurrences has placed a considerable constraint in providing a discernible, general pattern When preliminary data were re-examined closely, however, a seasonal trend (summer and wet) was noted Juveniles were generally observed in relatively high numbers during summer months (when seawater temperatures are assumed to be relatively higher) in most regions. The observed peak of juveniles in the study during the summer is consistent with a number of work elsewhere. Robertson (1991) noted that the growth and survival of juvenile fish have become stabilized after spawning output of the adults seemed to track the seasonal change of the suitability of the benthic environment due to changes in temperature, among others. An annual seawater temperature cycle was observed to regulate the onset and duration of the breeding season for the blackspot sergeant Abudefduf sordidus in Hawaii (Stanton, 1985) and for the tropical damselfish Pomacentrus in the Great Barrier Reef, Australia (Doherty, 1983). In the coral trout Plectropomus leopardus, large densities of pre-settling

larvae were captured by light traps deployed in northern reefs off Cairns in the GBR, Australia, mainly during the summer (November), for two weeks, particularly around the new moon (Doherty et al. 1994).

Variation in ambient seawater temperature has been recognized to be influenced by the general water circulation pattern (e.g., Wyrtki, 1961; Pickard & Emery, 1982). The Philippines has an average annual variation of sea surface temperature of less than 2°C (Morgan & Valencia, 1983). Villanoy et al. (in prep.) reported seasonality in the sea surface temperature (SST) measurements in the South China Sea, including the Sulu Sea and part of the Celebes Sea. During the southwest monsoon, temperature difference was almost negligible at 1°C (29-30°C) while in the northeast monsoon, SST ranged from 26°C to 29°C. However, information to further elucidate the effects of physicochemical factors on fish recruitment in the Philippines is lacking.

In addition, although data are few, some spatio-temporal peak occurrences of juveniles in this study may also suggest a monsoonal pattern. Most of the regions observed to demonstrate peak occurrences during the northeast monsoon are found generally along the eastern coasts of the archipelago or on the windward side of any land mass (e.g., Iligan Bay) while regions with peak occurrences during the southwest monsoon are located on the windward side of the prevailing winds Apparently, local water circulation patterns which are virtually wind-driven (see Morgan & Valencia, 1983) influence the distribution of the juveniles. During the northeast monsoon (NE; October-March), water circulation pattern (Fig. 4) [with current speed ranging from 12 cm/sec to >100 cm/sec (Wyrtki, 1971)] may possibly transport pelagic larvae of groupers to suitable areas onshelf for settlement along some of the areas found on the eastern side of the Philippine shoreline (e.g., Lamon Bay) and potentially drive larvae to oceanic conditions on the western side of the archipelago; hence, the low abundance of juveniles on the leeward side during this time of the year (e.g., Manila Bay). Conversely, prevailing water currents during the southwest monsoon (SW; June-September) (Fig. 4) may bring the larvae onshore for settlement (eventually increasing the abundance of juveniles) along the western



Fig. 4. Water current patterns for the Southwest monsoon (June; top) and for the Northeast monsoon (October, bottom) in the Philippines (after Morgan and Valencia 1984)

side (e.g., Lingayen Gulf) and, concomitantly, larvae on the eastern side may be dispersed further away from their natal reefs. However, the SW monsoon, with current speed of up to 25 cm/sec (Wyrtki, 1971), has little effect on the general circulation pattern on the leeward side. This may reflect the presence of juvenile groupers albeit in very low numbers in areas like Guiuan at this time of the year. A small percentage of respondents in the area recounted that juveniles can be observed throughout the year and peak around the summer months. Aside from the temperature rise during summer, predominant current speeds are generally slower with the shift of the monsoons (April-May). On this premise, it is not very surprising to expect that in at least some of the central islands in the Philippines (Visayas), recruitment may appear to occur during both monsoons. This would reflect recruits arriving from two different upstream source areas in any one year. Results suggest that both monsoons influence the pattern of distribution of the juveniles, temporally and spatially Aliño et al. (1992), using an ordination analysis correlated with localized environmental parameters, pinpointed the northeast (NE)-southwest (SW) monsoons as responsible for the observed groupings of coral reef fish species Doherty et al. (1994) explained that the "pulse" in the supply of *Plectropomus* larvae downstream to Arlington and Green Reefs in Cairns, Australia, was correlated with the northerly winds albeit the absence of a mechanism to determine the influence of water circulation. Dight et al. (1988) showed that patterns of passive juvenile recruitment and the maintenance of the cross-shelf species distribution of fish within the central Great Barrier Reef, Australia, were explained by models of larval dispersal primarily due to hydrodynamic processes in the area. However, evidence of the active role of larvae in settlement (in Leis, 1991) provided additional mechanisms to the patchy distribution of reef fishes. Sweatman (1983) showed that larvae of some coral reef fish actively choose settlement sites which were not habited by adult pomacentrid Dascyllus.

Although the recruitment patterns presented above were derived solely from the survey, the results were promising and should dictate a more refined protocol to verify the spatio-temporal variations of juvenile groupers in the Philippines. Distribution, abundance, and biomass of juvenile groupers at the species level may be obtained by visual counts using transects (English et al., 1997) or by sampling using light-traps (e.g., Doherty et al., 1994). Future studies should sample both monsoons and select sites at both shorelines (western and eastern) which emerged in the present study as showing signals of peak juvenile occurrence.

#### **Spawning patterns**

The variability in the recruitment patterns presented earlier may be reflective of the variability in the

spawning patterns of groupers in the Philippines (as the latter was inferred mainly from the former). It has been consistently observed that there is a close linkage between spawning and recruitment for coral reef fishes in general. Robertson et al. (1988) reported the close linkage between spawning activity and settlement based on contemporaneous measurements of clutch size and recruitment of damselfish in Panama. An Australian damselfish, Pomacentrus displayed matching periodicity of both spawning and settlement cycles (Doherty, 1991). Although there was no close comparison between both cycles, it generally suggested that production processes may have controlled the timing of settlement. For Plectropomus, Doherty et al. (1994) observed that the synchrony between spawning effort of the adults and the pattern of larval replenishment was due to a regional entrainment of spawning probably triggered by thermal and lunar cues. Seasonality of spawning for the Philippine groupers has been deduced to be bi-annual as noted in the banded grouper Epinephelus sexfasciatus (Pauly & Ingles, 1982) Recruitment pattern for the banded grouper was derived from the same overall shape of the "spawning pattern".

While some areas in this study were observed to have groupers with restricted spawning seasonalities (mainly based on the assumption that spawning periodicity and seasonality and occurrence of juveniles [settlement episodes] are closely matched), others displayed variation exemplified by biannual seasonality (e.g., region IV) or extended periods of spawning (e.g., region XI) which led to overlapping of seasonalities (Fig. 3) This suggests that some groupers in the Philippines may have spawned more than once in a year as in the case of the banded grouper E. sexfasciatus (Pauly and Ingles, 1982). However, these results (biannual seasonality and extended periods) are in contrast to the previously known seasonality of spawning common in groupers. All groupers for which there was evidence spawned during a restricted period (generally between early spring and summer in low latitudes [e.g., Australia] and somewhat later in the year in higher latitudes [e.g., the Caribbean]) (see reviews by Shapiro, 1987; Williams & Russ, 1991). On the other hand, spawning records show that some grouper species are known to spawn over 6-8 months (Nagelkerken, 1979; Loubens, 1980; Thompson & Munro, 1983).

Moreover, some artifacts in the local spawning patterns of the present study (Fig. 3) may have been introduced in part due to the manner the regions are subdivided, which was based on political classification rather than natural biogeographic criterion. This is shown in the case of Region IV which covers a large area ranging from Palawan in the western side influenced by the South China Sea to Quezon Province in the eastern side facing the Pacific Ocean (Fig. 1). The two provinces located at opposite shorelines showed two varying inferred spawning patterns which resulted in the display of a biannual seasonality for Region IV. Finally, the year round spawning period for Region XI was rather unreliable. This result may be indicative of the poor sampling scheme of the survey.

An interspecific difference in the behavior of groupers with regard to their spawning activity may explain the observed variability in the spawning episodes. This is difficult to discern, however, since this study depended mainly on the fisher's traditional knowledge which may constrain species level identification

Although spawning patterns of groupers were presented for several areas in the Philippines, these were preliminary and far from providing conclusive results A need to verify these results therefore exists Verification studies include determination of gonado-somatic index (GSI), gonad histology analysis of samples, and actual study of spawning behavior since most species of groupers studied previously displayed spawning aggregations (e.g., Shapiro, 1987; Samoilys, 1997).

## CONCLUSION

Recruitment patterns of groupers in the Philippines which were inferred from the peak occurrences of juveniles derived from a survey among fishers and traders varied greatly with area/region, masking an overall, general trend. Few, less discernible observations were noted, however. The spatiotemporal recruitment patterns of the juvenile groupers appeared to be related to changes in seasons (e.g., temperature) and monsoons as these seemed to affect the distribution of the juveniles. Concomitantly, spawning patterns appeared highly variable. Inferred patterns varied with most groupers spawning during a restricted period once or twice a year while others may presumably have extended spawning period. Although preliminary in nature, the results of this study not only give a broad snapshot of the juvenile grouper occurrence, but also some hypotheses which may stimulate future local studies with refined question-specific sampling programs. In addition, the results are nonetheless promising since the study is the first attempt to investigate the spatiotemporal dynamics of recruitment for the commercially important groupers in the Philippines. There is also a need to determine local oceanographic processes in the different regions to help explain the variation in spatiotemporal recruitment. Retention of significant numbers of larvae throughout their entire pelagic phase is affected by the topography and hydrodynamics (e.g., flushing times) in areas like bays or lagoons (see Hamner and Wolanski, 1988). Behaviour may also play a major role in larval distribution, aside from the more obvious cause of passive drift with mainstream currents, as well as spawning activities of adults of different grouper species.

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