Replenishment and connectivity of reef fish populations in the central Philippines

Thesis submitted by
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Statement on the Contribution of Others

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I performed the research for Chapter 2 in collaboration with SUAKCREM in Dumaguete City, Negros Oriental, Philippines. The monthly spawning surveys were conducted with the assistance of Claro Renato Jadloc. Mr. Jadloc was instrumental in obtaining monthly fish samples, development of gonad staging scales, identification of the different oocyte stages and estimation of batch fecundities of the four species that were studied. Mr. Jadloc will be a co-author of the paper to be submitted for publication based on Chapter 2. He will also be a co-author of a paper (separate from this thesis) on the reproductive biology of the four species that were studied, which formed part of his MSc thesis at Silliman University.

I performed the research for Chapter 4 in collaboration with SUAKCREM and the University of the Philippines-Marine Science Institute (UPMSI). Brian Stockwell of SUAKCREM collected the data on reef fish species distributions across the Bohol Sea and gave his consent for the use of this data for Chapter 4. The data on benthic habitat were collected by myself and several SUAKCREM staff: Brian Stockwell, Claro Renato Jadloc, Jasper Maypa, and Marco Innocencio. The code for the Lagrangian (particle tracking) larval dispersal model was originally written in C by Prof. Cesar L. Villanoy of UPMSI. Initial testing of the model for the Bohol Sea was done by Erlinda Salamante and Charina Repollo of UPMSI. The final model used in the simulations was developed from early model configurations by Lawrence Bernardo of UPMSI in consultation with Prof. Villanoy and myself. Mr. Bernardo made improvements to the advection-diffusion and interpolation schemes, streamlined the code so it could be efficiently run on cluster computing systems, generated the needed input data, and adapted the model to meet the objectives of this research. The application of the model to address questions about the

physical oceanography of the Bohol Sea is part of Mr. Bernardo's MSc thesis at UPMSI. Mr. Stockwell, Prof. Villanoy and Mr. Bernardo will be co-authors of the paper to be submitted for publication based on Chapter 4.

The larval dispersal model developed for the Bohol Sea in collaboration with Mr. Bernardo and Prof. Villanoy of UPMSI was modified to address the research questions in Chapter 5. Mr. Bernardo and Prof. Villanoy will be co-authors of the paper to be submitted for publication based on this Chapter.

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Abstract

The dynamics of reef fish populations at lower latitudes are not well understood, particularly in the Coral Triangle (composed of the Philippines, Malaysia, Indonesia, Timor Leste, Papua New Guinea and the Solomon Islands), where the monsoons (shifting tradewinds) are potential drivers of seasonality of reproduction and recruitment. Such dynamics will also be influenced by the degree to which local populations self-replenish or rely on larval replenishment from other populations. However, few have investigated the effects of the monsoons on the replenishment of reef fish populations. Furthermore, the extent of ecologically-significant larval dispersal of reef fishes, in general, remains unclear. Understanding the patterns and key processes behind population replenishment and larval dispersal are critical to the application of no-take marine reserve networks as conservation and fisheries management tools. This thesis addresses knowledge gaps about the patterns of reproduction, recruitment and larval connectivity of reef fish populations in the central Philippines, the epicentre of reef fish biodiversity in the Coral Triangle.

The questions that this thesis addresses are especially relevant to the use of no-take marine reserves for reef conservation and fisheries management in the Philippines, a developing archipelagic nation with a vast coral reef area, a large and rapidly growing human population and a great number of small, community-based marine reserves. Most coastal communities in the Philippines are poor and have few employment alternatives. Many communities rely on coral reefs for food and livelihood. No-take marine reserves in the Philippines are regarded as a viable option to conserve and manage coral reefs that is acceptable to local stakeholders.

This thesis consists of four related studies. In the first study, I tested the prevailing notion that spawning peaks of reef fish at lower latitudes are timed to take advantage of weaker winds during inter-monsoonal periods, supposedly to limit advection and enhance survivorship of larvae. The monthly spawning patterns of four species of reef fish (2 fusiliers, 1 surgeonfish and 1 damselfish) were studied for 11-22 months. All four species showed protracted spawning periods. However, results suggested that the monsoons affect reproduction in ways that are not consistent with the above hypothesis. Conditions advantageous to larval survival may not be restricted to the inter-monsoonal periods. An alternative explanation is that the spawning patterns

probably reflected temperature, rainfall, wind or wave action more directly influencing the spawning of adults, as opposed to adaptation of the timing of reproduction to ensure higher survivorship of larvae in the pelagic environment. The complex effects of the monsoons on reproduction in reef fishes warrant further study.

In the second study, I investigated the patterns of recruitment (larval settlement) of 120 species of reef fish almost every month for 20 consecutive months at two island and two coastal locations. Recruitment was found to occur throughout the year. Most species exhibited protracted recruitment seasons (up to 9-11 months). However, a predictable annual peak in community-wide recruitment of reef fishes was detected, coinciding with the weakening of monsoon winds and higher sea surface temperature. The annual pattern of recruitment was fairly consistent across 11 sites and between the two years sampled. The same recruitment pattern was also found in the two families that dominated monthly recruitment to reefs, the damselfishes and the wrasses, notwithstanding a 10-fold difference in overall abundance of recruits of these two families. These findings implied a far-reaching influence of the monsoons on recruitment of reef fishes at lower latitudes.

In the third study, I determined the extent of potential larval connectivity among reef fish populations across a 300-km-wide region of the Bohol Sea in the central Philippine archipelago, by combining two very different methods: 1) analysis of species assemblage patterns (presence/absence of 216 species at 61 sampling sites) and associated habitat patterns; and 2) modelling of reef fish larval dispersal patterns. The results of the two methods independently suggested probable connectivity within a large group of sites situated in an internal sea where a dominant westward current is present. The presence of potentially significant connectivity among these sites, and their lack of strong connectivity with other sites were probably strongly influenced by the local oceanographic setting and habitat. The results were consistent with present knowledge of the spatial scales of ecologically-relevant larval dispersal in reef fishes (10's of kilometres). The study provided a framework for connectivity within existing networks of no-take marine reserves in the region.

In the final study, I estimated the probable extent of recruitment subsidy (net larval export) and larval connectivity of 39 small (< 1 km^2) no-take marine reserves within a more limited (135 x 70 km) region of the Bohol Sea in the central Philippines. The reserves were estimated to occupy about 6% of total reef area in that region. I used a simple exponential model of population recovery to estimate the increase in larval

production of large predatory reef fishes inside reserves over time. Larval dispersal and recruitment were simulated using a larval dispersal model. The model simulations showed that a 3.5-fold (~250%) increase in recruitment to fished areas may result from a 55-fold increase in larval production inside reserves if all reserves were effectively protected for 20 years. Lesser larval subsidies are likely to more than replace losses in yield due to reserve creation but they will be difficult to detect because of temporal and spatial variation in recruitment. The strength of larval connectivity between reserves increased dramatically (up to ~20-fold) with greater larval production. These findings highlight the importance of protecting reserves over the long-term (decades) and establishing reserve networks that interact effectively via larval exchange in order for reserves to sustain reef fisheries in highly overfished areas and the reserve networks of which they are a part.

A synthesis of the results of this thesis highlighted the importance of the monsoons and local geographic setting in shaping the patterns of replenishment and connectivity of reef fish populations in the Coral Triangle. The implications of potential relationships between the monsoons and the dynamics of reef fish populations amidst a changing climate were also explored. Finally, future research that can validate ecologically-relevant larval connectivity within reserve networks and encourage the long-term protection of reserves were proposed.

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Chapter 1
General Introduction

Fishes that inhabit coral reefs generally occur in fragmented populations that may or may not be linked by the dispersal of larvae. For the past four decades, a major focus of reef fish ecology has been to determine the key processes affecting the dynamics and structure of these complex populations. Historically, reef fish populations were assumed to be 'open' non-equilibrial systems which relied on recruitment of larvae from sources external to local populations, as opposed to originating from local populations (Sale 1977; 1980; 1991). A hypothesis that developed from this assumption was that variation in exogenous recruitment would largely drive population dynamics and structure (i.e., the recruitment-limitation hypothesis) (Doherty 1981, 1991; Victor 1983). This hypothesis put forward the idea that recruitment was often insufficient for density-dependent, post-recruitment processes (e.g., competition and predation) to regulate populations. However, others have maintained the opposite view that post-recruitment processes are important in some situations and recruitment is unlikely to be all-important (Warner and Hughes 1988; Jones 1991; Hixon 1991). The consensus that emerged between these contrasting perspectives was that regulation of reef fish populations was likely to fall somewhere along a continuum, from populations with little or no density-dependence for much of the time to those with strong density-dependence for much of the time (Doherty and Fowler 1994; Caley et al. 1996; Schmitt and Holbrook 1999; Doherty 2002; Armsworth 2002; Hixon and Jones 2005; Jones et al. 2009).

A paradigm shift began in the late 1990's when two groundbreaking field studies demonstrated that reef fish populations can exhibit self-recruitment (i.e., recruits originating from the local population) to a significant degree (Jones et al. 1999; Swearer et al. 1999). These were soon followed by further studies suggesting that many reef fish populations may be more 'closed' than 'open' (Cowen et al. 2000; Jones et al. 2005; Almany et al. 2007). In the last decade, a considerable amount of attention has therefore been directed towards examining the extent of larval dispersal in reef fishes and its potential demographic consequences (Swearer et al. 2002; Mora and Sale 2002; Palumbi 2003; Sale et al. 2005; Cowen et al. 2006; Jones et al. 2009). There has been a

dramatic increase in studies that used a wide variety of methodologies that aimed to investigate the extent of self-recruitment and connectivity among reef fish populations (e.g., Taylor and Hellberg 2003; Paris and Cowen 2004; Paris et al. 2005; Patterson et al. 2004, 2005; Cowen et al. 2006; Almany et al. 2007; Gerlach et al. 2007; Patterson and Swearer 2007; Planes et al. 2009; Christie et al. 2010; Liu et al. 2010; Saenz-Agudelo 2011). However, large gaps in knowledge of the extent of demographically-significant larval dispersal remain (Gaines et al. 2003; Sale et al. 2005; Jones et al. 2009). Current evidence suggests that ecological-scale larval connectivity in reef fishes is more likely to occur within scales of 10's of kilometres and its pattern will more strongly depend upon local geographic setting rather than species-specific traits (Cowen et al. 2006; Almany et al. 2007; Jones et al. 2009; Saenz-Agudelo et al. 2011).

The shift in focus of research towards measuring the extent of larval dispersal was also stimulated by widespread interest in the use of networks of no-take marine reserves as tools for conservation and fisheries management on coral reefs (Plan Development Team 1990; Carr and Reed 1993; Roberts and Polunin 1991, 1993; Roberts 1997; Allison et al. 1998; Russ 2002; Sale et al. 2005; Almany et al. 2009; Jones et al. 2009). The utilisation of reserves in a network requires knowledge of the extent of demographically-relevant larval dispersal in order to make decisions about where, how large and how far apart reserves should be to effectively protect species throughout their entire life history, or to provide larval benefits to fished areas (i.e., 'recruitment subsidy' or 'recruitment effect') (Carr and Reed 1993; Roberts 1997, 2000; Allison et al. 1998; Botsford et al. 2001, 2009; Russ 2002; Gaines et al. 2003; Shanks et al. 2003; Halpern and Warner 2003; Sale et al. 2005; Jones et al. 2007; Almany et al. 2009). Reserves within a network will also be more effective if their larval dispersal 'kernels' interact, supplementing recruitment to both reserves and non-reserves (Man et al. 1995; Sladek-Nowlis and Roberts 1999; Crowder et al. 2000; Roberts 2000; PISCO 2007; Steneck et al. 2009). Although not a silver bullet to the myriad of problems that threaten coral reefs (Allison et al. 1998; Boersma and Parrish 1999; Hughes et al. 2003; Bellwood et al. 2004; Jones et al. 2004; Carpenter et al. 2008; Steneck et al. 2009; Agardy et al. 2011), the use of reserves in reef management is much advocated and generally accepted worldwide as a means to counteract biodiversity loss and overfishing (Alcala 1988; Plan Development Team 1990; Dugan

Figure 1.1 Map of the Coral Triangle region, which is composed of 6 countries, namely the Philippines, Malaysia, Indonesia, Timor-Leste, Papua New Guinea and the Solomon Islands. Source: Coral Geographic, Veron et al. unpublished data.

and Davis 1993; Roberts and Polunin 1993; Bohnsack and Ault 1996; Russ 2002; Hughes et al. 2003; Gell and Roberts 2003). In developing countries, the establishment of no-take reserves is regarded as one of the few viable strategies to protect reef biodiversity and manage reef fisheries that are acceptable to local stakeholders (Alcala 1988; Alcala and Russ 1990, 2006; Roberts and Polunin 1993; McManus 1997; Russ 2002).

This thesis primarily addresses two interrelated factors that have critical roles in the dynamics and spatially-explicit management of reef fish populations. The first is replenishment, which, in the general sense, is a function of reproduction and recruitment. The second is larval connectivity, which is the successful exchange of larvae among local populations (Sale et al. 2005). To be more specific, this thesis tackles knowledge gaps about the patterns of reproduction, recruitment and larval connectivity of reef fish populations in the central Philippines.

The geographic context of this work is important. The central Philippines (Visayas region) is the epicentre of reef fish biodiversity of the Coral Triangle (Carpenter and Springer 2005; Allen 2008; Nañola et al. 2010), the region shared by several countries (Philippines, Malaysia, Indonesia, Timor Leste, Papua New Guinea and the Solomon Islands) that has the richest marine biodiversity globally (Veron 1995; Hoegh-Guldberg et al. 2009; Veron et al. 2009) (Figure 1.1). The central Philippines is

estimated to harbour more than 1600 species of coral reef fish (Allen 2008; Nañola et al. 2010). Its reef fisheries are vital to sustaining local human communities that are poor and have few livelihood opportunities (Alcala 1981; Alcala and Luchavez 1981; Alcala and Russ 2002; Green et al. 2003, 2004; Alcala et al. 2005; Russ et al. 2004; Abesamis et al. 2006a). Its coral reefs, where they are well-managed, provide much needed income and employment to local communities through tourism (Vogt 1997; White 1988; Alcala 1998; Russ et al. 2004; White et al. 2007). Tragically, it is an area that is in serious need of urgent conservation and management measures due to decades of overexploitation, reef destruction and coastal habitat degradation, the root causes of which are a rapidly growing human population and severe poverty in many coastal communities (Bryant et al. 1998; White et al. 2000, 2007; Alcala and Russ 2002, 2006; Burke et al. 2002; Allen 2008; Nañola et al. 2010).

The central Philippines is also the birthplace of the first community-based no-take marine reserves in the Philippines (Alcala 1981, 1988, 2001; White 1986, 1988; Russ and Alcala 1999; Alcala and Russ 2006). The lessons from marine reserve management and effectiveness at two small islands (Sumilon and Apo) within this region served as templates for reserve establishment in other parts of the Philippines and were pivotal in shaping national marine resource management policy (Russ and Alcala 1999; Alcala 2001; Alcala and Russ 2006; White et al. 2007). To date, the major islands in the central Philippines, particularly Cebu, Bohol and Negros, have the highest concentrations of individual, small (< 1 km^2) no-take reserves anywhere in the world (Aliño et al. 2002; Alcala and Russ 2006; Alcala et al. 2008; Weeks et al. 2010a). Estimates vary as to how many no-take reserves have been established in Philippine waters (> 1300 reserves in Aliño et al. 2007 and Campos and Aliño 2008; 985 reserves in Weeks et al. 2010a). However, a high proportion of these reserves are located in the Visayas region (564 reserves in Alcala et al. 2008).

There are few studies of the dynamics of reef fish populations in the Philippines and the Coral Triangle region in general, compared to the less biologically-diverse coral reef regions of the Indo-Pacific and the Atlantic oceans. A recent literature search using the Aquatic Sciences and Fisheries Abstracts (Cambridge Scientific Abstracts) Database showed that the number of scientific publications on reproductive biology, recruitment and population connectivity of reef fishes in the Coral Triangle region lags considerably behind the Great Barrier Reef and the Caribbean (Figure 1.2a). Although

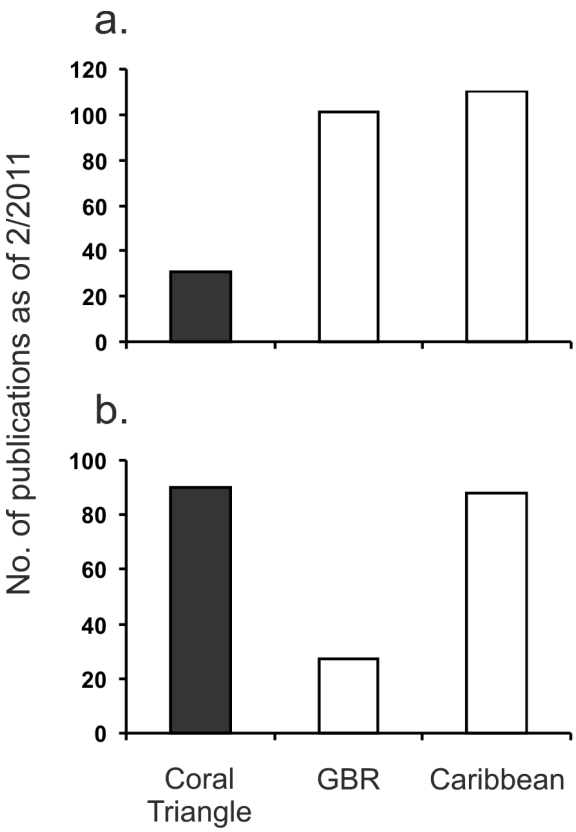


Figure 1.2 Results of a literature survey to determine the number of publications (as of 2/2011) on the topic of a) reef fish population dynamics (keywords: reef fish AND reproduction OR recruitment OR connectivity OR larval dispersal) and b) marine reserves or marine protected areas (keywords: coral reef AND marine reserve* OR marine protected area*) in the Coral Triangle versus the Great Barrier Reef (GBR) and the Caribbean. Coral Triangle countries include: Philippines, Indonesia, Malaysia, Papua New Guinea, Timor Leste and Solomon Islands. The literature search was done in the Aquatic Sciences and Fisheries Abstracts (Cambridge Scientific Abstracts) Database. The results only provide an indication of interest on the two topics .The survey was by no means exhaustive. Publications in a) were restricted to peer-reviewed (ISI) papers, while those in b) included peer-reviewed papers and 'grey' literature. The * after keywords denotes 'wildcard' search.

this is probably indicative of the large discrepancy in institutional capability to do research between the poorer and richer countries associated with each of the three regions, it is inconsistent with the significance of the Coral Triangle to global marine biodiversity and to local livelihoods in the poorer countries that share this region. However, a survey of the literature on marine reserves (or marine protected areas) showed that the number of publications on reserves in the Coral Triangle is slightly higher than in the Caribbean and about three times greater than in the Great Barrier Reef (Figure 1.2b). This is probably indicative of considerable interest to evaluate reserve effectiveness and a strong advocacy to utilise reserves in the Coral Triangle, where countries are less successful in implementing conventional approaches to reef fisheries management and conservation. Not surprisingly, however, the majority (~60%) of the publications on marine reserves in the Coral Triangle was based on research in the Philippines. The strong interest in marine reserves in the Coral Triangle but scant scientific knowledge on reef fish population ecology in the same region is a glaring gap that needs to be addressed.

The dynamics of reef fish populations in the Coral Triangle and other equatorial regions are likely to differ from those at higher latitudes because of dissimilar annual patterns of reproduction and recruitment (Srinivasan and Jones 2006). In general, seasonality of spawning and recruitment of reef fishes decreases from higher to lower latitudes (Robertson 1991). At higher latitudes (e.g., southern Great Barrier Reef, ~23º S), the annual patterns of spawning and recruitment are typically unimodal, coinciding with warmer water temperatures, with little spawning activity outside of the peak period (Russell et al. 1977; Doherty and Williams 1988; Williams et al. 2006). In contrast, spawning and recruitment at lower latitudes (within 18º N or S of the equator) tend to occur continuously throughout the year, with one or two peaks that are not obviously correlated with changes in temperature (Munro et al. 1973; Johannes 1978; Munro 1983; Robertson 1990; McManus et al. 1992; Sadovy 1996; Srinivasan and Jones 2006). Furthermore, reproduction and recruitment of reef fishes within the Coral Triangle may be strongly influenced by the Asian monsoons (shifting tradewinds) (McManus et al. 1992; Srinivasan and Jones 2006), which are major drivers of seasonality of wind direction, rainfall and surface currents in the Indo-Pacific region (Wyrtki 1961; Wang et al. 2001; Wang and LinHo 2002; Wang et al. 2006; Cook et al. 2010; Wahl and Morrill 2010; Villanoy et al. 2011). The shifting monsoon winds may also dramatically alter patterns of larval dispersal over large spatial scales from season to season (McManus 1994). Although the potential effects of the monsoons on the reproduction, recruitment or larval dispersal of marine fishes have long been recognised (Johannes 1978; Pauly and Navaluna 1983), these effects are likely to be complex, varying spatially and across different taxonomic groups (Srinivasan and Jones 2006). Few have seriously examined the patterns of reproduction, recruitment or potential larval connectivity in reef fishes in relation to changes in environmental parameters caused by the monsoons (McManus et al. 1992; McManus 1994; Srinivasan and Jones 2006).

A significant part of this thesis examined probable patterns of larval connectivity within existing networks of no-take marine reserves situated along the coasts of several major islands in the central Philippines (Alcala and Russ 2006; White et al. 2006; Weeks et al. 2010a). This provided an opportunity to: 1) evaluate the probable magnitude and spatial scales of recruitment benefits from an existing reserve network; and 2) examine the extent to which reef fish populations inside and outside existing reserves are potentially connected via larval dispersal in an archipelagic

setting, which is typical of reefs in the Coral Triangle. It is critical to address these two points because two major goals of establishing reserve networks are: 1) to enhance surrounding fisheries via net larval export (Roberts and Polunin 1993; Carr and Reed 1993; Man et al. 1995; Allison et al. 1998; Roberts 1997, 2000; Russ 2002; Sale et al. 2005); and 2) to promote reef resilience by ensuring that reserves in a network interact with each other through ecological-scale larval dispersal in order to allow for recovery from disturbances (Man et al. 1995; Crowder et al. 2000; Roberts 2000; Sale et al. 2005; Almany et al. 2009; McCook et al. 2009; Steneck et al. 2009). These two goals of reserve networks also imply the need to optimise the size, spacing and placement of reserves (Allison et al. 1998; Crowder et al. 2000; Almany et al. 2009; McCook et al. 2009). In order to achieve these goals, reserves must first accumulate substantial biomass of reef fish targeted by fisheries, resulting in much greater reproductive output per unit area compared to non-reserves. There is ample empirical evidence for reserves increasing the density and biomass of exploited species within their boundaries (Roberts and Polunin 1991, 1993; Russ 2002; Gell and Roberts 2003; Halpern and Warner 2003; Lester et al. 2009; Molloy et al 2009; Babcock et al. 2010; Russ and Alcala 2010). There also seems to be good evidence for higher spawning output per unit area within reserves compared to fished areas for targeted invertebrates and fishes (e.g., Wallace 1999; Kelly et al. 2000; Paddack and Estes 2000; Manriquez and Castilla 2001; Evans et al. 2008; Taylor and McIlwain 2010). However, the empirical evidence for reserves subsidising recruitment to fished areas is still very limited especially for fishes (Gell and Roberts 2003; Sale et al. 2005; Cudney-Bueno et al. 2009; Pelc et al. 2009, 2010; Christie et al. 2010). Likewise, the empirical evidence for reserves interacting with each other through larval dispersal is sparse (Cudney-Bueno et al. 2009; Planes et al. 2009; Christie et al. 2010). A case study on the development, magnitude and spatial scales of recruitment subsidy from, and connectivity within, an existing network of reserves in the central Philippines may be useful to a wide audience including reef fish ecologists, conservation planners and reserve managers because: 1) the rates of biomass build-up within reserves in this region are well-documented (Russ and Alcala 1996, 2003, 2004, 2010; Russ et al. 2005); 2) the distances between reserves are thought to be within the expected spatial scales of ecologically-relevant larval dispersal (Weeks et al. 2010a); and 3) the sizes and locations of these reserves were results of real-world socio-economic constraints and compromises that had little to do

with reserve network planning or optimisation (Alcala 1988; Russ and Alcala 1999; Alcala and Russ 2006).

The main body of this thesis is organised into four independent but not mutually exclusive studies. Primary data for each study were gathered using different methods including fishery-dependent spawning surveys, intensive recruitment surveys and computer modelling. Secondary data came from a wide range of sources such as regional biogeographic surveys, weather and sea temperature monitoring stations and global ocean circulation models. The four studies were written up as stand-alone scientific papers intended for publication.

In Chapter 2, I investigated the annual pattern of reproductive cycles and spawning of four species of reef fish to test the often-cited hypothesis that reef fish reproduction is timed to take advantage of inter-monsoonal periods, when weaker winds may reduce advection of larvae away from natal reefs and increase larval survivorship (Johannes 1978). The patterns of reproduction were also related to environmental variables such as sea surface temperature, rainfall and wind speed. Explanations based on larval biology or adult biology were examined in attempting to understand apparent relationships between environmental factors and the temporal patterns of reproduction and spawning.

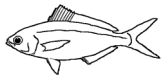
In Chapter 3, I investigated the annual pattern of community-wide recruitment of reef fishes to complement the preceding study on reproduction and spawning. Surveys of newly-settled fish were carried out almost every month at multiple sites in two island and two coastal locations over 20 consecutive months that included two monsoon cycles. The temporal patterns of recruitment were also examined with respect to changes in sea surface temperature, rainfall and wind speed associated with the monsoons.

In Chapter 4, I determined potential larval connectivity between populations of reef fishes inside and outside marine reserves across a 300-km-wide region in the central Philippines that included a major internal sea (Bohol Sea). I combined two very different techniques for this study: 1) analysis of species assemblage patterns (presence/absence of 216 species of reef fish at 61 sampling sites) and associated

habitat patterns; and 2) modelling of larval connectivity patterns using an individual-based biophysical model of dispersal of reef fish larvae. The main expectation of this study was mutual validation of probable connectivity, where it exists, by the two independent approaches.

In Chapter 5, I examined the extent of potential recruitment subsidy (net larval export or the 'recruitment effect') and larval connectivity of 39 small (< 1 km^2) community-based marine reserves. Probable levels of larval production from these reserves were estimated using the known rates of biomass recovery of large predatory reef fishes inside reserves measured almost annually over more than two decades. Using the larval dispersal model developed for the preceding study, I estimated the levels of recruitment subsidy from, and degrees of larval connectivity among, the reserves for different durations of protection, including the actual (ca. 2008) management status of the reserves in question.

The thesis concludes with a General Discussion (Chapter 6), synthesizing the results of the study overall, discussing some of their implications, and suggesting important directions for future research.



Chapter 2

Seasonality of spawning of coral reef fishes in a monsoonal environment

Abstract. The annual patterns of spawning of four species of coral reef fish in the Bohol Sea, central Philippines were investigated. Protracted breeding seasons were evident but the timing of inferred spawning peaks in relation to the seasonal monsoon winds varied between species. Spawning peaks of *Pterocaesio pisang* (Caesionidae) coincided with the longer inter-monsoonal period of the year (April-June) and the north-east monsoon (November-March). *Caesio caerulaurea* (Caesionidae) showed a spawning peak during the south-west monsoon (July-September) extending to the following shorter inter-monsoonal period (October). The annual pattern of spawning of *Naso minor* (Acanthuridae) was less clear, but there was a weak suggestion of higher spawning activity during the north-east monsoon. Spawning activity of *Pomacentrus moluccensis* (Pomacentridae) was high throughout the year except during the north-east monsoon. These results do not provide strong support for the notion that reproduction of reef fishes in monsoonal environments is timed to take advantage of the inter-monsoonal periods when winds are weaker, which presumably results in higher survivorship of pelagic larvae. The patterns of spawning indicate that conditions favourable to larvae may not be restricted to inter-monsoonal periods. For instance, periods of higher primary production may result from upwelling induced by monsoon winds. Alternatively, the observed spawning patterns may reflect temperature, rainfall, wind or wave action more directly affecting the spawning of adults, rather than adaptation to ensure greater larval survivorship. The influence of the monsoons on reef fish reproduction and its importance to the dynamics of populations warrants further study.

2.1 Introduction

Patterns of reproduction in coral reef fishes are remarkably diverse and highly variable at several temporal scales (Munro et al. 1973; Thresher 1984; Robertson 1991; Sadovy 1996). The degree to which these patterns influence the dynamics of populations is of primary interest to reef ecologists and fishery biologists (Robertson et al. 1988; Sadovy 1996; Levin and Grimes 2002; Meekan et al. 2003). Data on where, when and how often reproduction occurs in a species and the number of offspring (eggs and larvae) produced per spawning are essential to understand how populations persist and to what extent they are connected to each other by larval dispersal (Paris et al. 2005; Cowen et al. 2006).

In general, the strength of spawning seasonality in reef fishes at the community level decreases with decreasing latitude (Robertson 1991). The annual pattern of spawning (and recruitment) at higher latitudes (e.g., southern Great Barrier Reef, ~23º S) is typically unimodal, with little or no spawning activity outside of the peak period (Russell et al. 1977; Doherty and Williams 1988; Williams et al. 2006). At lower latitudes (within 18º N or S of equator), spawning tends to occur continuously throughout the year (Munro 1983; Robertson 1990; Sadovy 1996; Srinivasan and Jones 2006). One or two protracted peaks in spawning activity may be evident (Munro et al. 1973; Johannes 1978; Munro 1983).

Attempts to explain how seasonal patterns in spawning could have evolved in marine teleosts have focused on the potential consequences of environmental variables on the survival of pelagic larvae (Hjort 1914, 1926; Qasim 1956; Cushing 1982; Johannes 1978; Bakun et al. 1982; Walsh 1987; Lobel 1989). These variables include temperature, wind, currents, and available food for larvae in the plankton, which could (independently or in combination) enhance or decrease larval survivorship (Munro et al. 1973; Cushing 1982; Johannes 1978; Peterman and Bradford 1987; Sponaugle and Cowen 1996; Wilson and Meekan 2002; Sponaugle et al. 2006). However, geographic variation in the annual pattern of community-level spawning of reef fishes at the latitudinal scale is not consistently related to seasonal change of many of these environmental variables (Munro et al. 1973; Robertson 1991). Furthermore, variation in the seasonality of spawning is evident among closely-related species at the same locality or within species at different locations (Munro 1983; Robertson 1991; Clifton 1995). These patterns are difficult to explain based solely on larval biology (Robertson

1991). Alternative explanations for annual patterns of spawning in reef fishes may lie in how seasonality in the environment could affect the spawners (adults) themselves and/or in the intrinsic limitations of adult biology (Robertson 1990, 1991; Petersen and Warner 2002).

The monsoons are major drivers of seasonality in the tropics that appear to influence the patterns of reproduction and recruitment of fishes (Johannes 1978; Pauly and Navaluna 1983). The monsoons associated with the Asian continent cause dramatic changes in wind direction, rainfall, surface current patterns and plankton productivity in tropical marine regions south of the continent, from the western Indian Ocean to Southeast Asia/western Pacific Ocean (Wyrtki 1961; McManus 1994; Wang et al. 2001; Wang and LinHo 2002; Wang et al. 2006; Cook et al. 2010; Villanoy et al. 2011). Few studies have investigated potential relationships between spawning or recruitment of reef fishes and seasonal changes in environmental variables in these regions, especially at lower latitudes (Pauly and Navaluna 1983; McManus et al. 1992; Anand and Pillai 2002, 2005; Emata 2003; McIlwain et al. 2006; Arceo 2004; Abesamis and Russ 2010). The lack of studies probably reflects the persuasiveness of Johannes's (1978) argument that in monsoonal environments, reproduction in reef fishes has adapted to take advantage of inter-monsoonal periods when winds and currents are generally weaker, presumably to increase the chances of larval survival and settlement back to suitable habitat. The gap in knowledge on reproduction of reef fishes in many regions south of the Asian continent (i.e., the Indo-West Pacific, especially Southeast Asia) is not trivial because of the global significance of reef fish biodiversity of the Coral Triangle and the tremendous local importance of reef fisheries of these regions (McManus 1996, 1997; Carpenter and Springer 2005; Hoegh-Guldberg et al. 2009; Nañola et al. 2010).

The main objective of this study was to describe the annual patterns of spawning of four species of coral reef fish in one locality within the central Philippines. Monthly patterns of gonad maturation were examined to test the hypothesis that peaks in reproduction of reef fishes in monsoonal environments are timed to coincide with the inter-monsoonal periods (Johannes 1978; Pauly and Navaluna 1983). Patterns of gonad maturation were related to several gross environmental parameters (i.e., sea surface temperature, rainfall and wind speed) to seek potential explanations for the inferred patterns of spawning in relation to both larval and adult ecology. Estimates of batch fecundity (i.e., number of eggs released per spawn) for each species are also given.

2.2 Materials and methods

2.2.1 Geographic setting of the study area

This study was conducted off south-eastern Negros Island in the western part of the Bohol Sea, central Philippines (9.06-9.43 °N, 123.23-123.40 °E; Figure 2.1). Like the Philippines in general, the reversing monsoon wind pattern is a major characteristic of climate in this area (Wyrtki 1961; Wang et al. 2006). From November to early March, the prevailing wind comes generally from the north-east (north-east monsoon), then from July to September, it comes from the south-west (south-west monsoon). April to June and October are usually the inter-monsoonal periods when winds are much lighter and more variable in direction. Sea surface temperature in the Bohol Sea fluctuates by about 3 °C annually (about 27-30 °C) (NOAA Coral Reef Watch Program http://coralreefwatch. noaa.gov/satellite/index.html). Temperatures are highest from June/July to October/November, partly coinciding with the south-west monsoon. Temperatures are coolest from January to March during the northern hemisphere winter, partly coinciding with the north-east monsoon. There are no distinct wet and dry seasons in this area unlike other regions in the Philippines. However, long-term data suggest that rainfall is usually lower from November to April compared to the rest of the year [Type III climate based on classification by the Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA) http://kidlat.pagasa.dost.gov.ph/cab/cab.htm)]. Data from the U.S. Navy Layered Ocean model (www7320.nrlssc.navy.mil/global_nlom) suggest that the current patterns in the study area are partially influenced by the monsoons. Throughout the year, the general direction of currents is south/south-westward because of the strong mainstream currents that flow from the Bohol Sea and Tañon Strait to the Sulu Sea (Figure 2.1). On average, these currents are strongest during the north-east monsoon, slightly weaker during inter-monsoonal periods and weakest during the south-west monsoon (see Figure 4.2 in Chapter 4).

2.2.2 Study species

The temporal patterns of gonad maturation and female fecundity of two species of fusilier, *Pterocaesio pisang*, *Caesio caerulaurea* (Family Caesionidae), one species

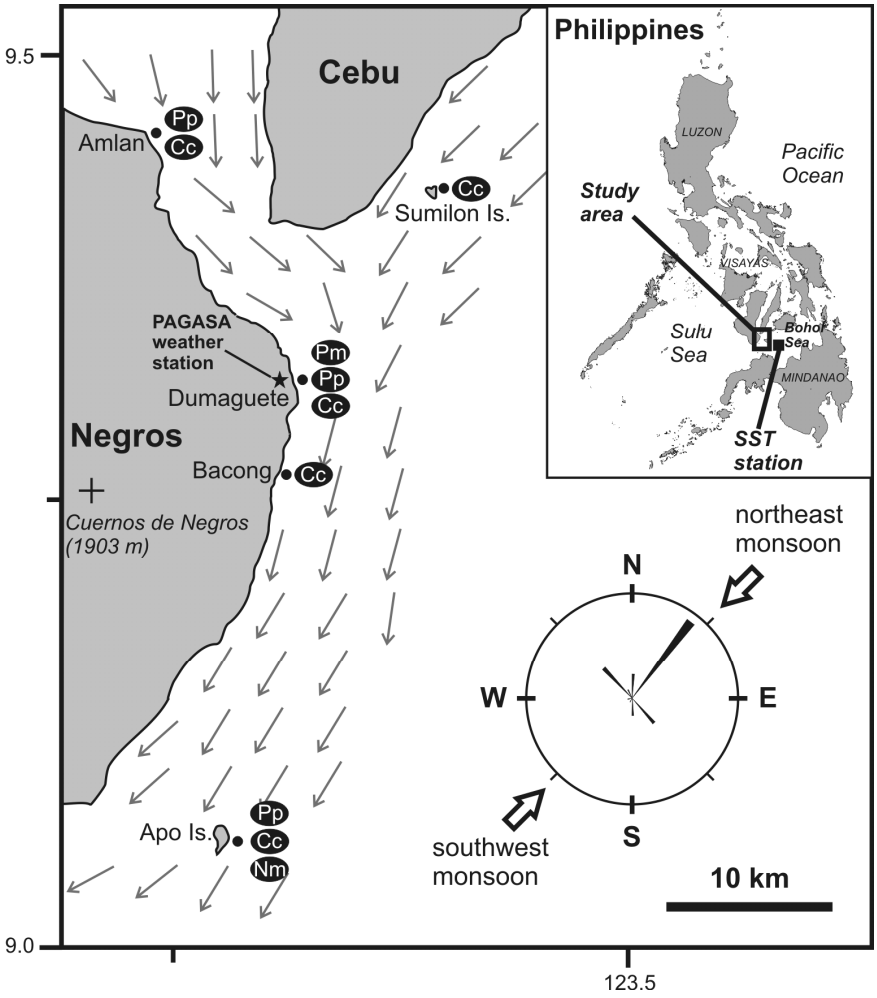


Figure 2.1 Map of the study area showing the sites (black dots) where fish samples were obtained for the spawning surveys. Letters enclosed in black ovals indicate where samples of each species were caught: Pp – *Pterocaesio pisang*; Cc – *Caesio caerulaurea*; Nm – *Naso minor*; Pm – *Pomacentrus moluccensis*. The wind chart shows the frequency distribution of daily wind direction for 1 year (January to December 2008) recorded at a weather station in Dumaguete. Note that in Dumaguete, winds from the south-west are blocked by tall mountains (*Cuernos de Negros*) in Negros Is. Arrows in grey show the general direction of currents throughout the year. Inset map shows the location of the study area in the Philippines. The inset map also shows the location of the sea surface temperature (SST) virtual monitoring station (a 0.5º longitude x 0.5º latitude area) of the NOAA Coral Reef Watch Program (see Materials and methods).

Table 2.1 Known maximum size of *P. pisang*, *C. caerulaurea*, *N. minor* and *P. moluccensis* and the size ranges of male and female individuals of each species in monthly samples. Maximum sizes were based on species descriptions by Lieske and Myers (1997), Allen et al. (2003) and Kuiter and Debelius (2006).

Species	Known maximum size (cm, TL)	Male size range (cm, TL)	Female size range (cm, TL)
Pterocaesio pisang	16-21	8.3-17.8 (n = 327)	8.9-17.0 (n = 487)
Caesio caerulaurea	25-35	19.1-27.6 (n = 144)	18.0-29.4 (n = 176)
Naso minor	19-30	17.5-22.1 (n = 69)	17.0-21.2 (n = 153)
Pomacentrus moluccensis	7-9	4.9-7.4 (n = 678)	4.5-6.6 (n = 411)

of unicornfish, *Naso minor* (Acanthuridae), and one species of damselfish, *Pomacentrus moluccensis* (Pomacentridae), were investigated. All four species are relatively small in size (maximum sizes shown in Table 2.1). Also, all four species are gonochoristic. The sex of mature individuals of each species can be readily identified by examining gonads using the naked eye. *P. pisang*, *C. caerulaurea*, and *N. minor* are targeted by local commercial and subsistence fisheries (Alcala and Luchavez 1981; Bellwood 1988; Carpenter 1988; Alcala and Russ 1990; Abesamis et al. 2006a) while *P. moluccensis* is occasionally targeted for the aquarium trade or for subsistence in some sites. *P. pisang, C. caerulaurea* and *N. minor* also differ from *P. moluccensis* in terms of reproductive and ecological characteristics. The first three species are pelagic spawners. They are zooplanktivores that are usually found off steep coral reef slopes up to a depth of > 30 m (Allen et al. 2003). In the Bohol Sea, *P. pisang* and *C. caerulaurea* are common at both coastal and offshore sites while *N. minor* tends to be restricted to offshore sites (i.e., reefs around small islands) (R. Abesamis, personal observation). The temporal pattern of spawning of *P. pisang* has been previously studied by Cabanban (1984) at two offshore sites (Apo and Sumilon islands, Figure 2.1) in the Bohol Sea. She found spawning activity of *P. pisang* to be greater from March to June and October (the latter only at Sumilon), coinciding with inter-monsoonal periods. On the other hand, *P. moluccensis* is a benthic spawner. It is an omnivore which feeds on zooplankton, benthic algae and coral propagules (Lieske and Myers 1997; Pratchett et

al. 2001). It lives in close association with live branching hard coral between depths of 2-10 m (Lieske and Myers 1997). *P. moluccensis* is also one of the most widespread coral reef fishes in the Bohol Sea (Chapter 4). Its annual pattern of recruitment in relation to the monsoons has been documented (Abesamis and Russ 2010; Chapter 3).

2.2.3 Monthly sampling

Sampling for *P. pisang*, *C. caerulaurea* and *N. minor* was dependent on catch of local fisheries. The period of sampling for these three species spanned 22, 15 and 15 months, respectively, which included 3-4 inter-monsoonal seasons. Fish were purchased 2-3 times per month, mainly from fishers and fish dealers, at several locations in southeastern Negros Is. (Figure 2.1). Fish were occasionally purchased from local markets. The fish were usually captured by local fishers using gill nets and fish traps, sometimes hook-and-line or spears. A minimum sample size of 20 male and 20 female fish per month was targeted for each species. However, there were months when samples were lacking or absent due to conditions unfavourable for fishing. Monthly sample sizes of *N. minor* were also often lower compared to *P. pisang* and *C. caerulaurea* because of its more limited distribution. Most (61%) of the samples of *P. pisang* were obtained from sites along the coast of Negros (Amlan and Dumaguete) while most (75%) of the samples of *C. caerulaurea* were obtained from Apo Is. (Figure 2.1). All samples of *N. minor* were caught at Apo Island.

Sampling for *P. moluccensis* was conducted at one coastal site (Dumaguete) in Negros Island for 11 consecutive months that included two inter-monsoonal seasons (Figure 2.1). This site is exposed to winds during the north-east monsoon and sheltered during the south-west monsoon hence wave action there is highly seasonal (Figure 2.1). Fish were captured by a local fisher using a bottom-set gill net. Sampling was limited to a reef about 3 ha in size, situated between depths of 2-4 m. The timing of monthly sampling for *P. moluccensis* was determined within the first month of sampling when the gonads of 20-30 males and females were examined 2-3 times every week for one lunar cycle (total of 10 sampling days). The results of this pilot survey indicated that the ovaries of most female *P. moluccensis* were ripening or ripe (and largest on average) near the full or new moon. Monthly sampling during succeeding months was therefore timed during or near (within 3 days before or after) the new and full moons, 2-3 times per month. Minimum monthly sample sizes of 20 male and 20 female individuals were targeted.

2.2.4 Macroscopic examination of gonads

Fish were kept in ice soon after capture and dissected in the laboratory within 24-36 hours of capture. Before dissection, the total, fork and/or standard body lengths (whichever were most appropriate for the species) of each fish were measured to the nearest mm. Whole body weight was measured to the nearest 0.1 g using an electronic balance. The gonads of each fish were then examined to determine sex and estimate gonad maturity stage. A five-point (Stages I-V) macroscopic gonad staging scale was developed for each species during the early part of monthly sampling. This gonad staging scale was modified from the scheme proposed by (Holden and Raitt 1974) for partial spawners (Table 2.2). This scheme was used because the four species were assumed to have asynchronous development of gametes (oocytes) and protracted periods of spawning at lower latitudes. Gonads of immature fish were classified into Stage I. Classification of gonads of a sexually-mature fish into Stage II (Resting) indicated that the fish would not spawn and gonads were 'inactive'. Classification of gonads into Stage III (Ripening), IV (Ripe) and V (Spent), on the other hand, indicated that spawning of the fish was imminent or had occurred recently and the gonads were 'active'.

A gonadosomatic index (GSI) was also calculated for each female fish to provide a supplementary indicator of gonad maturity. Ovaries were dissected from the fish then weighed to the nearest 0.001 g using an electronic balance. GSI was calculated using the equation:

$$GSI = \frac{W_g}{W_b} \times 100\% \qquad \text{(Equation 2.1)},$$

where W_g is the gonad weight and W_b is the whole body weight.

Sex ratios (male : female) were calculated for each species using only sexually-mature individuals (i.e., operational sex ratio). A chi-squared test ($\alpha = 0.05$) (Zar 1999) was used to test for significant deviation from an expected sex ratio of 1 male : 1 female.

2.2.5 Histological examination of ovaries

Subsamples of ovaries classified into Stages II, III, IV and V were obtained during the first half of the sampling period of each species. These were fixed in 10%

Table 2.2 Maturity stages of gonads of *Pterocaesio pisang*, *Caesio caerulaurea*, *Naso minor* and *Pomacentrus moluccensis*. Descriptions of external appearance of the ovary and testis were based on the scheme proposed by Holden and Raitt (1974) for partial (heterochronal) spawners. Gonads of sexually mature individuals are considered 'inactive' at Stage II and 'active' at Stages III, IV and V.

	External appearance	
Stage	Ovary	Testis
	A. *Pterocaesio pisang* and *Caesio caerulaurea*	
I-Immature	- Difficult to distinguish sex; gonads are small, elongated or ribbon-like; light pink or translucent	
II-Resting	- Small, cylindrical; pink; oocytes not visible	- Small, flat; whitish; milt not present
III-Ripening	- Larger, cylindrical, more firm; yellowish-pink; blood vessels visible; oocytes becoming visible	- Larger, thicker; white; exudes milt when cut but not when pressed
IV-Ripe	- Very large, full; yellow-pink to orange; oocytes are visible, may be extruded with slight touch	- Large, very thick, wrapped around intestine; creamy white; exudes milt when pressed
V-Spent	- Flaccid, with 'loose' walls; reddish orange to dark pink; oocytes visible in some 'spent' ovaries	- Shrunken and flaccid; reddish to pinkish-white; milt may be present
	B. *Naso minor*	
I-Immature	- Not seen	
II-Resting	- Small, lobe-shaped but not flat; pink; oocytes not visible	- Small, lobe-shaped, flat; pinkish-white; milt not present
III-Ripening	- Larger, more cylindrical in appearance; pink; blood vessels visible; oocytes becoming visible	- Larger, still relatively flat but thicker; exudes milt when cut but not when pressed
IV-Ripe	- Large and full, very soft; pink; oocytes plainly visible and may be extruded with slight touch	- Larger, fuller; readily exudes milt when pressed
V-Spent	- Not seen	- Flaccid; pinkish; milt may be present; difficult to distinguish from Stage II
	C. *Pomacentrus moluccensis*	
I-Immature	- Difficult to distinguish sex; gonads are very small and thread-like; translucent	
II-Resting	- Very small, oval-shaped; pink to dark pink; oocytes not visible	- Very small, thread-like; whitish; milt not present
III-Ripening	- Larger, fuller, oval to irregular shape; pinkish orange; oocytes becoming visible	- Larger but not very thick; whitish; milt present
IV-Ripe	- Large and full, irregular shape; orange; oocytes plainly visible	- Larger; whitish to white; milt freely flowing
V-Spent	- Appears shrunken, soft, with 'loose' walls; dark pink	- Shrunken, flaccid; pinkish-white; milt sometimes present

formalin for 7-10 days then transferred to 75% ethanol. Ovaries were prepared for histology following conventional procedures of dehydrating, embedding, sectioning and staining with hematoxylin and eosin. Between 25-50 transverse sections (depending on the size of the ovary) ~7 µm thick were obtained through the mid-section of each ovary. The histological sections were then examined microscopically to assess the accuracy of staging whole ovaries. Under microscopic examination, the most advanced oocyte stages that should be present in Stage II, III and IV ovaries should be as follows: Stage II – previtellogenic oocytes (i.e., chromatin nucleolar, perinucleolar to germinal vesicle stages); Stage III – vitellogenic oocytes (i.e., yolk globule stages); Stage IV – ripe oocytes (i.e., migratory nucleus and hydrated oocyte stages). Stage V ovaries ('spent') were expected to have post-ovulatory follicles. Classification into the different Stages was based on the presence of the most advanced oocyte that was expected for a particular stage, not on quantitative criterion based on the relative frequencies of oocytes stages. Identification of the different oocyte stages and other histological features of the ovary were based on West (1990), Ganias et al. (2004) and Choi et al. (1996). Correction factors based on the relative frequency (%) of correct and incorrect classification (macroscopic versus histological examination) of the subsamples per ovary maturity stage (Results, Table 2.3) were applied to the larger data set on macroscopic classification of ovaries to improve accuracy of gonad staging.

2.2.6 Examination of temporal patterns of spawning

For each species, the monthly relative frequency of individuals in the different gonad maturity stages and the monthly average female GSI were examined in relation to monsoon and inter-monsoonal periods to determine any seasonal pattern. Gonad maturation patterns were also compared to available data on monthly average sea surface temperature (SST) and monthly total rainfall for the study area. Absolute and relative changes in temperature are often implicated as an important factor in the spawning of reef fishes (Munro et al. 1973; Sadovy 1996) and the growth and survival of their larvae (Bergenius et al. 2002; Meekan et al. 2003). Rainy periods, on the other hand, may be associated with increased availability of planktonic food (due to nutrient input into coastal waters by terrestrial runoff), which could result in increased spawning activity for planktivorous fishes (Tyler and Stanton 1995) and better survival of larvae (Gallego et al. 1996). Data on SST were obtained from the NOAA Coral Reef Watch Program (http://coralreefwatch.noaa.gov/satellite/index.html) which archives SST data

measured by a 'virtual' monitoring station (0.5º longitude x 0.5º latitude in area) in the vicinity of the study area (Figure 2.1). The temporal resolution of this data was bi-weekly, giving 7-8 measurements per month for each monthly average value. Daily data on rainfall was obtained from a weather station in Negros (Dumaguete) that is operated by the PAGASA. This weather station is located almost at sea level < 1 km from the coast (Figure 2.1). The monthly pattern of total rainfall reflected major rainy periods due to the inter-tropical convergence zone and occasional typhoons, as opposed to just localized rain in the Dumaguete area. The gonad maturation patterns of *Pomacentrus moluccensis* were further compared to data on monthly average wind speed obtained from daily wind data recorded by the PAGASA weather station. The sampling site for *P. moluccensis* was located < 1km away from this weather station. Data on wind speed was used as a proxy for wind stress, which causes seasonality of wave action in the site where *P. moluccensis* was sampled.

Spearman rank correlation (r_s) (Zar 1999) was used to assess synchrony between monthly proportions of individuals with active testes, active ovaries and monthly average GSI. The same statistical procedure was used to determine the relationships between each of these indicators of gonad maturation versus each of the environmental variables of interest.

2.2.7 Estimation of batch fecundity

For each species, a subsample (n = 13-14) of ovaries classified as Stage IV (Ripe) was preserved in 10% formalin. Estimates of batch fecundity (number of eggs per spawning) were obtained from these ovaries using the gravimetric (or hydrated oocyte) method developed by Hunter et al. (1985) for multiple spawners. This method uses counts of hydrated oocytes per replicate subsample of ovary tissue of known weight. The counts are then extrapolated to the total weight of the ovary to estimate the total number of hydrated eggs that would have comprised a spawning batch. When hydrated oocytes were not present in the subsample (e.g., in all *P. moluccensis* and some *P. pisang* and *C. caerulaurea*), the largest yolked oocytes were counted because it can be assumed that these oocytes would have comprised a single batch of eggs in one spawning (Hunter et al. 1985). In *P. pisang* and *C. caerulaurea*, the largest yolked oocytes (and their abundance) in a given subsample were determined by constructing a size-frequency histogram based on oocyte diameters (Hunter et al. 1985). To determine if counts of hydrated (or largest) oocytes differed between lobes and among regions of

the ovary, subsamples were taken from the anterior, median and posterior regions of the left and right lobes of a smaller sample of ovaries (n = 6 ovaries per species). Significant differences in the density of hydrated (or largest) oocytes between lobes and between regions of the lobe were determined using a 2-way ANOVA (Zar 1999). Potential relationships between body length and batch fecundity were determined using simple linear regression (Zar 1999).

2.3 Results

2.3.1 Sample size, size range and sex ratio

A total of 814, 320, 222 and 1089 sexually mature individuals of *P. pisang*, *C. caeurulaurea*, *N. minor* and *P. moluccensis*, respectively, were obtained. Species-specific comparisons between the size ranges of males and females in the entire sample and maximum known size based on literature indicated that for all species except *N. minor*, the largest individuals in the population were probably sampled (Table 2.1). Sex ratios computed from the entire sample of mature individuals were found to be female-biased in *P. pisang* (1 male : 1.5 females; $\chi^2 = 31.9$, $p > 0.05$) and male-biased in *P. moluccensis* (1.6 males: 1 female; $\chi^2 = 65.5$, $p > 0.05$). Sex ratio in *Naso minor* was strongly female-biased (1 male: 2.2 females; $\chi^2 = 31.8$, $p > 0.05$). Sex ratio did not significantly differ from the expected ratio of 1 : 1 for *C. caerulaurea* (1 male: 1.2 females; $\chi^2 = 3.20$, $p < 0.05$).

2.3.2 Accuracy of macroscopic staging of ovaries

In subsamples of inactive (Stage II) ovaries, only few or no ovaries (0-33%) were incorrectly classified as active (Stage III-V) (Table 2.3). However, in all species except *P. pisang*, there were many instances when subsamples of inactive ovaries were mistaken to be active. This error occurred more frequently in late Stage II ovaries that had oocytes already at the germinal vesicle stage, which were incorrectly classified as Stage III (i.e., ovaries with vitellogenic oocytes) (Table 2.3). There was also some difficulty in distinguishing between Stage III and Stage IV ovaries in the subsamples (Table 2.3). In *P. pisang* and *C. caerulaurea*, ovaries (and testes) that appeared shrunken, reddish to dark pink and/or flaccid were classified into Stage V (‘spent’) (Table 2.3). Vitellogenic and/or near-ripe oocytes were present in a substantial proportion of the subsamples of ovaries classified into Stage V, which indicated partial

Table 2.3 Results of microscopic examination of ovaries to assess the accuracy of estimating maturity stage based on external appearance. Percent of correctly and incorrectly classified ovaries per ovary maturity stage are given in parentheses. The latest oocyte stage (and gonad maturity stage, in parentheses) and other features seen in incorrectly classified ovaries are also indicated. Gonads of sexually mature individuals are considered 'inactive' at Stage II and 'active' at Stages III, IV and V.

Ovary maturity stage	n	Correct	Incorrect	
A. *Pterocaesio pisang*				
II-Resting	11	10 (90.9)	1 (9.1)	- 1º yolk globule stage (early III)
III-Ripening	9	6 (66.7)	2 (22.2)	- migratory nucleus stage (IV)
			1 (11.1)	- perinucleolar stage (II)
IV-Ripe	21	10 (47.6)	10 (47.6)	- 3º yolk globule stage (late III)
			1 (4.8)	- germinal vesicle stage (II)
V-Spent	8	1 (12.5)	6 (75.0)	- 3º yolk globule stage (III)
			1 (12.5)	- migratory nucleus stage (IV)
B. *Caesio caerulaurea*				
II-Resting	13	12 (92.3)	1 (7.7)	- 1º yolk globule stage (early III)
III-Ripening	8	1 (12.5)	7 (87.5)	- germinal vesicle stage (late II)
IV-Ripe	17	10 (58.8)	7 (41.2)	- 3º yolk globule stage (late III)
V-Spent	6	2 (33.3)	3 (50.0)	- 1º-3º yolk globule stages (III)
			1 (16.7)	- germinal vesicle stage (II)
C. *Naso minor*				
II-Resting	3	2 (66.7)	1 (33.3)	- 3º yolk globule stage (late III)
III-Ripening	16	8 (50.0)	8 (50.0)	- germinal vesicle stage (late II)
IV-Ripe	12	6 (50.0)	5 (41.7)	- 3º yolk globule stage (late III)
			1 (8.3)	- perinucleolar stage (II)
V-Spent	-	-	-	-
D. *Pomacentrus moluccensis*				
II-Resting	14	14 (100.0)	-	-
III-Ripening	16	8 (50.0)	8 (50.0)	- perinucleolar to germinal vesicle stage (II)
IV-Ripe	18	4 (22.2)	14 (77.7)	- 2º-3º yolk globule stages (late III)
V-Spent	-	-	-	-

spawning in these species. These results became the basis for correction factors that were applied to the data on macroscopic classification of ovaries of each species.

2.3.3 Temporal patterns of spawning

In *P. pisang*, active testes and ovaries were present during every month that was sampled (Figures 2.2c,d). Stage V ('spent') testes and ovaries were also present during many months. A higher percentage of individuals had active gonads during the first inter-monsoonal season (March-June 2008) and the second north-east monsoon season extending to the third inter-monsoonal monsoon season (November 2008-May 2009) of the period that was sampled (Figure 2.2c,d). Average GSI of females also peaked within these seasons, in May 2008 and January 2009 (Figure 2.2e). Peaks in gonad maturation and GSI occurred within 2-3 days before or after the new moon or the full moon (Figure 2.2). Correlations between the monthly percent frequency of active testes, active ovaries and monthly GSI were moderate to high (Table 2.4). There was no clear relationship between the pattern of gonad maturation and fluctuations in SST (Figure 2.2a,c-e). SST was increasing or decreasing to lowest levels as percent frequency of active gonads and average GSI reached peak levels, but monthly percent frequency of active gonads and average GSI were low when SST was highest (during the south-west monsoon season). There was, however, some indication that the seasonal pattern of gonad maturation was tracking the pattern of rainfall (Figure 2.2b-e). Gonad maturation patterns had a weak negative correlation with SST and a weak positive correlation with rainfall, but these relationships were only statistically significant for GSI (Table 2.4).

In *C. caerulaurea*, active testes and ovaries were also present during all months sampled. The percent frequency of active testes was higher during a 9-month period that encompassed consecutive south-west monsoon, inter-monsoon and north-east monsoon seasons (July 2008 to March 2009) (Figure 2.3c). Stage IV (ripe) testes were more frequent in the first 5 months of this period (south-west monsoon to early north-east monsoon season). The frequency of active ovaries was also usually higher during this 9-month period but peaks occurred during the south-west monsoon and inter-monsoonal seasons (August and October 2008) (Figure 2.3d). Average GSI of females peaked during the south-west monsoon (August 2008) (Figure 2.3e). There was some indication that percent frequency of active ovaries and average GSI were higher near the new moon (Figure 2.3). Correlations of monthly frequency of active testes versus frequency of active ovaries and average female GSI were low to negligible, but high

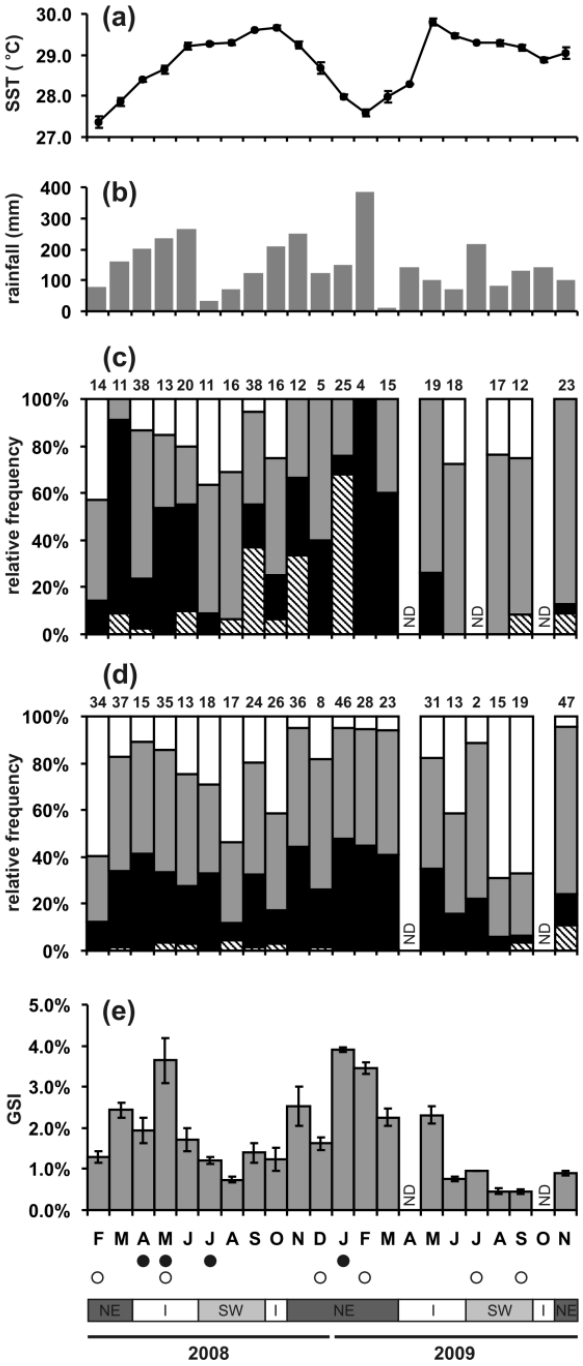


Figure 2.2 Monthly gonad maturation patterns of *Pterocaesio pisang* versus environmental variables: average monthly sea surface temperature (SST) (a); total monthly rainfall (b); relative frequency of individuals in different gonad maturity stages for males (c) and females (d); average monthly female GSI (e). Legend for (c) and (d): Stage II (Resting) – white; Stage III (Ripening) – grey; Stage IV (Ripe) – black; Stage V (Spent) – diagonal lines. Numbers on top of bars in (c) and (d) indicate sample size. Monsoons (seasonal wind regime) and inter-monsoonal periods are indicated by different shades of grey on the bar at the bottom of the figure, parallel to the x-axis (months): NE – north-east monsoon, SW – south-west monsoon, I – inter-monsoon. If more than 50% of the samples in a particular month were caught within 2 days before or after the day of the new moon or full moon, a black circle (for new moon) or white circle (for full moon) is indicated under the letter representing that month.

Table 2.4 Spearman rank correlations (r_s) of monthly proportions of individuals with active gonads (represented by ♂ for testes and ♀ for ovaries) and monthly female gonadosomatic indices (represented by $♀_{GSI}$) versus monthly average sea surface temperature (SST), total rainfall or average wind speed. $^{*}p < 0.05$; $^{**}p<0.01$, $^{***}p<0.001$, $^{\dagger}p = 0.06\text{-}0.08$.

		♀	$♀_{GSI}$	SST	Rainfall	Wind speed
Pterocaesio	♂	0.80^{***}	0.66^{**}	-0.29	0.33	-
pisang	♀	-	0.67^{**}	-0.37	0.37	-
	$♀_{GSI}$	-	-	-0.46^{*}	0.50^{*}	-
Caesio	♂	0.21	-0.08	0.25	-0.10	-
caerulaurea	♀	-	0.90^{***}	0.65^{*}	-0.62^{*}	-
	$♀_{GSI}$	-	-	0.45	-0.70^{*}	-
Naso	♂	0.61	0.73^{*}	0.30	-0.09	-
minor	♀	-	0.48	0.29	0.52	-
	$♀_{GSI}$	-	-	0.26	-0.05	-
Pomacentrus	♂	0.92^{***}	0.93^{***}	$0.55^{\dagger}$	0.11	$-0.55^{\dagger}$
moluccensis	♀	-	0.93^{***}	$0.58^{\dagger}$	0.07	-0.49
	$♀_{GSI}$	-	-	$0.55^{\dagger}$	- 0.04	$-0.58^{\dagger}$

between monthly frequency of active ovaries and GSI (Table 2.4). Patterns of gonad maturation had a tendency to be positively correlated with SST and negatively correlated with rainfall (Table 2.4). The correlations of maturation of ovaries and female GSI with these environmental variables were stronger and more often statistically significant (Table 2.4).

The annual pattern of gonad maturation in *N. minor* was difficult to discern due to lack of samples during several months (Figure 2.4). The available data, however, suggested that active ovaries were present in all months that were sampled. Active testes were present during most months. Percent frequency of active ovaries and average GSI were usually higher near the new moon (Figure 2.4). There was some suggestion of higher frequency of active ovaries during the earlier part of the second north-east monsoon season (November-December 2008) (Figure 2.4). Outside of this season, active testes were absent or less frequent (March, May and September 2008). Differences in the frequencies of active gonads and average female GSI between north-east monsoon and inter-monsoonal seasons were not apparent (Figure 2.4). Correlations between monthly percent frequency of active testes, active ovaries and monthly GSI were low to moderate (Table 2.4). Maturation of testes, ovaries and average GSI had weak positive relationships with SST but none of these relationships were statistically significant. Correlations between gonad maturation patterns and rainfall were negligible except for frequency of active ovaries which had a positive (but not statistically significant) relationship with rainfall.

In *P. moluccensis*, a strong seasonal pattern was detected in the maturation of testes and ovaries and the fluctuations in female GSI (Figure 2.5). The percent frequency of active gonads and average GSI were much higher during the south-west monsoon and inter-monsoonal seasons (Figure 2.5c-e). Conversely, the percent frequency of inactive gonads and average GSI were lowest from December to January, during the north-east monsoon. The inferred seasonal pattern of spawning appeared to be directly proportional to SST and inversely related to wind speed. Strong correlations were detected between the patterns of maturation of testes and ovaries and the patterns of GSI (Table 2.4). Gonad maturation and GSI had moderate positive relationships with SST and moderate negative relationships with wind speed, but these were not statistically significant (p ranged from 0.06 to 0.08). Correlations between gonad maturation and GSI versus rainfall were negligible (Table 2.4).

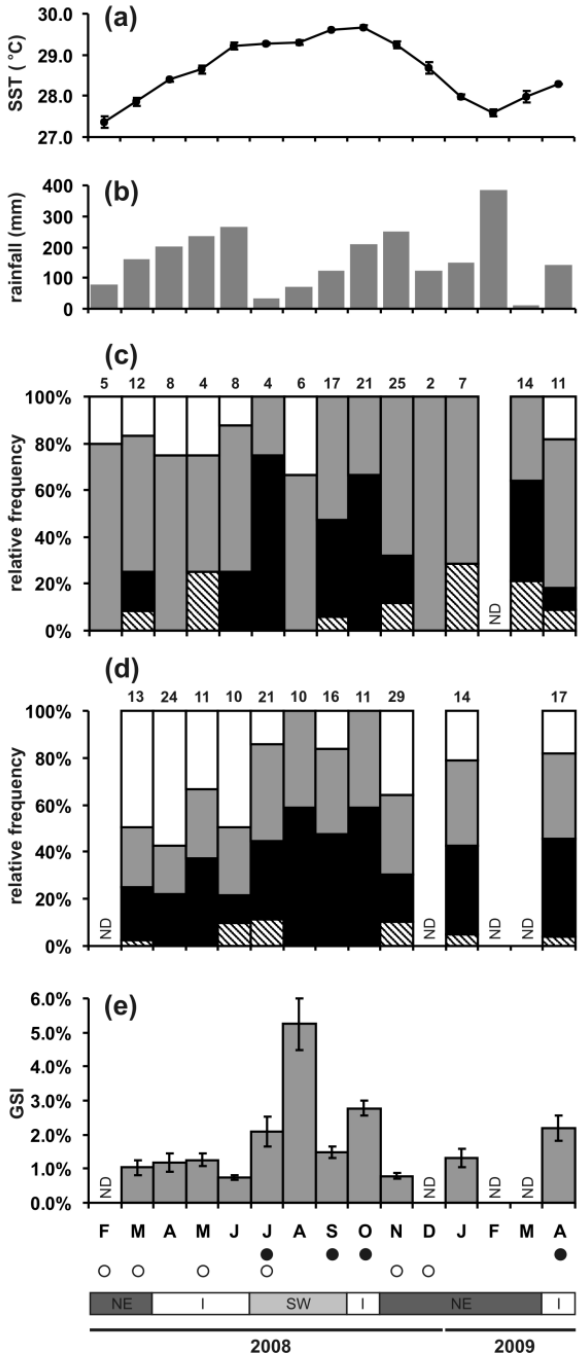


Figure 2.3 Monthly gonad maturation patterns of *Caesio caerulaurea* versus environmental variables. Labels and legends are the same as in Figure 2.2.

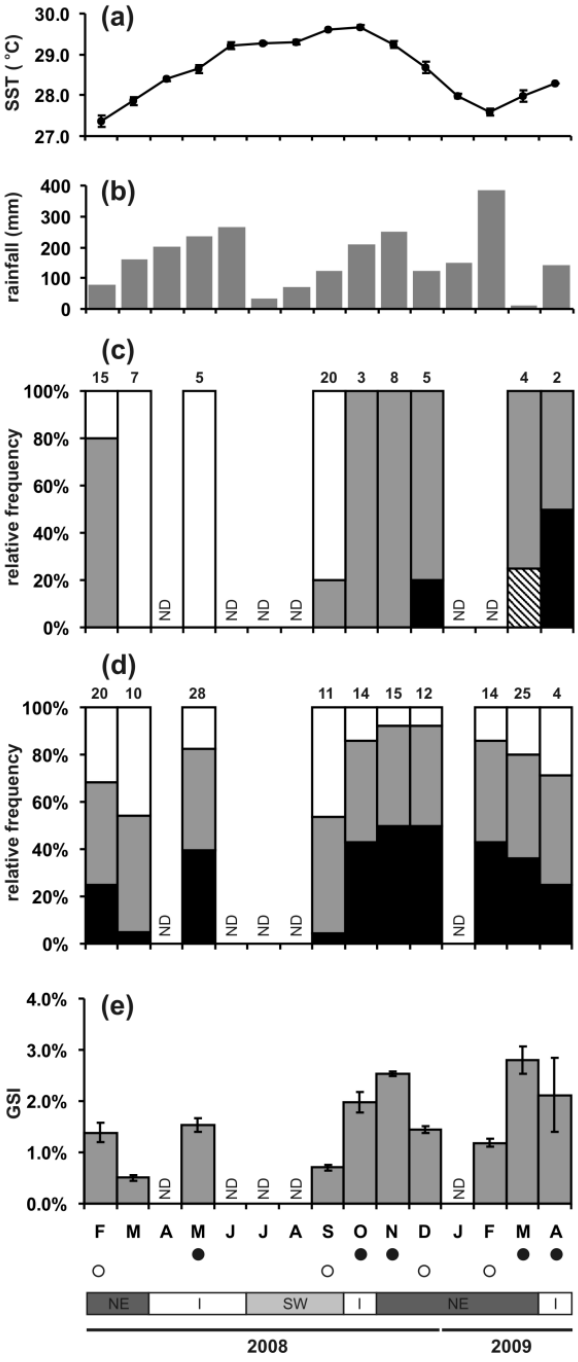


Figure 2.4 Monthly gonad maturation patterns of *Naso minor* versus environmental variables. Labels and legends are the same as in Figure 2.2.

2.3.4 Estimates of batch fecundity

No significant differences in the density of hydrated (or largest) oocytes (number of hydrated oocytes per gram ovary tissue) were found among the regions of the lobes (i.e., anterior, median and posterior) and between the lobes of the ovaries of *C. caerulaurea*, *N. minor* and *P. moluccensis* (Table 2.5). In *P. pisang*, however, a significant difference was detected between regions, but not between lobes (Table 2.5). There was a decreasing trend in the density of oocytes from the anterior to the posterior region of the ovaries of *P. pisang*. A post-hoc test (Tukey's test) indicated that oocyte density was significantly higher (by 23%) in the anterior region than in the posterior region. For each species, batch fecundity was estimated using counts of hydrated (or largest) oocytes taken from 3 replicate subsamples of ovary tissue, one each from the anterior, median and posterior regions, of a randomly selected lobe of the ovary. Estimates of average batch fecundity per species are given in Table 2.6. Batch fecundity was highest in the largest species, *C. caerulaurea* and lowest in the smallest one, *P. moluccensis*. Batch fecundity was more variable in *C. caerulaurea* and *N. minor* and less variable in *P. moluccensis* and *P. pisang* (Table 2.6). Batch fecundity was found to increase with size in the two species of fusilier, but this relationship was weak (and not statistically significant) in *P. pisang*. Batch fecundity and body size had no apparent relationship in *N. minor* and *P. moluccensis* within the ranges of size that were examined. However, the size range that was examined for each species was small (Table 2.6).

2.4 Discussion

The expectation of protracted breeding seasons of coral reef fishes at lower latitudes was confirmed. The gonads of all four species were in spawning condition almost every month that was sampled. Broad spawning peaks were evident. However, the timing of inferred spawning peaks in relation to the monsoons varied between species. Only *P. pisang* showed a spawning peak in one year that coincided with the longer inter-monsoonal period of the year – a pattern that is consistent with the findings of Cabanban (1984) for this species in the same area. In the following year, the spawning peak of *P. pisang* occurred during the north-east monsoon and may have extended to the succeeding inter-monsoonal period. In *C. caerulaurea*, a probable spawning peak occurred during the south-west monsoon and the following (shorter)

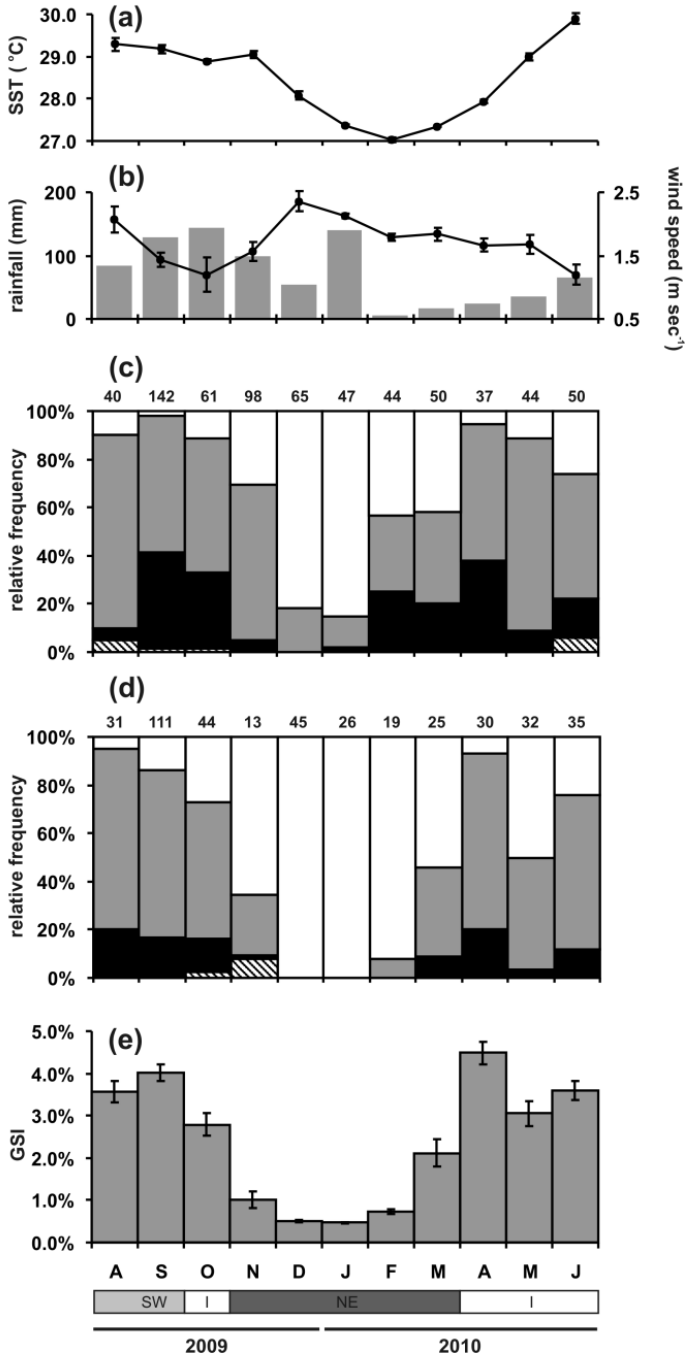


Figure 2.5 Monthly gonad maturation patterns of *Pomacentrus moluccensis* versus environmental variables: average monthly sea surface temperature (SST) (a); total monthly rainfall and wind speed (b); relative frequency of individuals in different gonad maturity stages for males (c) and females (d); average monthly female GSI (e). Other labels and legends are the same as in Figure 2.2.

Table 2.5 Results of 2-way ANOVA testing for significant differences in the density of hydrated (or largest) oocytes among regions of the lobe (i.e., anterior, median and posterior) and between the lobes of ovaries of *Pterocaesio pisang*, *Caesio caerulaurea*, *Naso minor* and *Pomacentrus moluccensis* (n = 6 replicate fish per species). A post-hoc test (Tukey's HSD) revealed a significant difference between the anterior and posterior regions of the ovary of *P. pisang*. A = anterior, M = median and P = Posterior.

	P. pisang		*C. caerulaurea*		*N. minor*		*P. moluccensis*	
2-way ANOVA								
Effects	F	p	F	p	F	p	F	p
Lobe	0.72	0.40	0.66	0.42	0.37	0.55	1.70	0.20
Region	3.55	0.04	0.06	0.94	0.02	0.98	2.85	0.07
Lobe x Region	0.22	0.80	0.03	0.97	0.01	0.99	1.57	0.23
Tukey's HSD								
Region	A > P	0.03						
	A = M	0.36						
	M = P	0.32						

Table 2.6 Estimates of batch fecundity for *Pterocaesio pisang* (PP), *Caesio caerulaurea* (CC), *Naso minor* (NM) and *Pomacentrus moluccensis* (PM). The potential relationship between batch fecundity and body size was determined using simple linear regression. *Fork length (cm FL) was used for PP, CC and NM, while standard length (cm SL) was used for PM.

		Size range*	Batch fecundity			Batch fecundity vs. size relationship
Species	n	(cm)	Range	Ave. ± SD	CV	
PP	14	12.4-15.5	5,787 to 32,916	21,603 ± 6,541	30%	weakly positive $R^2 = 0.25$, $F_{1,12} = 4.0$, $p = 0.07$
CC	13	18.5-25.1	27,500 to 154,923	67,870 ± 37,754	55%	positive $R^2 = 0.75$, $F_{1,11} = 32.0$, $p < 0.001$
NM	14	16.0-18.4	5,209 to 26,214	13,483 ± 6,025	45%	no relationship $R^2 = 0.08$, $F_{1,12} = 1.0$, $p = 0.34$
PM	14	4.0-5.4	1,360 to 3,426	2,506 ± 569	23%	no relationship $R^2 = 0.01$, $F_{1,12} = 0.1$, $p = 0.79$

inter-monsoonal period. The annual pattern of spawning was less clear in *N. minor*, but there was a weak indication of spawning activity being slightly higher during the north-east monsoon. In *P. moluccensis*, spawning activity was high throughout the year except during the north-east monsoon. Taken together, these results do not provide strong support for the notion that the timing of reproduction in reef fishes in monsoonal environments tracks the inter-monsoonal periods.

If the timing of spawning of reef fishes in the area that was studied has adapted to take advantage of optimum conditions for survival of larvae, then the results indicate that such conditions are not restricted to the inter-monsoonal periods. A study on recruitment of reef fishes in the same locality partly supports this suggestion. Abesamis and Russ (2010) (Chapter 3) showed that for many species, the best 'window' for recruitment is during a period of 4-6 consecutive months that includes the two inter-monsoonal periods and the south-west monsoon (May to October). They concluded that warmer temperatures and weaker winds (locally) during this recruitment window are critical to larval survival. However, assuming that the same 4-6 month period is important for the larvae of all four species considered here, it would appear that only *C. caerulaurea* and *P. moluccensis* have adapted to take advantage of this period. Note that a reasonable case for adaptation can be made for *P. moluccensis* since this species dominated recruit densities in the study by Abesamis and Russ (2010) (but alternative explanations for the seasonal pattern of spawning in this species are given below).

Other conditions beneficial to larvae that occur outside of the inter-monsoonal periods are possible, which may explain the patterns of spawning in the other two species, particularly *P. pisang*. For instance, the monsoons may result in regional or local upwelling depending on the degree of exposure and orientation of a site to prevailing winds (Wang et al. 2006, Cabrera et al. 2011, Villanoy et al. 2011). McIlwain et al. (2006) found that four demersal species of fish in Oman (Arabian Sea) appeared to match their spawning with the south-west monsoon. They hypothesised that the timing of spawning in these four species maximizes larval survivorship due to the increased primary productivity brought by upwelling (McIlwain et al. 2006). Such a possibility would further weaken the argument for the importance of inter-monsoonal periods and complicate the detection of an adaptive response of reef fishes to favourable conditions for their larvae. Clearly, the potential effects of the monsoons on survival of reef fish larvae warrant further investigation.

Alternatively, the patterns of spawning described here possibly reflect temperature, rainfall, wind or wave action more directly affecting the spawning of adults, as opposed to adaptation of reproduction to ensure higher survivorship of larvae in the pelagic environment. Potential relationships between spawning and environmental variables were evident in *P. pisang*, *C. caerulaurea* and *P. moluccensis*. The nature of these relationships varied among species, which suggests that responses of adults were species- and/or location-specific. The relationship between environmental factors and spawning in *N. minor*, however, requires further study.

The results indicate that temperature and rainfall were correlated in opposite ways to the temporal pattern of spawning in the two more closely-related species, the fusiliers *P. pisang*, and *C. caerulaurea*. At first glance, these results are difficult to explain. However, a closer examination shows that the first peak of spawning of *P. pisang* occurred when SST was increasing. Similarly, the peak of spawning of *C. caerulaurea* was positively correlated with SST. Increasing temperatures may therefore be an important cue for spawning in fusiliers. This assertion is supported by previous studies on reproduction in fusiliers. The spawning season of *C. caerulaurea* in Okinawa, Japan (26º N) coincides with increasing temperatures around June (Yokoyama et al. 1995). Another species of fusilier, *Pterocaesio digramma*, also has a spawning period that occurs around the same time of year in the same locality (Yokoyama et al. 1994; Choi et al. 1996). The annual pattern of spawning in *P. pisang* previously documented by Cabanban (1984) at two offshore sites in the Bohol Sea (Apo and Sumilon Is.) could then be due to increasing temperatures from February to June.

In the present study, a second spawning peak in *P. pisang* occurred when temperature was decreasing, suggesting the influence of other environmental factors. Results point to food availability driven by rainfall as a factor that is likely to affect spawning activity in *P. pisang*. The spawning of this species had a weak but statistically significant positive correlation with rainfall. Abundance of plankton in tropical areas can vary seasonally with rainfall because the latter usually increases terrestrial run-off and nutrient input into coastal areas (Sander and Steven 1974; Grahame 1976; Sammarco and Crenshaw 1984). Spawning activity has been positively correlated with freshwater discharge in coastal populations of a planktivorous reef fish (*Abudefduf abdominalis*) in Hawaii (Tyler and Stanton 1995). Furthermore, food availability has a direct relationship with reproductive activity in reef fishes (Clifton 1995; Tyler and

Stanton 1995). In the present study, rainfall may have had an indirect positive influence on the pattern of spawning of *P. pisang* but a similar situation was not apparent in *C. caerulaurea* (a negative correlation between rainfall and spawning was detected). This discrepancy may be partly explained by geographic location, i.e., degree of exposure of sampling sites to major sources of terrestrial run-off. The majority (61%) of the *P. pisang* samples came from sites along the coast of Negros (Amlan and Dumaguete, Figure 2.1), closer to several rivers and many streams. On the other hand, the majority (75%) of the *C. caerulaurea* samples came from an offshore site (Apo Is.) 7 km away from the nearest coast. However, degree of exposure to terrestrial run-off cannot explain the negative correlation between rainfall and spawning activity in *C. caerulaurea*. Future studies should attempt to measure spawning activity of planktivorous reef fishes at different sites and relate the information to data on concentrations of planktonic prey, rainfall, freshwater discharge, and other factors such as monsoon-induced upwelling.

In *P. moluccensis*, the depression of spawning activity during the north-east monsoon may have been a direct or indirect consequence of environmental stresses specific (but not unique) to the site where this species was studied. Spawning was negatively correlated with wind but positively correlated with temperature (both not significant statistically), suggesting three possible mechanisms driving the annual pattern of spawning. First, heavy wave action due to north-east monsoon winds may make nesting difficult or disadvantageous for *P. moluccensis*, especially in shallower water. A similar point was made by Robertson (1990) to explain the lower spawning output of two species of damselfish (*Stegastes partitus* and *S. diencaeus*) at a Caribbean site in San Blas, Panama during periods when that site was exposed to heavy wave action brought by the dry season tradewind. The second potential mechanism is related to the first. Heavy wave action during the north-east monsoon may result in lower abundance of the benthic algae that is eaten by *P. moluccensis*, resulting in decreased reproductive output or failure to store enough energy reserves for spawning. This type of mechanism involving food limitation was demonstrated convincingly by Clifton (1995) in an herbivorous reef fish (the parrotfish *Scarus iserti*) at two Caribbean sites in San Blas that differed in their exposures to the dry season tradewind. In the exposed reef that Clifton studied, strong wave action may have reduced algal food levels directly by physical removal or indirectly by decreasing water clarity (increasing turbidity). The third mechanism could be related to lower temperatures during the north-east monsoon.

For instance, Robertson (1990) showed that the spawning output of two species of damselfish (*Stegastes acapulcoensis*, *S. flavilatus*) at a Pacific site in Panama was lower during periods when temperature was lower. However, the drop in temperature at that Panamanian site is considerable (from average of 30 ºC to just 14-18 ºC) due to local upwelling, which casts some doubt about the importance of temperature in the pattern of spawning of *P. moluccensis* in the present study (annual temperature difference in the Dumaguete site is < 3 ºC). Future studies on the reproduction of *P. moluccensis* and other shallow-water reef fishes in monsoonal environments should investigate these three potential mechanisms. A comparative approach would be most useful, wherein populations subject to different degrees of exposure to the two monsoons are sampled.

The protracted spawning seasons described in this study may be typical of smaller-bodied species of reef fish. For instance, in her review of the temporal patterns of spawning of reef fishery species, Sadovy (1996, p. 35-36) found an inverse relationship between body size and duration of spawning season among species within three families (i.e., groupers, emperors and snappers). Robertson (1990) argued that smaller-bodied species may be limited by shorter lifespans and low capacity to store resources for future egg production, which could prevent a strategy of timing spawning peaks to coincide with periods that would favour survivorship of larvae. Comparative studies on the patterns of reproduction between smaller- and larger-bodied species of reef fish in relation to the monsoons are required to elucidate size-related temporal spawning strategies.

The possible influence of lunar patterns of spawning on the inferred annual patterns of spawning in *P. pisang*, *C. caerulaurea* and *N. minor* deserves a brief discussion. There were indications that the percent frequency of active ovaries and average GSI were higher around the full moon and new moon for *P. pisang,* and around the new moon for *C. caerulaurea* and *N. minor* (Figures 2.2-2.4). However, gonad maturation patterns in the two species of fusilier did not have a predictable relationship with the lunar cycle. For instance, in *P. pisang*, the frequency of active ovaries and average GSI were low around the time of the full moon during several months (February 2008, July 2009 and September 2009) (Figure 2.2). For *C. caerulaurea*, the highest average GSI, which was recorded in August 2008, did not occur around the time of the new moon (Figure 2.3). Furthermore, daily observations by Yokoyama et al. (1994, 1995) on the reproductive behaviour of two species of fusilier (*P. digramma* and *C. caerulaurea*) suggested that spawning in fusiliers is not associated with the lunar

cycle. Thus, in the present study, the inferred annual patterns of spawning of *P. pisang* and *C. caerulaurea* were probably not indicative of lunar patterns of spawning. On the other hand, the possible influence of the lunar cycle on the inferred annual pattern of spawning in *N. minor* cannot be ruled out. No studies on the lunar patterns of spawning of *N. minor* are available.

In conclusion, the monsoons may play an important role in the timing of reproduction of reef fishes, but it is clear from this study that peaks in spawning activity are not necessarily restricted to the inter-monsoonal periods. The influence of the monsoons on spawning seasonality is likely to be complex. Many environmental variables change with the monsoons. These variables also vary at several spatial scales. Although it cannot be denied that some species appear to take advantage of inter-monsoonal conditions presumably to increase survivorship of larvae (Johannes 1978), the effect of the monsoons on reproduction is obviously not uniform across all species. However, the lack of a consistent pattern between species may also be partly due to the limited number of species that were examined and the limited time of the study, which did not allow the documentation of inter-annual variability. We still know very little about the annual patterns of spawning of reef fishes in monsoonal environments and how important these patterns are in the dynamics of reef fish populations. Protracted spawning periods are likely to be typical of reef fishes situated at lower latitudes (Robertson 1991) but the ways in which the monsoons may influence the spatial and temporal patterns of reproduction and recruitment in reef fishes warrant further investigation.

Chapter 3

Patterns of recruitment of coral reef fishes in a monsoonal environment*

Abstract. The abundance of newly settled recruits of coral reef fishes was monitored at a total of 11 sites at two islands and two coastal locations in the central Philippines for a 20-month period (February 2008 to September 2009) that included two monsoon cycles. Recruitment occurred throughout the year. Most of the abundant species exhibited protracted recruitment seasons. This confirms the expectation of extended breeding of reef fishes at lower latitudes (see Chapter 2). The annual pattern of recruitment of reef fishes as a group was reasonably predictable. Annual fluctuations of sea surface temperature and wind strength largely explained the pattern. Rainfall, however, did not significantly influence the pattern of recruitment. Peaks in density and species richness of recruits occurred during the southwest monsoon and the second inter-monsoonal period of the year (July to October) when temperatures were highest and when most of the sites were sheltered from winds or when winds were weak. Conversely, lowest density and species richness of recruits were observed during the northeast monsoon (November to March) when temperatures were lowest and most sites were exposed to winds. The same pattern could also be seen in the recruitment of both damselfishes (Pomacentridae) and wrasses (Labridae), notwithstanding a 10-fold difference in abundance of recruits between the two families. The pattern was fairly consistent across most sites, among most of the species that were examined, and between the two years that were sampled. This study is one of the few to provide insights into the influence of environmental factors on the recruitment patterns of fishes on Indo-Pacific coral reefs situated at lower latitudes.

*This thesis chapter has already been published:

Abesamis RA, Russ GR (2010) Patterns of recruitment of coral reef fishes in a monsoonal environment. Coral Reefs 29:911-921

3.1 Introduction

The demographic structure and population dynamics of marine species with a pelagic larval phase and a benthic adult phase can be heavily influenced by recruitment (i.e., the addition of juveniles to a population) (Doherty and Williams 1988; Roughgarden et al. 1988; Underwood and Fairweather 1989). Recruitment is highly variable in time and space at many scales, reflecting the variability and unpredictability of processes in the pelagic environment that affect growth and survivorship of larvae (Doherty 1991; Caley et al. 1996). The degree of seasonality of the environment can influence the annual timing of recruitment. Timing of reproduction may also be adapted to match oceanographic conditions that are favourable to the survival of larvae (Johannes 1978; Cushing 1987). In coral reef fishes, seasonality of recruitment is most obvious on reefs closer to the limits of the tropics (23.5º N and S). Highly seasonal recruitment is typical of populations at higher latitude reefs, where most juveniles settle within a relatively short period during the warmer half of the year, forming distinct 'year-classes' (e.g., southern Great Barrier Reef, ~23.5º S, see Russell et al. 1977; Williams and Sale 1981). In contrast, recruitment on lower latitude reefs is less seasonal and there may be no period without some settlement (e.g., Victor 1986; Robertson et al. 1993 in the Caribbean Panama, ~9.5º N). The importance of recruitment in modifying population structure and dynamics will likely differ between higher and lower latitude reefs (Srinivasan and Jones 2006). However, it is difficult to make generalizations about what environmental conditions have the strongest effects on the variability of spawning and recruitment (Doherty 1991; Robertson 1991). The relative importance of environmental factors that determine the timing and strength of spawning activity and recruitment will likely vary among geographic locations at similar latitudes and even among closely-related species (Robertson 1990; Clifton 1995; Lemberget et al. 2009).

Coral reefs closer to the equator are subject to monsoonal conditions that are characterised more by annual wind and precipitation cycles than by changes in ambient sea temperature. Reef fishes in equatorial regions may time their spawning during periods when winds and currents are at their weakest, presumably to limit the advection of larvae away from natal reefs and increase the chances of settlement to suitable habitats (Johannes 1978). Fishes may also time spawning activity to take advantage of upwelling events caused by monsoon winds (McIlwain et al. 2006). Furthermore, even

at lower latitude reefs, temperature may still play a role in mediating settlement success of reef fishes by increasing larval growth rates (Wilson and Meekan 2002). However, few studies have assessed the role of the monsoons in the dynamics of recruitment of reef fishes. Most of the studies that have related patterns in spawning, larval supply and settlement with environmental variables at lower latitudes were conducted in the Caribbean (Robertson 1990; Clifton 1995; Sponaugle and Cowen 1996, 1997; Robertson et al. 1999; Wilson 2001). Surprisingly, little is known about the patterns of spawning and recruitment of reef fishes at lower latitudes in the Indo-Pacific region and the extent to which monsoonal conditions influence these patterns. To date, the only study which related environmental data with observed patterns of recruitment of reef fishes in a low latitude location in the Indo-Pacific region is that of Srinivasan and Jones (2006) (Kimbe Bay, Papua New Guinea, ~5.5º S). The paucity of knowledge is regrettable considering Indo-Pacific coral reefs that are close to the equator, such as those in Southeast Asia, have the most diverse fish communities (Myers 1999; Carpenter and Springer 2005), and yet are some of the most threatened reefs in the world (Burke et al. 2002; Hoegh-Guldberg et al. 2009). Addressing this knowledge gap must begin with gathering basic information on temporal and spatial patterns of reproduction (see Chapter 2) and recruitment.

The main objective of this study was to determine the temporal (annual) pattern of recruitment of common coral reef fishes in the central Philippines, where two monsoon seasons occur per year. Density and species richness of newly settled recruits were monitored for 19 separate months over a 20-month period at offshore (island) and inshore (coastal) locations separated by up to 40 km. Temporal variability of recruitment was evaluated against fluctuations in sea surface temperature, wind speed and rainfall to determine which (if any) of these environmental variables could have a strong effect on the pattern of recruitment.

3.2 Materials and methods

3.2.1 Geographic setting of the study area

This study was conducted off south-eastern Negros Is. in the Bohol Sea, central Philippines (9.06-9.43 °N, 123.23-123.40 °E; Figure 3.1). As with the Philippines in general, this area is influenced by the reversing wind pattern of the Asian monsoon (Wang et al. 2001). From November to early March, strong winds from the northeast

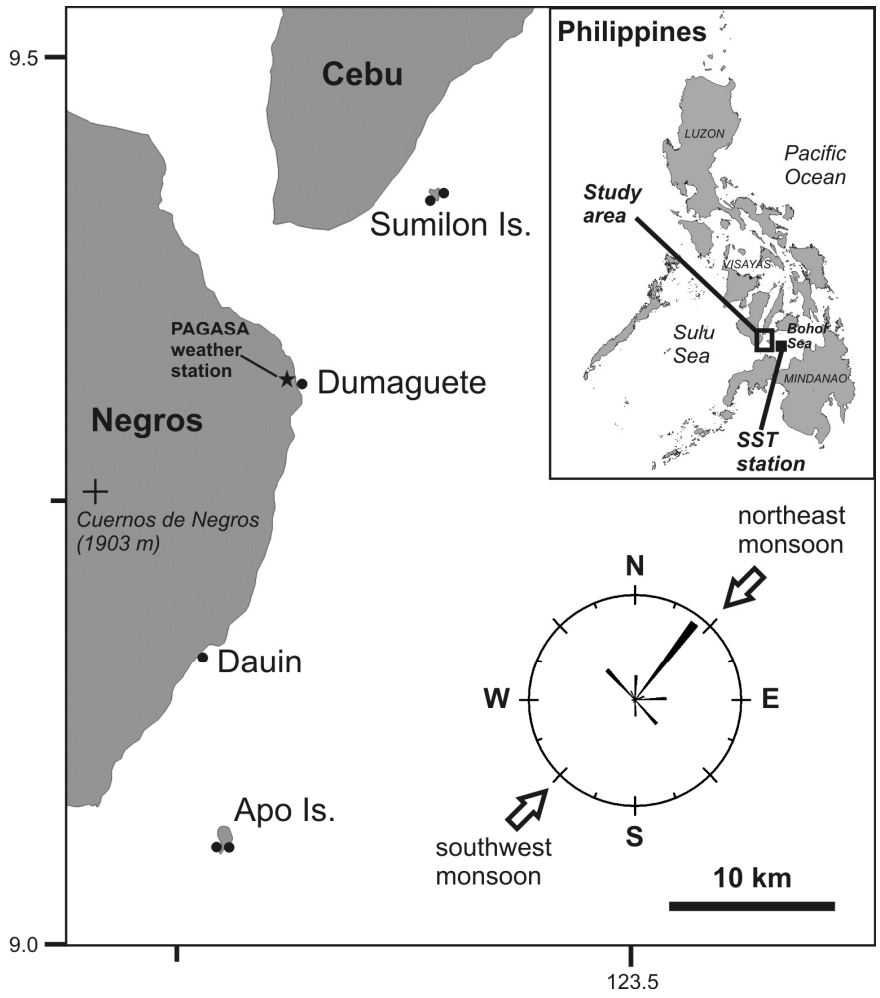


Figure 3.1 Map of the study area showing the two islands (Sumilon and Apo) and two coastal locations (Dumaguete and Dauin) where recruitment of reef fishes was monitored over a 20-month period. Black dots also indicate the locations of sites on the two sides of each island that differed in their exposure to the two monsoons. The wind chart shows the frequency distribution of daily wind direction for one year (January to December 2008) recorded at a weather station in Dumaguete. Inset map shows the location of the study area in the Philippines. The inset map also shows the location of the sea surface temperature (SST) virtual monitoring station (a 0.5º longitude x 0.5º latitude area) of the NOAA Coral Reef Watch Program (see Materials and methods).

(northeast monsoon) predominate, while from July to September, strong winds blow from the southwest (southwest monsoon). However, much of the study area is sheltered from the southwest monsoon due to tall mountains in south-eastern Negros (e.g., Cuernos de Negros, elevation: 1,903 m; Figure 3.1). Winds during inter-monsoonal months (April to June and October) are lighter and more variable in direction. Sea surface temperature fluctuates by about 3 °C annually (about 27-30 °C) (NOAA Coral Reef Watch Program, http://coralreefwatch.noaa.gov/satellite/index.html) (Figure 3.2a). Temperatures are lowest from January to March during the northern hemisphere winter. During this period, the northeast monsoon brings cool winds from mainland Asia. Temperatures are highest from June/July to November, during and towards the end of the southwest monsoon. The wet and dry seasons that are typical of many regions of the Philippines are not very pronounced in this area, but from November to April rainfall is usually lower compared to the rest of the year [Type III climate based on classification by the Philippine Atmospheric, Geophysical and Astronomical Services Administration (PAGASA) (http://kidlat.pagasa.dost.gov.ph/cab/cab.htm)]. The area may also be affected by several typhoons annually, but it is situated away from the main path of typhoons (up to 20 typhoons may affect the Philippines throughout the year).

3.2.2 Study sites

Two small islands and two coastal locations 15-40 km apart were surveyed in order to gain insights into recruitment patterns within the ~300 km^2 study area (Figure 3.1). The two islands were Sumilon (0.2 km^2) and Apo (0.7 km^2). They are about 40 km from each other and about 2 and 7 km away, respectively, from their nearest neighbouring large island (Negros and Cebu, respectively). Coral reefs surround much of Sumilon and Apo to a depth of more than 50 m. Reefs are steeper and more developed along the southern half of the two islands. The two coastal locations were situated along the south-eastern coast of Negros in Dauin municipality and Dumaguete City. Dauin and Dumaguete are about 20 km apart. The reefs in both coastal locations are found less than 300 m from shore between depths of < 1 to 30 m and are patchily distributed, separated by sand or seagrass.

3.2.3 Visual census of recruits

Samples of monthly recruit abundance of coral reef fish were taken by an experienced observer (R.A.A.) by counting all non-cryptic recruits along 50 m long x 2

m wide belt transects laid parallel to the shoreline following a depth contour. The sampling strategy aimed to include as many species and reef habitat types as practically possible. Sampling took place at 11 sites that were unequally distributed among the four locations, two depths (reef slope and reef flat) and two wind exposures (northeast and southwest). North-eastern (NE) and south-western (SW) Sumilon, and south-eastern (SE) and south-western (SW) Apo were sampled. At each of these sides of the two islands, two depths (3-4 m, 10-12 m) were sampled, each with three replicate transects. Hard coral cover in the deeper sites (reef slope) of the two islands ranged from 35-70% except on NE Sumilon where sand, dead coral and rock dominated benthic cover. Soft corals and/or coral rubble dominated benthic cover in the shallower (reef flat) sites. All transects in SW Sumilon and SE Apo were situated inside a no-take marine reserve. In Dauin, surveys were done on coral patches (50-120 m long x 20-80 m wide) found within a stretch of coast about 1 km long. Only two depths were sampled (3-4 m, 8-12 m), each with five replicate transects. Hard coral cover on those coral patches ranged from 30-60%. Almost all transects in Dauin were situated inside two no-take marine reserves. In Dumaguete, the seaward edge of a shallow coral patch (about 200 m long x 100 m wide) was surveyed. Only one depth (3-4 m) was sampled with three replicate transects. Hard coral cover on this coral patch ranged from 30-35%.

Surveys of recruits were conducted for 19 separate months over a 20-month period (late February 2008 to early September 2009). The only month that was not sampled was February 2009 due to inclement weather. Unfavourable weather also prevented surveys at certain sites during some months: February 2008 (Dumaguete site); January 2009 (Sumilon and Apo sites); July 2009 (SW Sumilon at 3-4 m); August 2009 (SW Apo sites); and September 2009 (Dauin at 3-4 m). Moreover, replicate samples were incomplete in Dauin during two months: August 2009 (only 3 transects at 8-12 and 3-4 m) and September 2009 (only 3 transects at 8-12 m). Due to logistical constraints, random sampling among sites could not be performed but the order in which islands and coastal locations were surveyed during each month was not fixed. Within each site, transects had a random starting point wherever practical but the same general area was sampled almost every month. Sites were located every month with the aid of fixed natural (rocks, big coral bommies, etc.) and man-made (mooring buoys) markers at the surface or underwater.

Recruits of a particular month are fish that settled during, and survived to the end of, a lunar cycle. Past studies and reviews indicated that larval settlement on reefs

tends to be higher around the new moon and lower around the full moon (Victor 1986; Doherty 1991; Wilson 2001). This lunar periodicity of larval settlement was confirmed in a pilot study at Dauin where the abundance of new recruits settling on 15 individually-marked branching coral colonies were monitored every 2-3 days over 2 lunar cycles (Appendix 3.1). Surveys of recruits were therefore performed around the full moon (2 days before to 7 days after) in order to capture the peak settlement periods within each lunar cycle. All sites were sampled within 3-4 days except when field work was delayed for 2-3 days because of inclement weather. The time interval between consecutive monthly surveys at each site was about 4-5 weeks (26-35 days; mode = 28 days or 4 weeks). Consistent timing of monthly surveys was used to help reduce variability in the data caused by mortality of early recruits (due to predation).

In order to avoid counting older fish that did not settle within the previous 4-5 weeks, only those fish that were below an arbitrary threshold size were counted. For many species the threshold size was set at < 20 mm total length (TL), e.g., damselfishes (Pomacentridae), wrasses (Labridae), parrotfishes (Scaridae), etc. For species that had larger recruits, e.g., butterflyfishes (Chaetodontidae) and surgeonfishes (Acanthuridae), threshold sizes were set at < 30-40 mm TL, respectively. These size limits allowed for several mm of growth after settlement. Estimates of threshold sizes were guided by family-level information on sizes of late stage pre-settlement larvae and newly settled recruits (e.g., Leis and Rennis 1983; Leis and Trnski 1989; Victor 1991; Paddack and Sponaugle 2008). Data on sizes of newly settled recruits from the pilot study supplemented the basis for these threshold sizes. Threshold size was set at < 20 mm TL for species that had no information available on sizes at the recruit stage. In order to maintain the accuracy of size estimates, the observer always used a ruler attached to the top of his recording slate as a guide. Recruits that were too small to identify to the species level were identified to the genus or family level (e.g., Apogonidae).

Benthic composition along each transect was estimated during the first five months of the survey period. The type of substrate (e.g., hard coral, soft coral, macroalgae, dead coral, rock, sand, etc.) at every 0.5 m point intercepted by the 50-m transect was recorded and expressed as a percentage of all points per transect (% cover). The purpose of the benthic surveys was to provide a baseline description of reef habitat at each site in order to detect changes in habitat caused by disturbances (e.g., coral bleaching, typhoons) that could affect recruit abundance during the study. However, additional benthic surveys were not conducted after the first five months of

the study because the few disturbances (i.e., 3 typhoons) that affected the study area did not cause major damage to the reef habitat at each site.

3.2.4 Weather data and sea surface conditions

Data on sea surface temperature (SST) for the period covered by the recruitment surveys were obtained from the NOAA Coral Reef Watch Program (http://coralreefwatch.noaa.gov/satellite/index.html). The program has a 'virtual' SST monitoring station located in the Bohol Sea close to the study area (Figure 3.1). The SST monitoring station is a 0.5º longitude x 0.5º latitude area. Data on SST are derived from nighttime measurements made by the Advanced Very High Resolution Radiometer (AVHRR) carried on NOAA's Polar Orbiting Environmental Satellites (POES). The temporal resolution of the data was bi-weekly, giving 7-10 days of SST measurements for every 4-5 week period covered by the monthly recruitment surveys. Daily data on wind velocity and rainfall during the recruitment surveys were obtained from a weather station at Dumaguete airport operated by the PAGASA. This weather station is located almost at sea level < 1 km from the coast and about 1-30 km away from the individual recruitment monitoring sites (Figure 3.1). The data on wind showed that wind speed was highest in January and February during the northeast monsoon and weakest around July during the southwest monsoon (Figure 3.2b). This wind pattern is due to the fact that when south-westerly winds predominate, Dumaguete is on the leeward side of Negros (see wind chart in Figure 3.1). However, the pattern in wind speed also directly reflects the seasonal change in sea surface conditions within much of the study area. Wind stress (i.e., drag caused by wind moving over water) causes seasonality of wave action. Surface waters east of Negros are generally more turbulent during the northeast monsoon than the southwest monsoon (R. Abesamis, personal observations over > 2 years). The sheltering effect of Negros during the southwest monsoon is most noticeable in Dumaguete but can still be felt at Dauin and Sumilon. Occasionally, however, the two latter sites can be affected by storm surge when the southwest monsoon is intensified by typhoons. Apo Is., on the other hand, is not sheltered by Negros during the southwest monsoon. Thus, surface waters around Apo can be rough during both monsoons. The data on rainfall was probably an accurate index of rain intensity for the entire study area. Peaks in rainfall during certain months were caused by the intertropical convergence zone and several typhoons and storms that affected the area, as opposed to just localized rain in the Dumaguete area (Figure 3.2b).

Heaviest rainfall was recorded in early February 2009, when a storm brought more than 250 mm of rain in just one day.

3.2.5 Data analyses

The temporal pattern of 'collective recruitment' (i.e., recruits of all species combined) was described by averaging monthly total recruit density and species richness across all 11 sites. Significant differences among monthly average values (19 months) were then determined using one-way ANOVA. Planned contrasts were made after each ANOVA to determine inter-annual and seasonal differences. For inter-annual comparisons, data from March to September in 2008 were contrasted with data from the same months in 2009. For comparisons between seasons, data from northeast monsoon (November to March), southwest monsoon (July to September) and inter-monsoonal months (April, May, June and October) were contrasted with each other. The overall temporal pattern of recruitment of two common families, the damselfishes and the wrasses, were compared. Special interest was given to these two families because they dominated recruit species composition and comprised 80% of cumulative recruit abundance. Monthly recruit densities of the damselfishes and wrasses were summarised and analysed following the same approach as that for total recruit density.

Potential effects of SST, wind speed (as a proxy for wind stress) and rainfall on the temporal pattern of collective recruitment were tested using multiple regression analyses. Average recruit density and species richness values were computed for each location (Sumilon, Apo, Dauin and Dumaguete) for every month surveyed, giving a sample size of n = 73 for each regression. Monthly values for each environmental variable were computed by averaging (for SST and wind speed) or summing (for rainfall) bi-weekly or daily values within each 4-5 week period that corresponded to each monthly recruitment survey. The potential effects of SST, wind stress and rainfall on the temporal pattern of recruitment of the damselfishes and wrasses were also tested following the same procedures.

Most variables were transformed in order to conform to the assumptions of parametric statistical procedures [log (x + 1) for total recruit density, damselfish density, wind speed, rainfall; $(x)^{1/2}$ for species richness; $(x + 0.001)^{0.25}$ for wrasse density]. All statistical analyses were performed in Statistica (ver. 8).

Species-level analysis of temporal patterns of recruitment was limited to the most abundant species, i.e., species that had a cumulative abundance of ≥ 50 recruits

recorded from all sites. Only the data from sites where each species was most abundant were used in this analysis. The duration of the recruitment period of each species was estimated by counting the number of months when recruitment was considered significant. To determine which months had significant recruitment, two arbitrary thresholds of abundance were applied. The first threshold was set at ≥ 1 % of the adjusted total abundance in one year. This was adapted from Srinivasan and Jones (2006) and was used in the present study in order to directly compare results between the central Philippines and Kimbe Bay, Papua New Guinea. The second threshold was set at ≥ 5 % of the adjusted total abundance in one year to provide more conservative estimates of duration of the recruitment period. To compute the adjusted total abundance of a species in one year, average abundance values for each month that was surveyed for two years (March-September) were initially computed then added to the raw abundance values of other months. The abundance value of each month was then expressed as a percentage of the adjusted total abundance in one year.

3.3 Results

A total of 40,913 new recruits of 120 species of reef fish from 16 families were recorded during the surveys. Species composition was dominated by the damselfishes (43 species) and wrasses (35 species). Damselfishes comprised 73% of total recruit abundance, wrasses just 7%. The five most abundant species were four damselfish species (*Pomacentrus moluccensis*, *Chromis ternatensis*, *Chromis viridis*, and *Chromis retrofasciata*) and one species of anthias (*Pseudanthias tuka*, Serranidae, subfamily Anthiinae). Together, the recruits of these five species accounted for 54% of the total number of recruits recorded.

New recruits were observed during all months sampled, but a distinct temporal pattern was present. Peaks in total recruit density were recorded during the southwest monsoon and the second inter-monsoonal period of the year, in June-July, July-August and September-October 2008 and June-July 2009 (Figure 3.2c). Total density during peak months averaged between 100-140 recruits 100 m^{-2}. During other months, density was typically less than 30-50% of peak levels. Lowest levels of recruit density were observed during the northeast monsoon, in February and March 2008 and December-January and March-April 2009, averaging between 5-15 recruits 100 m^{-2} (Figure 3.2c). This temporal pattern was also evident in the density of recruits of damselfishes and

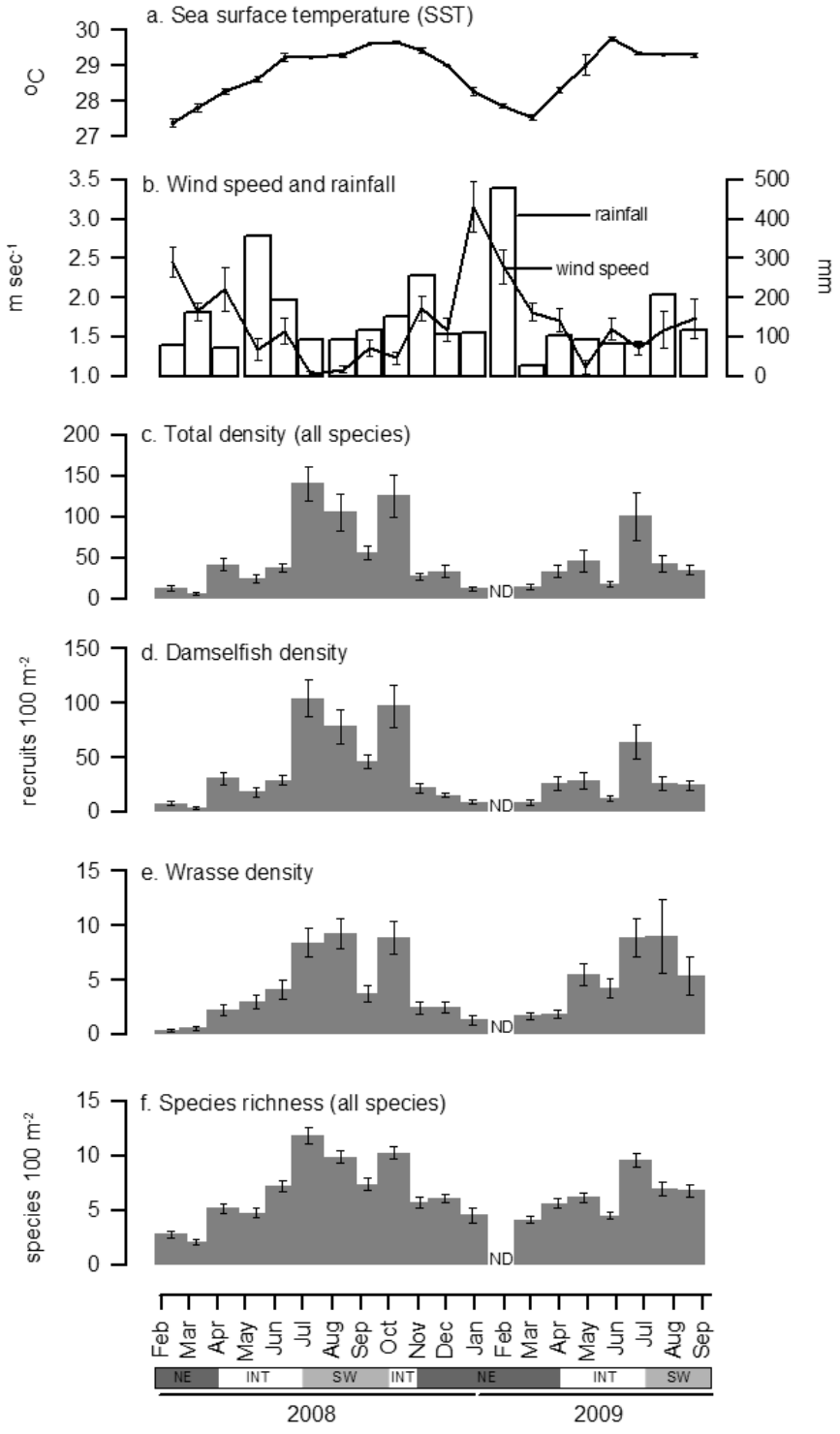


Figure 3.2 Temporal patterns of sea surface temperature, wind speed and rainfall (a, b) versus temporal patterns of recruit density (total, damselfishes, wrasses) and species richness averaged for all sites (c-f). Monsoons indicated by different shades of grey along x-axis. NE = northeast monsoon; SW = monsoon; INT = inter-monsoon. Position of plotted data between calendar months reflects change in timing of lunar months relative to calendar months. Error bars are ± SE. ND = no data.

wrasses, notwithstanding a 10-fold difference in abundance of recruits between the two families (Figure 3.2d-e). However, recruit density of wrasses also peaked in July-August 2009. The temporal pattern in species richness mirrored the temporal patterns in density (Figure 3.2f). On average, 10-12 species per 100 m^{-2} were recruiting during months of highest recruit densities. In contrast, only 2-7 species per 100 m^{-2} on average were recruiting during other months.

Significant differences in monthly levels of recruit densities (total, damselfish and wrasse) and species richness were detected among the 19 months that were sampled (Table 3.1). Total recruit density was significantly greater (by 64%) in 2008 than in 2009 (March to September). Similarly, damselfish recruit density was significantly higher (by 47%) in 2008 than in 2009. However, no significant inter-annual variation was detected for species richness of recruits and density of wrasse recruits. Significant variation in recruit densities and species richness was detected between all seasons that were compared (Table 3.1). Average recruit densities and species richness were always lowest during the northeast monsoon (November to March), highest during the southwest monsoon (July to September) and were at intermediate levels during the inter-monsoonal months (Table 3.1).

Peaks in recruit densities and species richness were recorded during or around the southwest monsoon, when SST values were highest and wind speed values lowest (Figure 3.2a-f). Conversely, lowest densities and species richness occurred during the northeast monsoon, when SST values were lowest and wind speed values highest. Regression models indicated significant effects of SST and wind speed on monthly average recruit densities and species richness (Table 3.2). SST always had a positive effect, and wind speed always had a negative effect, on recruitment. The models, however, did not suggest any significant effect of rainfall on recruit densities or species richness (Table 3.2, Figure 3.2b-f).

There was a good degree of spatial coherence in the general pattern of monthly collective recruitment (Figure 3.3). The peaks in recruit density during the southwest monsoon and the second inter-monsoonal period, and the troughs during the northeast monsoon were detected across most sites (Figure 3.3a). However, the peak in recruitment in June-July 2009 was obvious at only a few sites, and there were peaks during March-April in 2008 and 2009 that were recorded only in some sites.

Table 3.1 Summary of 1-way ANOVAs and subsequent planned contrasts to determine significant differences in average recruit densities and species richness among 19 months, between two years (2008 vs. 2009) and between seasons. Variables tested were the density and species richness of the recruits of all species combined and the densities of the recruits of damselfishes and wrasses. Average density (individuals 100 m^{-2} ± SE) and species richness (species 100 m^{-2} ± SE) values are indicated for years and seasons that were compared. NE = northeast monsoon (November to March), SW = southwest monsoon (July to September), INT = inter-monsoonal months (April, May, June and October).

		ANOVA	Planned Contrasts							
		(Months, df = 18)	2008	2009	NE	SW	NE	INT	SW	INT
a. Total density (all species)			60.0 ± 5.5	40.8 ± 5.2	18.0 ± 2.0	83.4 ± 8.1	18.0 ± 2.0	46.7 ± 4.9	83.4 ± 8.1	46.7 ± 4.9
	F =	23.4	9.9		186.2		40.6		63.5	
	p =	<0.001	0.002		<0.001		<0.001		<0.001	
b. Damselfish density			44.5 ± 4.1	27.1 ± 3.1	11.5 ± 1.2	60.1 ± 5.5	11.5 ± 1.2	34.8 ± 3.7	60.1 ± 5.5	34.8 ± 3.7
	F =	21.4	18.8		166.0		36.1		56.8	
	p =	<0.001	<0.001		<0.001		<0.001		<0.001	
c. Wrasse density			4.5 ± 0.4	5.0 ± 0.6	1.5 ± 0.2	7.4 ± 0.7	1.5 ± 0.2	4.3 ± 0.4	7.4 ± 0.7	4.3 ± 0.4
	F =	11.9	1.8		119.8		34.0		31.8	
	p =	<0.001	0.18		<0.001		<0.001		<0.001	
d. Species richness (all species)			6.9 ± 0.3	6.2 ± 0.2	4.2 ± 0.2	8.9 ± 0.3	4.2 ± 0.2	6.3 ± 0.2	8.9 ± 0.3	6.3 ± 0.2
	F =	27.4	1.3		220.4		31.7		100.7	
	p =	<0.001	0.25		<0.001		<0.001		<0.001	

Table 3.2 Summary of regression models to assess the potential effects of environmental variables on temporal patterns of recruitment. Dependent variables were the monthly total density (TD) and species richness (SR) of the recruits of all species combined and the monthly densities of recruits of the two families (damselfishes and wrasses – DD and WD, respectively) that dominated recruit species composition and overall abundance. Monthly density and species richness values were averaged for each location (Sumilon, Apo, Dauin and Dumaguete), resulting in n = 73 for each regression. Independent variables were monthly average sea surface temperature (SST), average wind speed (as the proxy for wind stress) and total rainfall. R^2_{adj} = adjusted R^2 value of the regression model, R_p = partial correlation coefficient of independent variable.

	Model			SST			Wind speed			Rainfall		
	R^2_{adj}	F	p	R_p	t	p	R_p	t	p	R_p	t	p
a. TD	0.45	20.71	<0.001	0.35	3.10	0.003	-0.41	-3.71	<0.001	-0.12	-1.03	0.30
b. DD	0.43	19.30	<0.001	0.33	2.90	0.005	-0.40	-3.64	0.001	-0.08	-0.67	0.50
c. WD	0.36	14.56	<0.001	0.37	3.34	0.001	-0.27	-2.36	0.02	-0.14	-1.15	0.25
d. SR	0.52	27.02	<0.001	0.42	3.84	<0.001	-0.43	-3.96	<0.001	-0.17	-1.44	0.16

A total of 37 species, representing 7 families, had a cumulative abundance of ≥ 50 recruits recorded from all sites during the study (Appendix 3.2). The species composition of this subset of species was still dominated by the damselfishes (23 species), followed by the wrasses (6 species). Most of these 37 species had protracted annual recruitment periods. Depending on the threshold value that was used, the majority of species (23-24 species in 5-6 families) had 5-7 or 9-11 months of significant recruitment (Figure 3.4a, b). The shortest recruitment periods were found only in a few species of damselfish (e.g., *Chromis amboinensis*, *Dascyllus trimaculatus*, *Neopomacentrus anabatoides*, *N. azysron*, *Pomacentrus smithii*) and the cardinalfishes (Apogonidae) (Figure 3.4a, b). There was considerable variation in the timing of peaks among species but most peaks occurred during the southwest monsoon and inter-monsoonal months, mainly in July and October (Figure 3.5). Most of the major peaks that contributed substantially to the cumulative annual abundance of each species were also recorded in July or October. Within the damselfishes, the timing of major peaks of *Neoglyphidodon*, *Neopomacentrus* and most *Pomacentrus* spp. differed from that of *Chromis*, *Chrysiptera*, and *Dascyllus* spp. in that the major recruitment peaks in the former group occurred earlier than in the latter group. At the family level, the timing of recruitment peaks of the damselfishes, wrasses, parrotfishes, anthiases and cardinalfishes were more similar to each other compared to the butterflyfishes and

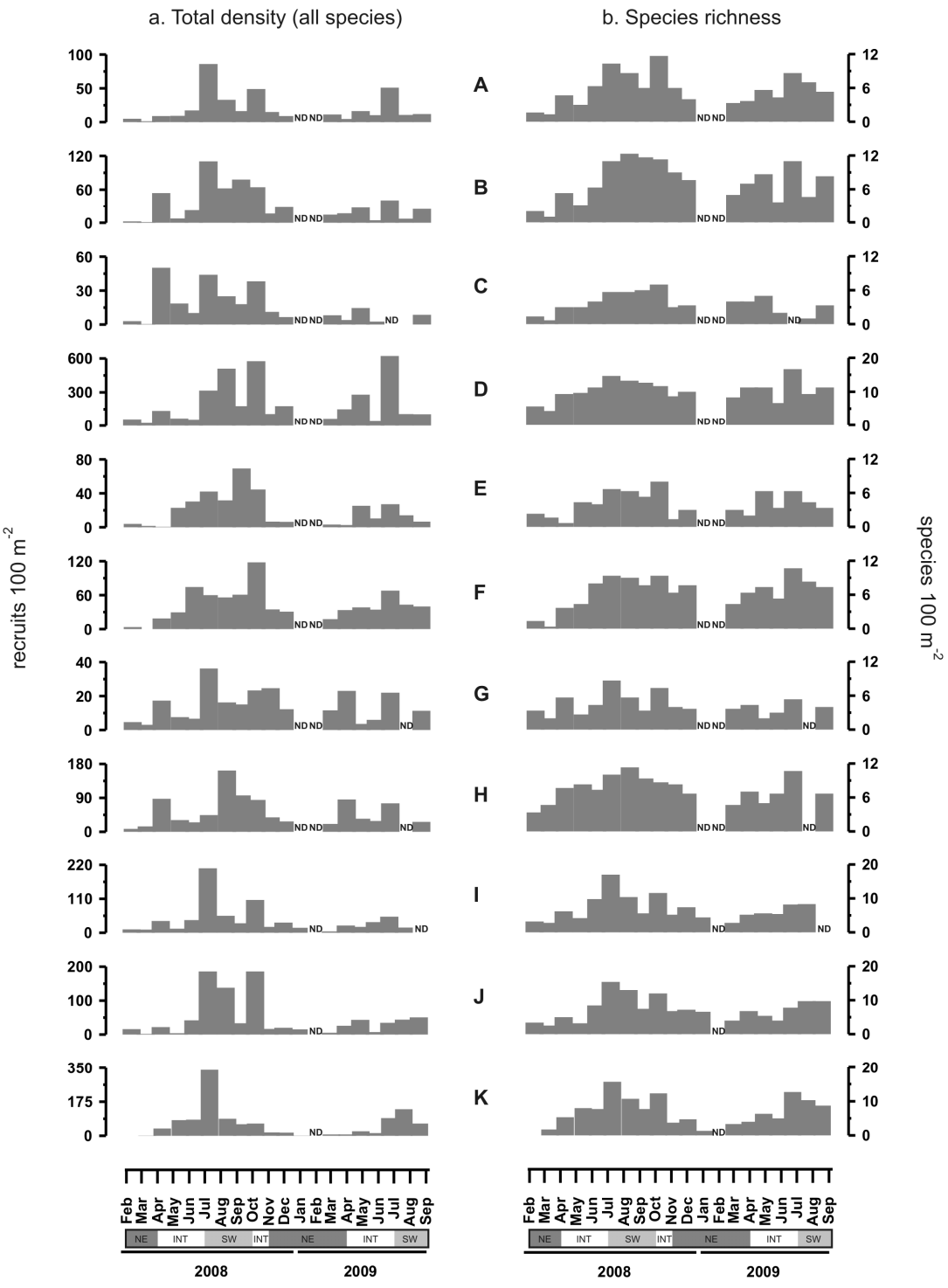


Figure 3.3 Temporal patterns of (a) total recruit density and (b) species richness at all sites. A = northeast Sumilon, 3-4 m; B = northeast Sumilon, 10-12 m; C = southwest Sumilon, 3-4 m; D = southwest Sumilon, 10-12 m; E = southeastern Apo, 3-4 m; F = southeastern Apo, 10-12 m; G = southwest Apo, 3-4 m; H = southwest Apo, 10-12 m; I = Dauin, 3-4 m; J = Dauin, 8-12 m; K = Dumaguete, 3-4 m. Monsoons indicated by different shades of grey along x-axis. NE = northeast monsoon; SW = monsoon; INT = inter-monsoon. ND = no data.

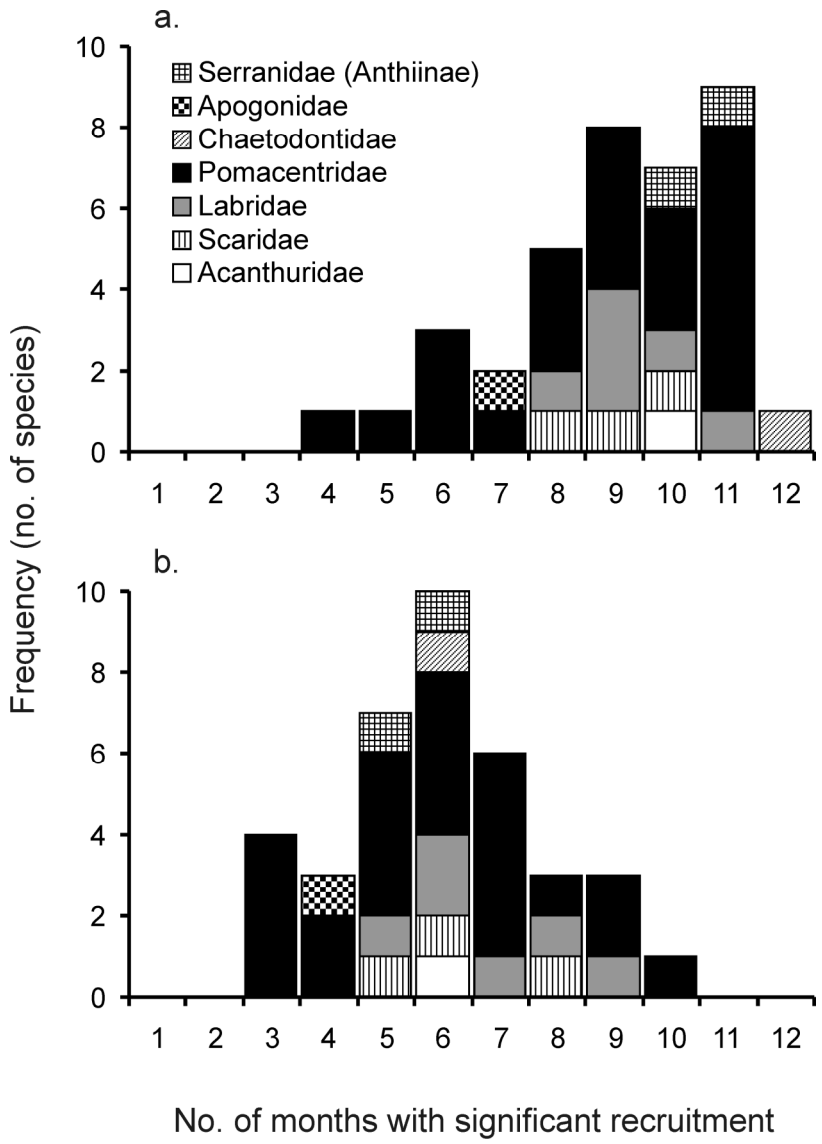


Figure 3.4 Durations of the recruitment period (months) of the 37 most abundant species (grouped into 7 families in this figure) estimated using two thresholds of recruit abundance per month: ≥ 1% (a) and ≥ 5% (b) of adjusted total abundance in one year (see Materials and methods).

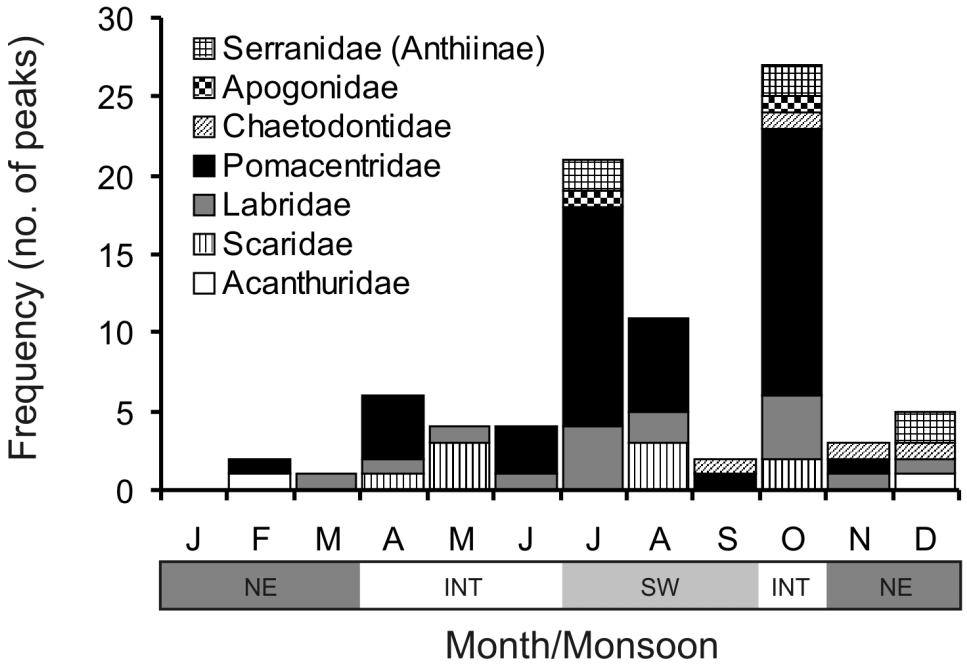


Figure 3.5 Summary of the timing of recruitment peaks of the 37 most abundant species (grouped into 7 families in this figure). Note that a single species may have more than one peak in recruitment within a year (also refer to Appendix 3.2). Monsoons indicated by different shades of grey along x-axis. NE = northeast monsoon; SW = monsoon; INT = inter-monsoon.

surgeonfishes (Appendix 3.2). Recruitment peaks of the two latter families, which were represented by one species each (*Chaetodon baronessa* and *Ctenochaetus binotatus*, respectively), only occurred in the earlier or later part of the year, almost all during the northeast monsoon (Figure 3.5).

3.4 Discussion

This study is one of the few to describe patterns of recruitment (settlement) of coral reef fishes in a location within the Indo-Pacific region where reversing monsoon winds strongly influence environmental conditions. Previous studies have suggested that the monsoons play a role in determining the annual pattern of recruitment of fishes, particularly in the Philippines (Pauly and Navaluna 1983; McManus et al. 1992; Arceo 2004; Cabaitan et al. 2008). However, the present study is the first in the Philippines that related observed patterns of recruitment of fishes directly to environmental data.

New recruits were observed throughout the year and the majority of species that were examined exhibited protracted recruitment seasons. These results confirm the expectation of extended annual breeding of reef fishes at lower latitudes (Robertson 1990; Doherty 1991; Srinivasan and Jones 2006; see also Chapter 2). Of greater significance, the annual pattern of collective recruitment was predictable. Annual variability in SST and wind strength can largely account for the pattern. There was a good degree of similarity in the pattern of recruitment among sites considering the distance separating them (up to 40 km), differences in exposure to prevailing monsoon winds, habitat and depth, and large differences (up to 20-fold) in maximum average recruit densities between some sites. This indicates that the effects of SST and wind were working at a broad spatial scale, most likely during the pelagic larval phase. Rainfall, on the other hand, did not have a significant effect on the patterns of recruitment.

Results strongly suggested that the best ‘window’ for survival and settlement of larvae of the most common reef fish species (mostly damselfishes and wrasses) is during a 4-6 month period within the year when water temperatures are warmest and when winds are weakest locally, i.e., during the southwest monsoon and inter-monsoonal periods. Small increases in water temperature can enhance growth rates of larval reef fishes (McCormick and Molony 1995; Wilson and Meekan 2002; Meekan et al. 2003; Bergenius et al. 2005; Sponaugle et al. 2006). Faster growth, in turn, can

result in higher survivorship because fewer predators would be capable of preying on larger larvae and the time spent in the pelagic environment is shortened (Houde 1987; Anderson 1988). For instance, Wilson and Meekan (2002) showed that in San Blas in the Caribbean Panama, where water temperature varies by only about 3 ºC, temperature is positively correlated with larval growth and magnitude of settlement of the damselfish *Stegastes partitus* (also see Bergenius et al. 2002). On the other hand, wind can result in two physical processes that have potential consequences for the pelagic larval phase. Firstly, wind stress can generate waves and turbulent mixing of surface waters which may be detrimental to survival. Some field studies have indicated that mortality rates in fish larvae are highest during windy conditions, probably because turbulence disrupts concentrated patches of food that are critical to the survival of first-feeding larvae (Peterman and Bradford 1987; Bailey and Macklin 1994). At very small spatial scales, mild turbulent mixing could increase the encounter rates between larval fish and their prey (MacKenzie and Kiorboe 1995; Utne-Palm and Stiansen 2002; Utne-Palm 2004). However, this may increase feeding success and result in faster growth rates in larval fish (Gallego et al. 1996), thus potentially enhancing settlement.

Secondly, prevailing winds can influence dispersal of larvae over larger spatial scales (10's to 100's of kilometres) (Sponaugle and Cowen 1996). There is some suggestion that the effect of the monsoon winds on surface current patterns in the Bohol Sea can partly explain the observed annual pattern of recruitment. In the Bohol Sea, there is a dominant westward flow produced by water entering from the Pacific Ocean and exiting to the Sulu Sea through the Negros-Mindanao strait (Wyrtki 1961). In the study area, this dominant current is manifested as a strong south-westward flow (Chapters 2, 4). Data from a sea surface circulation model [1/32º global Navy Layered Ocean Model (NLOM), see Shriver et al. 2007] indicate that this current is enhanced by the northeast monsoon, increasing the potential for flushing of eggs and early-stage larvae out of the study area (Figure 4.2). During the southwest monsoon and inter-monsoonal periods, the current weakens, potentially enhancing retention of larvae. If a good proportion of the recruits that settle on reefs that were studied are produced in the same general locality (as opposed to more distant reefs), then monsoon-induced seasonal variation in the strength of local currents will have a significant influence on the annual pattern of recruitment. In such a case, the potential effect of wind on local settlement is negative only when it enhances the dispersal of larvae away from nearby source reefs.

A comparison of the findings of the present study with similar studies from other locations close to the equator indicates that among environmental variables, wind has the most consistent effect on settlement patterns of reef fishes, particularly in damselfishes and wrasses. For instance, the annual patterns of recruitment of damselfishes and wrasses that were described here are similar to the recruitment patterns of several damselfish species and one species of wrasse (*Thalassoma bifasciatum*) in San Blas, Caribbean Panama (~9.5 ºN) (Robertson 1990; Robertson et al. 1999). Recruitment of these fishes in San Blas is lower during the dry season (December to April) when northerly tradewinds produce heavy wave action. Species-specific peaks in recruitment occur throughout the wet season (May to November) when winds are lighter. Other studies at San Blas have recorded similar seasonality of larval supply of damselfish and *T. bifasciatum* (Victor 1986; Wilson 2001). In northern Philippines, McManus et al. (1992) monitored monthly fish recruitment on the reef slope of the Bolinao reef system (~16.5 ºN) for four consecutive years. They found one annual peak in total recruitment in that area every year. The recruitment peak occurred between April and July, coinciding with the first inter-monsoonal period when winds are weakest in that area. Note that unlike the area that was surveyed in the present study, the Bolinao area is exposed to the north-east and south-west monsoon winds. Wind also appears to strongly influence the patterns of reef fish recruitment on lower latitude reefs in the southern hemisphere. In Kimbe Bay, Papua New Guinea (~5.5º S), recruitment of many species of wrasses (but not damselfishes) is lower between July and August when monsoon winds are strongest (Srinivasan and Jones 2006).

Some general effects of wind, water temperature, and rainfall emerge from the few studies of reef fish recruitment carried out at low latitude sites to date. The annual trend in wind strength in relation to temperature is somewhat similar between the Philippine and Caribbean sites studied (Lemberget et al. 2009; this study). It is likely that in other lower latitude sites with similar environmental conditions, wind and temperature interact to influence recruitment patterns of many species. However, further insights about temperature are precluded by the absence of an evaluation of its effect on fish recruitment patterns at other locations such as Kimbe Bay (the annual water temperature range there is < 2º C) (Srinivasan and Jones 2006). Studies to date suggest that rainfall is influential only in areas that have an extremely pronounced wet season. For example, in Kimbe Bay, strong rainfall may persist for many weeks, and reach more than 600 mm month^{-1} during the wet season (Srinivasan and Jones 2006).

Heavy rainfall at that site seemed to negatively affect the recruitment of damselfishes (Srinivasan and Jones 2006). In contrast, rainfall at the Philippine and Caribbean sites is considerably less during the wet season than in Kimbe Bay and had little effect on the recruitment of damselfishes and wrasses (Robertson 1990; Robertson et al. 1999; this study).

It is tempting to extrapolate the seemingly predictable effects of water temperature, wind and rainfall to the recruitment patterns of reef fishes in all equatorial regions. However, such predictable effects for all equatorial regions are unlikely. Recruitment patterns of one butterflyfish and one surgeonfish in this study were opposite to the dominant pattern, i.e. settlement in these species was more favourable during the cooler and windier months. Other studies conducted at lower latitude reefs, including those that investigated the effects of environmental variables on larval development and settlement success in detail, highlight species-specific responses and contrasting patterns even among closely-related species (Sponaugle and Cowen 1994, 1997; Robertson and Kauffman 1998; Bergenius et al. 2005; Lemberget et al. 2009).

There are few studies on the seasonal patterns of spawning and recruitment of reef fishes in the Philippines (Chapter 2). This limits an assessment of the degree to which spawning activity may affect patterns of recruitment in reef fishes within the Philippines. In the preceding study (Chapter 2), data on the annual spawning pattern of one population of *P. moluccensis* at one site (Dumaguete) where recruitment of this species was also monitored suggest minimal spawning activity during the northeast monsoon (Figure 2.5). Results of the present study indicate that this pattern of spawning is consistent with the annual pattern of recruitment of *P. moluccensis* at that site and at most sites where *P. moluccensis* recruits were abundant (Dauin and Apo Is.) (Figure 3.1). If the patterns of spawning and recruitment in *P. moluccensis* are strongly coupled, then the same pattern of spawning in this species should be evident at other sites. However, the findings of Chapter 2 imply that the annual pattern of spawning in *P. moluccensis* will vary among local populations depending upon their degree of exposure to the two monsoon winds. Furthermore, the present study indicates that patterns in recruitment are influenced more by environmental factors that are working at a broad spatial scale during the pelagic larval phase as opposed to environmental conditions at more local spatial scales. On the other hand, strong coupling between patterns of spawning and recruitment is exhibited by rabbitfishes in the Bolinao reef system. For instance, spawning migrations of the rabbitfish *Siganus fuscescens* occur

twice a year (March-May and August-September), resulting in two major annual recruitment peaks (Aragones 1987; McManus et al. 1992). The timing of spawning and recruitment in this species is remarkable because it appears to perfectly match the two inter-monsoonal periods within the year, when winds are weakest.

This study is an initial step in understanding the dynamics of recruitment of fishes on Indo-Pacific coral reefs situated in monsoonal environments. Similar studies in other equatorial locations that differ in the character of the monsoons and the degree of exposure to monsoonal conditions are needed. More attention should also be given to resolving the patterns of spawning at the same locations (Chapter 2) to test hypotheses about the degree of coupling between timing of reproduction and larval survival. A reliable understanding of the role of the monsoons, temperature and rainfall in shaping the seasonality of spawning and recruitment may prove useful in determining year-to-year recruitment strength, something that remains difficult to predict for fish populations at lower latitude reefs because of extended annual breeding periods. Better knowledge on the spatial and temporal patterns of reef fish reproduction and recruitment will also be valuable to conservation and fisheries management efforts, particularly the use of networks of no-take marine reserves that aim to preserve or enhance larval connectivity among local reef fish populations (Chapters 4 and 5).

Chapter 4

Predicting connectivity in a marine reserve network from reef fish assemblage patterns and larval dispersal models

Abstract. Connectivity through larval dispersal and recruitment may greatly influence the dynamics and management of marine populations. Two techniques were used together to determine potential larval connectivity between populations of coral reef fishes in a 300-km-wide region in the Philippines that included the Bohol Sea and adjacent bodies of water. A westward current flows through the Bohol Sea. This current possibly connects more than 100 no-take marine reserves by larval dispersal. The first technique investigated connectivity by analysing data on the presence/absence of 216 species of reef fish and habitat variables across 61 sampling sites. Hierarchical clustering of sites reflecting species assemblage patterns distinguished a major group of sites in the Bohol Sea (Bray-Curtis species assemblage similarity > 70%) from sites situated in adjacent bodies of water (i.e., bays, channels and a local sea). The grouping of sites could be partly explained by a combination of degree of embayment, % cover of sand and % cover of rubble (Spearman rank correlation, $\rho_w = 0.42$). The second technique predicted patterns of connectivity using an individual-based model that simulated dispersal of reef fish larvae monthly for 3 consecutive years (2006-2009) in the Bohol Sea. The results of simulations, using a range of pelagic larval durations (15-45 days), were consistent with hydrodynamic and reef fish species assemblage patterns. The sites in the larval dispersal model that showed strongest connectivity corresponded to the majority of sites that comprised the Bohol Sea group of sites based on fish assemblage analysis. Most sites in the model that exhibited weak connectivity were groups of sites which had fish species assemblages that were most dissimilar to those in the Bohol Sea group of sites. The coincident findings from the two independent techniques indicated a strong influence of the local hydrodynamic regime on potential patterns of population connectivity at a broad scale. However, resolution of connectivity was made difficult by the effect of local habitat on the structure of the reef fish assemblage.

4.1 Introduction

Connectivity is often defined as the linking of marine populations through dispersal and successful settlement (recruitment) of pelagic larvae (Sale et al. 2005). The extent of such connections is a central issue in the population dynamics, genetic structuring, biogeography and conservation of marine species (Doherty and Williams 1988; Roberts 1991; Planes 2002; Cowen et al. 2006; Carpenter et al. 2011; Kool et al. 2011). Demographic connectivity, which occurs at ecologically-relevant (as opposed to evolutionary) time scales, may largely determine how local populations persist amidst natural and man-made disturbances (Kritzer and Sale 2004; Botsford et al. 2009). Patterns of demographic connectivity can have tremendous implications for spatially-explicit management of marine resources, particularly the use of networks of marine protected areas or no-take marine reserves (Allison et al. 1998; Botsford et al. 2001; Palumbi 2003; Sale et al. 2005).

The recent interest in determining the spatial extent of population connectivity has been driven by the use of marine reserve networks on coral reefs as conservation and fisheries management tools (Jones et al. 2009). Coral reefs worldwide have been severely impacted by a plethora of anthropogenic activities (Hughes et al. 2003, 2007; Carpenter et al. 2008; Hoegh-Guldberg et al. 2009). Reserves can help reverse the degradation and build resilience of reefs by becoming net exporters of larvae to other reserves and to non-reserves (Roberts 1997; Russ 2002; Gell and Roberts 2003; Hughes et al. 2003; Sale et al 2005). From the standpoint of fisheries management, reserves may benefit reef fisheries through recruitment subsidy (Russ 2002; Gell and Roberts 2003). The rate at which net larval export from reserves can be achieved will depend upon how quickly populations within reserves recover (e.g., Russ and Alcala 2010). Rates of recovery of populations inside reserves can be strongly determined by rates of imported recruitment and 'self-recruitment' (i.e., larvae returning to natal reefs) (Jones et al. 1999, 2005; Jennings 2000; Almany et al. 2007). Ecologically-relevant larval dispersal should therefore be taken into consideration in order to determine the optimum locations, spacing and sizes of individual reserves to attain reserve network goals (Almany et al. 2009). Population connectivity in major coral reef taxa (corals and reef fishes) probably occurs within 10's to 100's of kilometres (Bode et al. 2006; Cowen et al. 2006; Jones et al. 2009; Planes et al. 2009; Saenz-Agudelo et al. 2011), but empirical studies are still lacking. Few existing individual marine reserves or

networks of marine reserves on coral reefs have incorporated quantitative estimates of larval dispersal and recruitment to their designs (Almany et al. 2009; McCook et al. 2009) or have convincingly demonstrated larval connections among reserves or between reserves and fished areas (e.g., Gell and Roberts 2003; Pelc et al. 2009, 2010; Planes et al. 2009; Christie et al. 2010).

Empirical studies of larval dispersal are hindered by many challenges inherent to larval biology. Most coral reef fishes, for instance, have minute larvae (typically < 20 mm in length before settlement) that undergo ontogenetic development away from reefs lasting from a few to several weeks, depending on the species (Leis and Rennis 1983; Victor 1991). Larval distributions in the marine environment are difficult to predict due to advection by currents and high rates of larval mortality (Leis 1991; Cowen et al. 2000). Also, many late-stage larval reef fishes are capable of sustained directed swimming that can modify transport trajectories indicated by hydrodynamic patterns (Stobutzki and Bellwood 1997; Wolanski et al. 1997; Cowen 2002; Leis and McCormick 2002; Paris and Cowen 2004; Leis 2006). Some of these tremendous challenges have been addressed by technological advancements in fields such as oceanography, genetics and chemistry. Various techniques are presently available to make inferences about connectivity (Jones et al. 1999, 2005; Thorrold et al. 2006; Almany et al. 2007; Cowen et al. 2007; Hellberg 2007; Werner et al. 2007; Jones et al 2009; Planes et al. 2009; Williamson et al. 2009; Christie et al. 2010; Saenz-Agudelo et al. 2011). Besides population genetics (particularly parentage analysis) and direct tagging of larval otoliths using chemical markers (e.g., Jones et al. 1999; 2005; Almany et al. 2007; Planes et al. 2009) the most applicable technique to measure connectivity at spatial scales relevant to networks of marine reserves (100's of kilometres) is biophysical (larval dispersal) modelling. The current consensus is that connectivity can be best incorporated into designs of reserve networks using sophisticated biophysical models that are cross-validated by genetic or otolith chemical tagging techniques that can relate individual juveniles to their parents (Jones et al. 2009).

Biogeographic studies may also provide clues about reef connectivity at spatial scales similar to those addressed by biophysical models (Jones et al. 2009). Such studies are expected to differ from biophysical models particularly in terms of the temporal scale of larval dispersal. Biophysical models may be limited to predicting patterns of larval dispersal within decadal time scales (James et al. 2002; Bode et al. 2006; Cowen et al. 2006), while some biogeographic studies (e.g., phylogeography)

may detect connectivity that probably occurred hundreds to thousands of years ago, or much longer (Planes 2002; Rocha et al. 2002; Carpenter et al. 2011). A straightforward biogeographic approach is to examine larval connectivity indirectly from patterns of distribution of species. This approach has been used to infer larval dispersal at oceanic spatial scales (1000's of km) that presumably occurred over longer time scales (Thresher and Brothers 1985, 1989). Species distributions have also been used to argue for the presence or absence of connectivity at more local spatial scales (100's of km, e.g., cross-continental-shelf distribution of reef fishes on the Great Barrier Reef and distributions of reef fish in the Red Sea, see Williams et al. 1986; Roberts 1991; Roberts et al. 1992). However, the time frame of connectivity that determines these patterns over shorter distances is almost impossible to know precisely from data on species distributions alone. An exception to this is the colonisation of the Hawaiian islands by introduced species of reef fish that occurred over a few decades (Randall 1987). A dearth of studies curtails a critical assessment of the usefulness of species distributions to infer patterns of population connectivity at scales most relevant to marine reserve networks.

The utility of species distribution patterns to infer larval connectivity will depend also upon the extent to which demographic patterns determined by larval supply are modified by post-recruitment processes. Demographic patterns in reef fishes may be influenced strongly by a suite of processes acting on the benthic (post-settlement) juvenile or adult phase (Jones 1991). One process that clearly has a considerable influence on the patterns of distribution of fishes on coral reefs is habitat selection (Williams 1991). Abundance and species diversity of reef fishes are usually correlated with habitat availability and structure (e.g., Carpenter et al. 1981; Roberts and Ormond 1987). Studies of larval connectivity that utilise species distribution patterns must therefore consider the potential effects of both larval supply and habitat. For two hypothetical sites in question, the interaction of larval exchange between sites and the characteristics of reef habitat at each site may result in either similar or dissimilar species assemblages, for a variety of potential reasons (Table 4.1). The probability, direction and strength of larval exchange can be predicted and examined using a biophysical model that includes a range of larval life histories. Habitat and species assemblage structure at each site, on the other hand, can be measured by field surveys. From these sets of data, one may infer if larval connectivity is likely to be present or absent, or if levels of connectivity are strong or weak, between sites (Table 4.1).

Table 4.1 Combinations of predicted larval exchange between, and measured habitat and species assemblage structure within, two theoretical sites. The final column lists possible conclusions about connectivitv between the two sites.

Case	Predicted larval exchange	Measured habitat	Measured species assemblage	Possible conclusions
1	Probable, strong	Similar	Similar	Connectivity likely to be significant
2	Probable, strong	Different	Dissimilar	Connectivity is uncertain
3	Improbable, weak	Similar	Dissimilar	Connectivity likely to be absent or weak
4	Improbable, weak	Different	Dissimilar	Connectivity likely to be absent or weak
5	Probable, strong	Similar	Dissimilar	- Failure to account for the most influential post-recruitment process (e.g. disturbances) - Failure to measure the most influential habitat parameter/s - Failure of biophysical model to predict connectivity accurately - Failure to measure species assemblage accurately
6	Probable, strong	Different	Similar	
7	Improbable, weak	Similar	Similar	
8	Improbable, weak	Different	Similar	

Connectivity is likely to be significant if larval exchange is probable and strong and the habitats at the two sites are similar, resulting in similar species assemblages between sites (Table 4.1, Case 1). However, detecting connectivity becomes uncertain when larval exchange is probable and strong but the habitats at the two sites are very different, resulting in species assemblages that are dissimilar between sites (Table 4.1, Case 2). Connectivity is likely to be absent or weak when larval exchange is predicted to be improbable or weak and species assemblages are dissimilar between sites, whether habitats at the two sites are similar or are different (Table 4.1, Cases 3 and 4). The four preceding cases assume that the predictions of the biophysical model, measurement of habitat parameters and representation of species assemblage patterns are all accurate. All four preceding cases also assume that habitat is the most influential post-recruitment factor structuring assemblages. Failure of any one of these assumptions may be suspected in four other cases (Table 4.1, Cases 5-8).

Current evidence suggests that patterns of demographic connectivity in coral reef taxa may be influenced more by local geographic setting than by other factors (e.g.,

size of reef habitat or pelagic larval duration) (Jones et al. 2009). Case studies of larval connectivity within specific networks of marine reserves may therefore be of value to both reef ecologists and managers. In this study, two techniques were used in conjunction to determine the extent of potential larval connectivity of reef fish populations within a 300-km-wide region in the central Philippines that has > 100 'no-take' marine reserves. The reserves in this archipelagic region were established with local (community-based) objectives with little consideration of reserve network planning, but their locations reflect potential connectivity suggested by large-scale hydrodynamic patterns (Indab and Suarez-Aspilla 2004; Alcala and Russ 2006; McCook et al. 2009) and relatively short distances (< 5-10 km) separating individual reserves (Weeks et al. 2010a). The first technique examined patterns of reef fish species assemblages and associated habitats across multiple sampling sites. A secondary aim of using this biogeographic approach was to test if species assemblage patterns are useful in elucidating patterns of larval connectivity at the spatial scale in question. The second technique used an individual-based larval dispersal model to predict patterns of connectivity and quantify levels of self-recruitment within, and larval exchange between, sites. The main expectation of this study was mutual agreement of probable connectivity, where it exists, by the two independent approaches.

4.2 Materials and methods

4.2.1 The study region

This study was conducted in a region of the central Philippines that included the Bohol Sea and adjacent bodies of water (Figure 4.1). The Bohol Sea spans about 300 km from east to west and has a mean depth of approximately 1500 m. It is one of the pathways of water from the Pacific Ocean to the Sulu Sea, connected to the Pacific by Surigao Strait (~20 km wide) and to the Sulu Sea by Negros-Mindanao Strait (~45 km wide) (Figure 4.1a). On its northern side, the Bohol Sea is linked to two internal Philippine seas (Visayan Sea and Camotes Sea) by three channels: Tañon Strait, Cebu-Bohol channel and Bohol-Leyte channel (Figure 4.1a). At least 16 major and minor bays are connected to the Bohol Sea. Most of these bays are coastal features of surrounding major islands: e.g., Sogod and Cabalian bays in Leyte; Cogtong, Guindulman, Maribojoc bays in Bohol; Gingoog, Butuan, Macajalar, Iligan and Murcielagos bays in Mindanao) (Figure 4.1b).

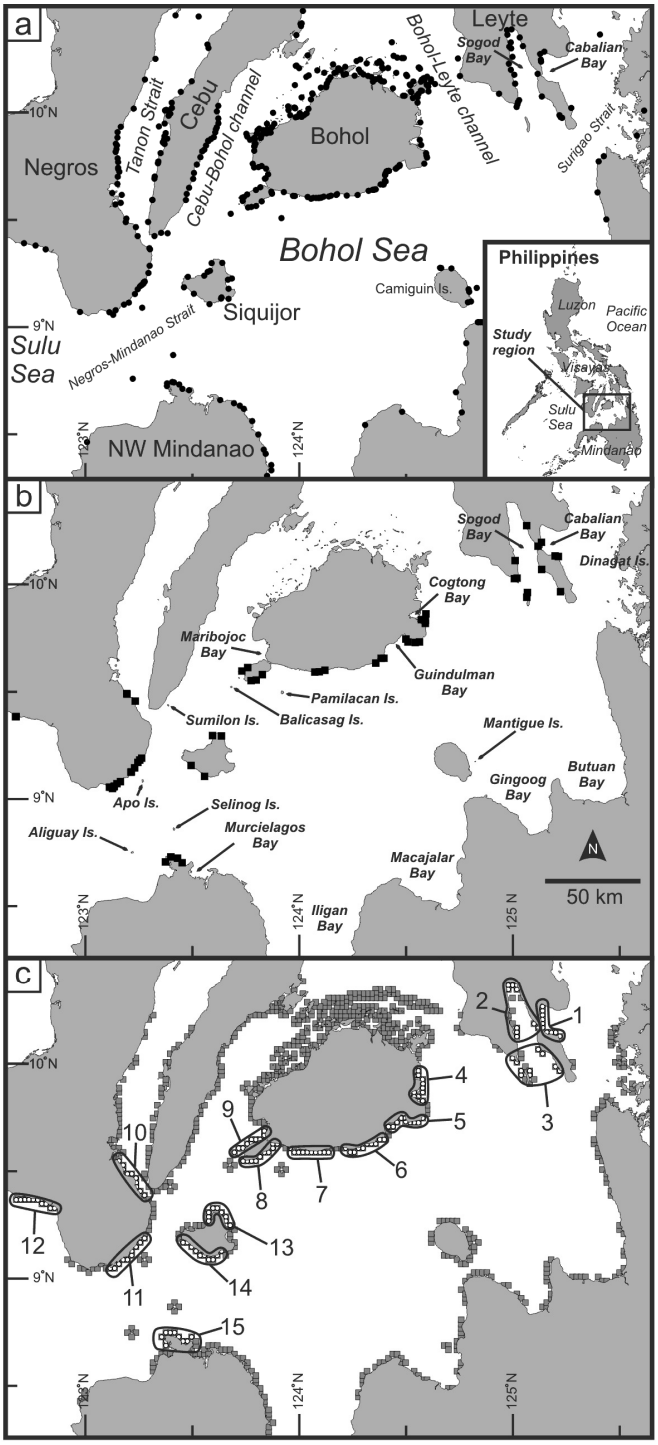


Figure 4.1 Maps of the study region (Bohol Sea and adjacent bodies of water). The top map (a) shows the names of major islands and adjacent bodies of water that were included in this study. It also shows the locations of numerous 'no-take' marine reserves (black circles). The middle map (b) indicates the locations of 61 sites where surveys of reef fishes and benthic habitat were undertaken (black squares). The names of numerous small islands and bays are indicated. The bottom map (c) shows the spatial domain of the biophysical individual-based (larval dispersal) model. It also indicates grid cells that were classified as areas of coral reef (grey squares). Coral reef grid cells that were designated as spawning sites for virtual larvae are marked by white circles. These spawning sites were grouped into 15 nodes (encircled).

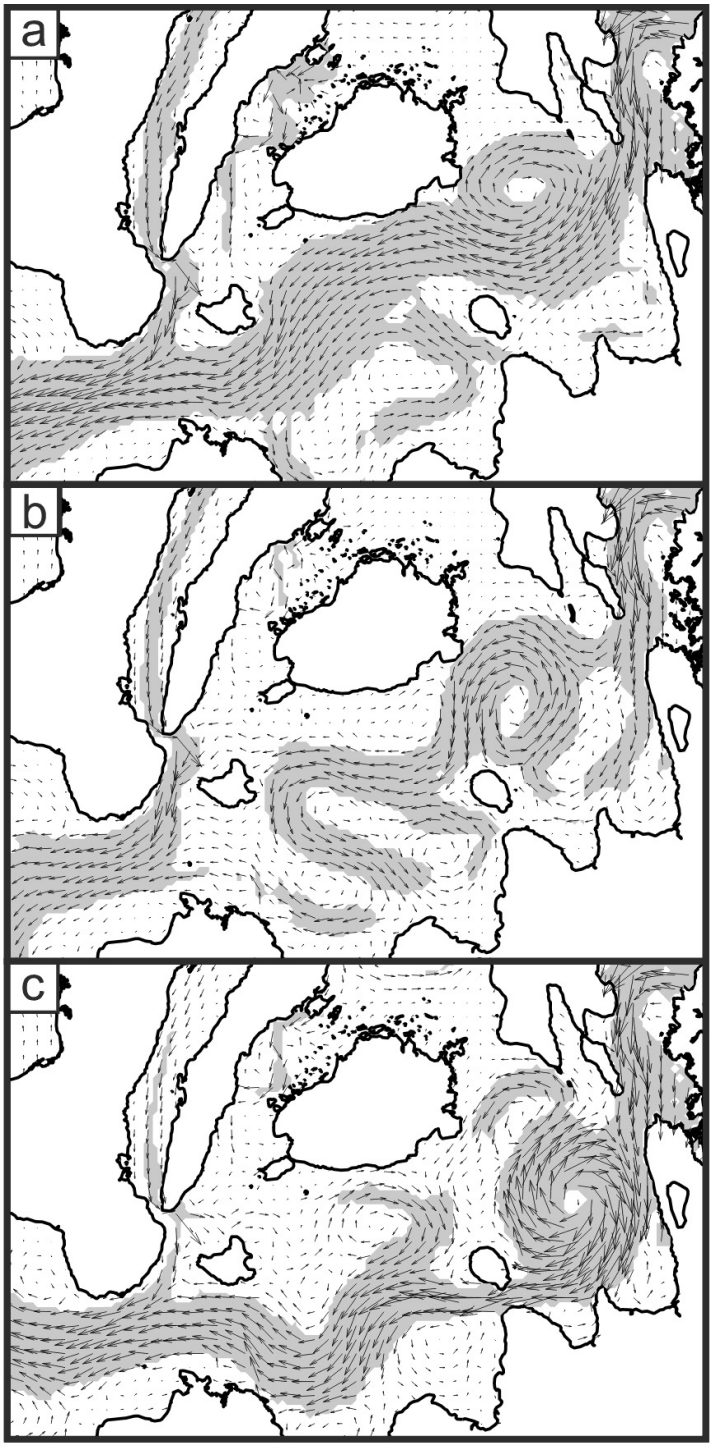


Figure 4.2 Annual trend in current patterns within the study region represented by three months: January (a), May (b) and August (c). January represents current patterns for 6 consecutive months of the year (November to April), coinciding with the northeast monsoon wind. May and August represent current patterns for inter-monsoonal and southwest monsoon (June to September) periods, respectively. Velocity vectors were averaged from 3 years (June 2006 to May 2009) of data interpolated from NLOM (see Materials and methods). Strongest currents (> 0.10 to 0.80 m sec^{-1}) are highlighted in grey. Maximum average velocities estimated for January, May and August were 0.80, 0.60 and 0.47 m sec^{-1}, respectively.

Wyrtki (1961) showed that the net flow of surface water in the Bohol Sea is westward throughout the year. This surface current pattern is also indicated by *in situ* data collected during oceanographic surveys (Cabrera et al. 2011; Lermusiaux et al. 2011). Data from the U.S. Navy Layered Ocean Model (NLOM) (www7320.nrlssc.navy.mil/global_nlom) indicate that this westward surface flow is usually strongest near the northern boundary of the sea for 6 consecutive months of the year (November to April), coinciding with the northeast monsoon (Figure 4.2a). During this period, the dominant current passes within the vicinity of the southern coasts of four major islands (Leyte, Bohol, Cebu and Negros), around a fifth island (Siquijor) and in the vicinity of the north-western tip of Mindanao, before exiting through the Negros-Mindanao Strait (Figure 4.2a). During inter-monsoonal periods
(e.g., in May), the westward mainstream current weakens slightly and meanders, forming eddies (Figure 4.2b). During the southwest monsoon (e.g., in August), it weakens further and may shift its position closer to the southern boundary of the Bohol Sea (Figure 4.2c).

The westward mainstream current has been hypothesised to be a dominant driver of the patterns of connectivity between coral reef populations in the Bohol Sea (Ablan 2005, 2006; Alcala and Russ 2006; McCook et al. 2009). This study focused on investigating potential larval connectivity among fish populations on coral reefs situated mainly along the northern boundary of the Bohol Sea due to the persistence of the westward mainstream current in that area (Figures 4.1 and 4.2). To date, there are an estimated 112 small (i.e., area < 1 km^2 per reserve) community-based no-take marine reserves located within that area (Alcala et al. 2008; Weeks et al. 2010a) (Figure 4.1a). The history of establishment and management status of these reserves are described in detail by Russ and Alcala (1999), White et al. (2002), Indab and Suarez-Aspilla (2004), Alcala and Russ (2006), Alcala et al. (2008) and Weeks et al. (2010a).

4.2.2 Reef fish and benthic habitat data

The data on reef fishes and benthic habitat for this study were selected from a large set of data collected during surveys of coral reefs in the central Philippines (Russ et al. 2005; Stockwell et al. 2009). The objective of most of these surveys was to investigate spatial variations in the effects of no-take marine reserves on reef fish communities. Data from 61 sites were used. The sites formed a transect spanning more than 300 km from east to west mostly across the northern part of the Bohol Sea (Figure

4.1b). Thirty-six of the sites were no-take reserves. The rest were areas of reef open to fishing. The selected sites were situated along the coasts of southern Leyte, Bohol, Negros, northern and southern Siquijor, and north-western (NW) Mindanao (Figure 4.1b). Seventeen of the sites were located within bodies of water connected to the Bohol Sea but not directly influenced by the mainstream westward current. These bodies of water were Cabalian Bay, Sogod Bay, Bohol-Leyte channel, Cebu-Bohol channel, Tañon Strait and Sulu Sea (note that Cabalian and Sogod bays are connected by a very narrow channel < 0.5 km wide) (Figures 4.1b, 4.2). All of the sites were situated on sloping fringing reefs of major islands and a few inshore shoals < 1 km away from these fringing reefs. Sites situated on reefs encircling small offshore islands (e.g., Sumilon, Apo, Balicasag in Figure 4.1b) and fringing reefs with near-vertical slopes were not used for this study in order to limit the potential effects of habitat on reef fish community structure.

Each of the 61 sites was sampled using six 50-m-long x 10-m-wide replicate transects except for one site (n = 5 transects), resulting in a total of n = 365 replicate transects for this study. At each site, three transects were laid on the reef slope at a depth of 3-4 m, while the other three transects were laid on the reef slope at 10-12 m. Surveys of fish were conducted by a single observer (B. Stockwell) using scuba. The observer swam slowly along each transect listing all non-cryptic reef fish species that were seen and counting individuals of each species. For this study, only those species belonging to the families Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Pomacentridae (damselfishes) and Labridae (wrasses), all Families not usually targeted by local fisheries, were included. These Families were selected to minimise the effects of mortality due to fishing and no-take protection in marine reserves on species assemblage structure. Benthic composition (% cover) of sites was estimated by a second observer who recorded the type of substratum at points every 0.5 m interval along each of the 50-m-long transects (i.e., 100 points transect^{-1}). Major substrate types included live hard corals, soft corals, dead coral, rock, rubble and sand. Minor benthic habitat components were classified as ‘others’ [i.e., other sessile invertebrates (e.g., clams and sponges), seagrass and macroalgae]. Surveys of the benthic habitat aimed to quantify broad patterns in benthic composition that could explain the strongest patterns (similarity and dissimilarity) in assemblage structure of reef fish between sites. Data on habitat structure (e.g. rugosity) were not available for all of the sites. In general, however, the structural complexity of reefs was expected to

correlate positively with % cover of live hard coral (all life forms considered) and negatively with % cover of sand and/or rubble (Abesamis et al. 2006b). The 61 selected sites were surveyed between February 2006 and May 2008.

4.2.3 Analyses of reef fish and environmental data

Multivariate analyses of fish and habitat data were carried out using the computer software package PRIMER (www.primer-e.com) (Clarke and Warwick 2001). Data on reef fish abundance and species composition from replicate transects were pooled for each of the 61 sites (total reef area per site = 2500-3000 m^2). Data were transformed to species presence/absence to further minimise the potential effects of fishing and reserve protection on fish species assemblage patterns. Degrees of similarity between sites based on species composition were examined first by constructing a resemblance matrix using Bray-Curtis similarity. Note that Bray-Curtis similarity is equivalent to Sorenson's similarity when used on presence/absence data. Furthermore, 'shared absences' between samples have no effect on the computation of Bray-Curtis similarity coefficients (Clarke and Warwick 2001). Hierarchical clusters of sites (agglomerative) were then generated from the Bray-Curtis resemblance matrix. A series of 'similarity profile' (SIMPROF) tests in PRIMER were used to identify statistically-significant clusters of sites. A non-metric multi-dimensional scaling (MDS) plot was then generated from the resemblance matrix. To highlight geographic patterns, the groupings of sites indicated by hierarchical clustering and MDS were illustrated on maps.

The BIO-ENV routine in PRIMER was used to examine the potential influence of local environmental conditions on species assemblage patterns indicated by hierarchical clustering. BIO-ENV computes weighted Spearman rank correlations (ρ_w) between the fish species Bray-Curtis resemblance matrix and a Euclidean distance matrix generated from data on habitat to identify the combination of habitat variables that could best explain the species assemblage patterns (Clarke and Ainsworth 1993; Clarke and Warwick 2001). Habitat variables that were included in the analysis were the % cover of each benthic component (live hard coral, soft coral, dead coral, rock, rubble, sand and 'others') averaged across replicate transects for each of the 61 sites. In addition to benthic habitat variables, a categorical measurement of the degree of embayment of each site was also included. This ranged from 1 to 3 (i.e., 1 – site is situated along an open coast exposed to monsoon winds and wave action; 2 – site is

sheltered to some extent by coastal features such as headlands; 3 – site is sheltered within a bay). Draftsman's plots in PRIMER indicated low degrees of skewness in the untransformed environmental data. Data were normalised before running BIO-ENV. Further examinations of the relationship between fish species assemblage patterns and environmental variables were made by overlaying the major site groupings indicated by hierarchical clustering of fish species data on a Principal Components Analysis (PCA) plot of the environmental data.

The species assemblage patterns and potential influence of local environment on these patterns were further investigated by examining the habitat preferences of the sets of reef fish species that differentiated between groups of sites. This was done first by applying the 'similarity/distance percentage' (SIMPER) routine in PRIMER, which uses Bray-Curtis dissimilarities between pairs of samples (i.e., groups of sites) to identify those species that contribute most (up to 90%) to differences (Clarke and Warwick 2001). Information on the habitat preferences of each species were then obtained from reef fish identification guides (Lieske and Myers 1997; Allen et al. 2003). Habitats preferred by each species were classified into 7 benthic (micro-) habitat categories that matched the classification of the major benthic components during surveys. Two additional categories of preferred habitat pertaining to degree of embayment were included: 'more sheltered' from winds and wave action – reefs within bays, inshore reefs or silty reefs; and 'more exposed' to winds and wave action – outer reefs and offshore reefs, or reefs with clearer water. Note that the habitat preferences of a species can be described by classification into more than one of the 9 (in total) categories. Simple pie charts were used to compare the composition of habitat preferences of the sets of species that differentiated between pairs of groups of sites.

4.2.4 Individual-based biophysical model

An 'off-line' 2-dimensional Lagrangian (particle-tracking) model was developed to predict larval exchange between sites where reef fishes and benthic habitat were surveyed. Hydrodynamic forcing for this model was based on daily surface (upper 100 m) current data obtained from the 1/32° (approximately 3 x 3 km) NLOM global circulation model and a tidal model. NLOM is forced by wind, solar radiation and buoyancy flux data and assimilates sea surface temperature and sea level data to improve model output. NLOM data from June 2006 to May 2009 (3 years) were used. The tidal model, on the other hand, was developed using the Delft3D system. Tidal

components obtained by Magno (2006) for the Bohol Sea were used. The tidal model provided hourly current variability and hydrodynamic forcing in areas where NLOM data were not available (i.e., shallower areas < 100 m deep) but where tidal forcing may be the dominant mechanism for advection.

The spatial domain of the offline model was bounded by 7.95º N, 122.63º E and 10.49º N, 125.65º E (Figure 4.1c), which included the Bohol Sea and significant portions of adjacent bodies of water. Hydrodynamics for the offline model were generated at a scale of 2.2 x 2.2 km, which was the grid resolution of the tidal model. NLOM velocity fields were interpolated to match this resolution using kriging interpolation. The final hydrodynamic data set was obtained through vector addition of the NLOM and tidal velocity fields within the offline model. The resulting grid size of the entire domain was 151 x 127 cells. Land boundaries of the model were defined using coastline data from the NOAA Coastline Extractor (http://rimmer.ngdc.noaa.gov). Grid cells representing coral reef areas in the model were identified using satellite images (LandSat 7 ETM+, available at http://landsat.gsfc.nasa.gov). Where information from satellite images was lacking, data from numerous surveys of coral reefs in the Bohol Sea were used (e.g. PhilReefs 2008; Alcala et al. 2008; this study).

Dispersal of early-stage (non-swimming) fish larvae was governed by Euler-type advection-diffusion equations adapted from Polovina et al. (1999):

$$x_{t+\Delta t} = x_t + (u_{x,y,t}\Delta t + \varepsilon\sqrt{k\Delta t}) \qquad \text{(Equation 4.1)}$$

and $$y_{t+\Delta t} = y_t + (v_{x,y,t}\Delta t + \varepsilon\sqrt{k\Delta t}) \qquad \text{(Equation 4.2),}$$

where x and y are the coordinates of a virtual larva, u and v are components of advection velocities (m sec^{-1}) obtained from the model hydrodynamics, Δt is the integration time step (sec), ε is a randomly generated number ranging from -1 to 1, and k is the eddy diffusion rate (m^2 sec^{-1}). These two equations were simplified from the original by assuming that the effect of the earth's curvature on advection is negligible within the study region since it is situated near the equator. The time step used was 75 sec. An eddy diffusion rate of 0.125 m^2 sec^{-1} was used. Eddy diffusion rate was assumed to be uniform throughout the model domain. Interpolation of the velocity components to the positions of larvae at each time step was done using bilinear interpolation.

Directed swimming ability of late-stage fish larvae was incorporated into the advection-diffusion equations by adding a velocity term for larval swimming to each of the advection velocity components. Swimming speed of larvae was set at 0.15 m sec^{-1}. This value is at the lower end of the range of swimming speeds measured *in situ* for settlement-stage larvae of several species belonging to the Pomacentridae and Chaetodontidae (Leis and Carson-Ewart 2003; Leis 2006). Swimming of virtual larvae was always directed towards the nearest reef grid cell found within a radius of 4.4 km from each larva's position. This value for larval 'sensory zone' is within the range of values used by James et al. (2002) and consistent with the spatial scales of potential larval sensory mechanisms (e.g., Kingsford et al. 2002; Gerlach et al. 2007) but more conservative than that used in other studies (e.g., 9 km in Paris et al. 2005; Cowen et al. 2006; Paris et al. 2007). Note that in the model, late-stage larvae do not swim when no reef grid cells are found within the sensory zone. Parameters for the onset of swimming and competency to settle were included in order incorporate a simple ontogenetic schedule for larvae into the model. Onset of directed swimming was set at 50% of pelagic larval duration (PLD). This is a coarse approximation of the development of swimming ability in the larvae of *Pomacentrus amboinensis* (Pomacentridae) (Fisher et al. 2000). On the other hand, competency to settle was set at 90% of the PLD (i.e., larvae cannot settle unless they are in the final 10% of their pelagic life). This allowed for some individual variation in the time (age) at which competent larvae settled.

4.2.5 Simulations of larval dispersal

Potential exchange of larvae between sites was investigated by first identifying reef grid cells in the model that corresponded to the positions of the 61 sites that were surveyed. To compare the results of the simulations with species assemblage patterns, these reef grid cells were grouped into 15 nodes (numbered 1 to 15) to represent (but not perfectly match) the grouping of sites determined by hierarchical clustering and MDS (Figures 4.1c and 4.4d). Each node was designated as a site for spawning (releasing) virtual larvae in the model. Nodes also functioned as settlement sites. The other reef grid cells in the model that were not grouped into nodes also functioned as settlement sites but not as spawning sites. Each node was standardised to have 10 reef grid cells each in order to equalise spawning output and available settlement habitat among nodes. Reef grid cells within each node formed a continuous string of cells which spanned about 22 km of coastline in the model except for 2 nodes (nodes 1 and 2

in Figure 4.1c). The latter 2 nodes occupied areas that had a maximum length of about 30 km. Larvae were released from each node every lunar month over the entire 3 years of simulated hydrodynamic data (n = 37 replicate lunar months), consistent with year-round spawning of reef fishes in the region (Abesamis and Russ 2010; Chapters 2 and 3). Spawning output was set at a constant value of 2000 larvae grid cell^{-1} month^{-1} (equivalent to 20 x 10^3 larvae node^{-1} month^{-1} or 300 x 10^3 larvae month^{-1} for the entire model). Spawning was timed around the new moon staggered over a four-day period (i.e., 5000 larvae released day^{-1} node^{-1}). Three sets of simulations were done using PLD values of 15, 30 and 45 days to evaluate different life history strategies of reef fish species.

4.2.6 Analyses of larval dispersal data

Successful settlement of virtual larvae to reef habitat was quantified in two ways. The first was 'self-recruitment', which were instances when larvae settled to the same node where they were spawned. Note that self-recruitment was quantified at a spatial scale of 22-30 km because this was the range of maximum lengths of the areas occupied by nodes in the model. The second was 'connectivity', which were instances when larvae settled to nodes other than where they were spawned. Connectivity from nodes to reef grid cells situated outside of nodes was not considered in this study. Probabilities of self-recruitment and connectivity were determined using a transition probability matrix where the 15 nodes were represented both as 'sources' (on the y-axis) or 'sinks' (on the x-axis) for virtual larvae. Each element of the matrix is given by the expression:

$$P_{ij} = L_{i \to j} / S_i \qquad \text{(Equation 4.3)},$$

where P_{ij} is the probability of larvae from node *i* settling to node *j*, $L_{i \to j}$ is the number of larvae that originated in node *i* (on the y-axis) and settled in node *j* (on the x-axis) within the specified PLD, and S_i is the total number of larvae spawned from node *i*. Probabilities of self-recruitment are represented by the elements of the matrix where node *i* = node *j*. Dispersal probability matrices were constructed for each of three sets of simulations (15, 30 and 45-day PLD) using average probabilities of self-recruitment and connectivity computed from the n=37 temporal replicates. Only those probabilities

(P_{ij}) ≥ 0.01 were plotted in the matrices in order to highlight the strongest patterns in the data.

The relative strength of connectivity was quantified using the equation suggested by Dupont et al. (2007) to define larval exchange between two populations (nodes) denoted by A and B:

$$\frac{L_{A\to B}}{\sum_i L_{i\to B} + L_B} + \frac{L_{B\to A}}{\sum_i L_{i\to A} + L_A} \qquad \text{(Equation 4.4),}$$

where $L_{i\to j}$ is the same term as in Equation 3, L_i represents the number of larvae that were spawned in node *i* and also settled in node *i*, and the two summations are the total number of larvae from all other nodes that settled into each of the two nodes considered. Connectivity quantified in this manner expressed the strength of larval exchange between nodes regardless of the direction of the exchange (i.e., exportation or importation). Symmetrical matrices were built for each of the three sets of simulations (15-, 30- and 45-day PLD) using values computed from Equation 4 averaged across the n = 37 temporal replicates (monthly simulations over 3 years). These symmetrical matrices enabled the calculation of an 'overall index of connectivity' for each node by summing (horizontally or vertically in the symmetrical matrix) the indices of strength of connectivity (but not self-recruitment) associated with each node. The nodes which had the strongest or weakest connectivity were then determined by ranking the nodes according to the overall index. The symmetrical matrices were also used to determine the strength of larval exchange between groups of nodes, such as those nodes in the model that corresponded to groups of sites indicated by hierarchical clustering and MDS.

The straight line (point-to-point) dispersal distance of each virtual larva was measured starting from the reef grid cell of the 'source' node where the larva was released to the reef grid cell of the 'sink' node where it settled. Average dispersal distances of larvae that originated from the same node were then computed for each of the three sets of simulations (15-, 30- and 45-day PLD, each with n = 37 temporal replicates). The modal range and maximal range ($P_{ij} \geq 0.01$) of these dispersal distances were determined from histograms.

The larval dispersal model was programmed in C. Summarisation and analyses of model outputs were done in MATLAB.

4.3 Results

The results are presented in two sections. The first section reports on general patterns that emerged from the analyses of the data from field surveys (i.e., fish species composition and habitat amongst sites) and the data from simulations of larval dispersal. In the second section, groups of sites generated by hierarchical clustering of species assemblage patterns are compared in pairs. The rationale for each pair-wise comparison was to examine potential presence (or absence) and strength of larval connectivity between groups of sites.

4.3.A General patterns

4.3.A.1 Fish species assemblage patterns

A total of 216 species of reef fish in the four families were recorded at the 61 sites. The species list was dominated by the wrasses and damselfishes (82 species each), followed by the butterflyfishes (37 species), and angelfishes (15 species). Sixty-four (30%) of the species were recorded in ≤ 10% of the sites. Sixty-one (28%) of the species were recorded in ≥ 70% of the sites. Only 3 species, all damselfishes (i.e., *Pomacentrus moluccensis*, *P. brachialis* and *P. amboinensis*), were recorded at all sites.

The hierarchical clustering and MDS plot (stress = 0.14) of the 61 sites using data on presence/absence of species suggested groups that reflected the bodies of water where sites were situated (Figures 4.3, 4.4). All sites were found to group together at 40% similarity (Figures 4.3, 4.4a). Higher levels of similarity resulted in the separation of a major Bohol Sea group from other groups that were located in adjacent bays, channels and the Sulu Sea. For instance, at about 60% similarity (Figures 4.3, 4.4b), sites situated in the Bohol-Leyte channel (group A) and within the two bays in southern Leyte (i.e., groups B and C in Sogod Bay and Cabalian Bay, respectively; group B-C is composed of sites that are situated very close to the narrow channel that connects the two bays) were the first ones to separate from a larger group (D) composed mostly of sites situated in the Bohol Sea. At around 70% similarity (Figures 4.3, 4.4c), this larger group (D) was further subdivided into groups representing Tañon Strait (E), Sulu Sea

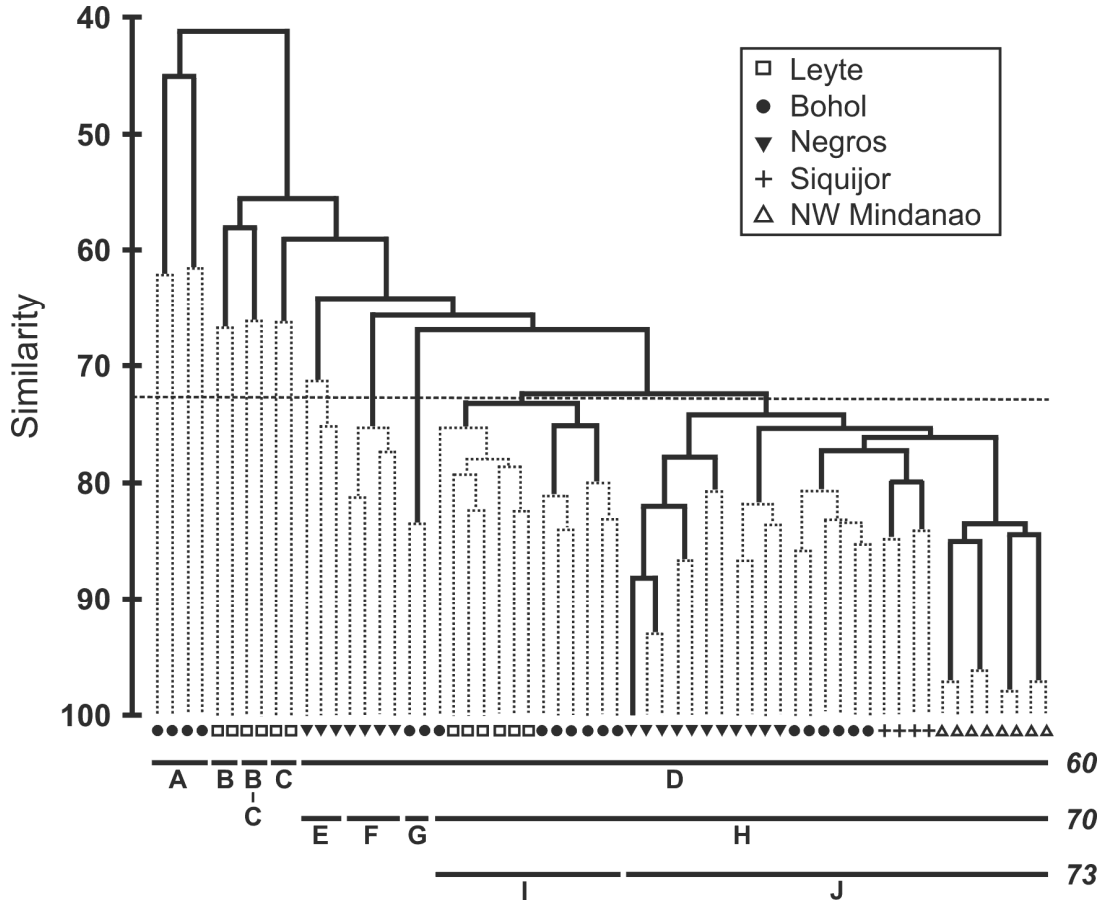


Figure 4.3 Dendrogram showing hierarchical clustering of 61 sites based on the Bray-Curtis similarity measure using data on reef fish species composition (presence/absence). Significant clusters determined by SIMPROF tests (see Materials and methods) are connected by solid lines to distinguish them from non-significant clusters (broken lines). Sites that grouped together at 60, 70 and 73% similarity are spanned by horizontal lines at the bottom of the figure labelled by letters. Groups indicated by letters A to J correspond to the groups denoted by the same letters in the MDS plots and maps in Figure 4.4. The broken horizontal line that runs across the dendrogram indicates 73% similarity. Legend indicates the major islands where sites are situated.

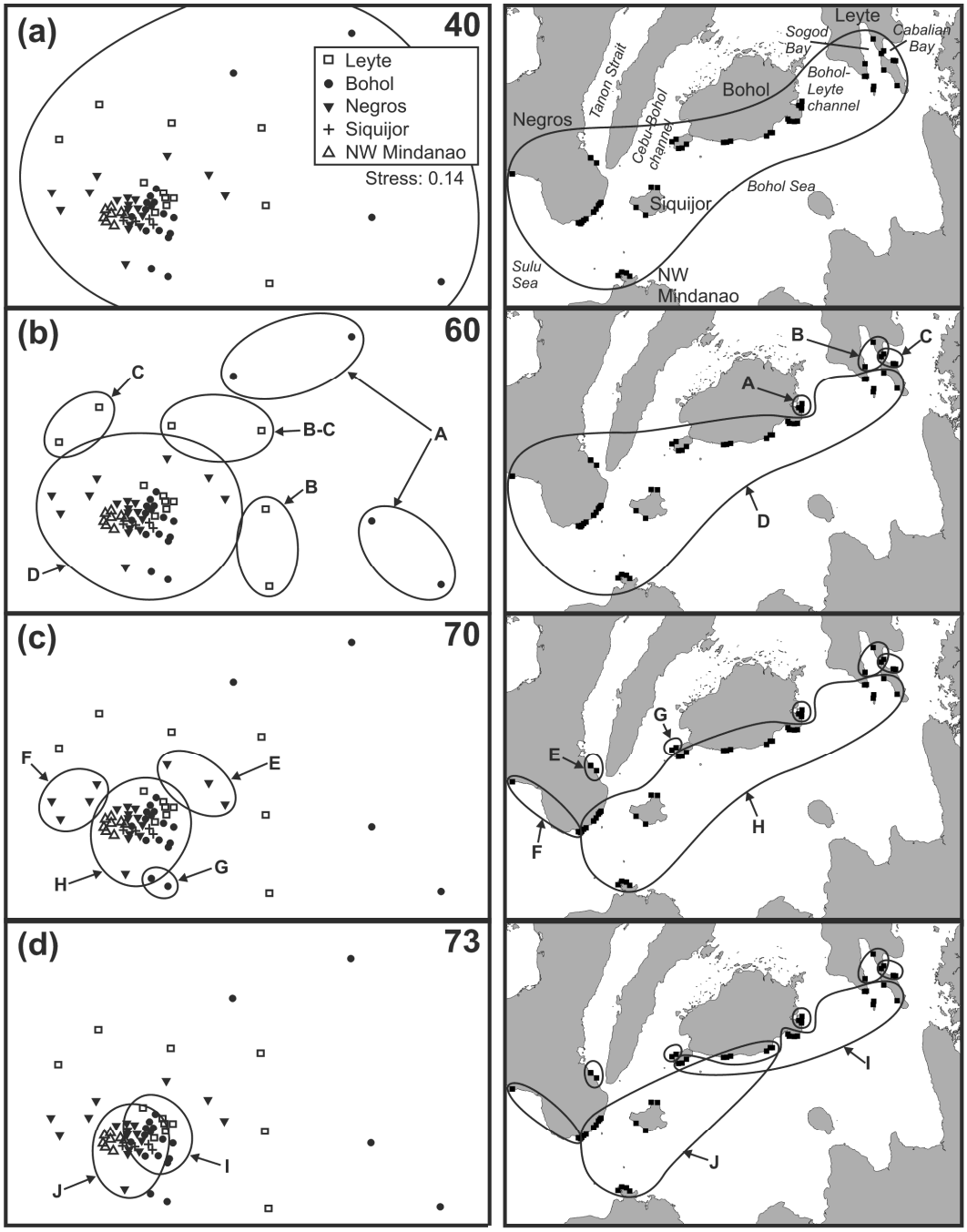


Figure 4.4 Left side of the figure shows Non-metric Multi-Dimensional Scaling (MDS) plots of species assemblages at each of 61 sites based on Bray-Curtis similarity measure. Within each plot, groups of sites that are formed at similarity levels of 40 (a), 60 (b), 70 (c) and 73 (d) are enclosed by ellipses and labelled by letters A to J (also refer to dendrogram in Figure 4.3). Legend indicates the major islands where sites are situated. Right side of the figure shows the geographic locations of groups of sites (black squares enclosed by ellipses) formed at each level of similarity (group B-C is the intersection between the ellipses for B and C). For clarity, further subdivisions of groups A, B, C, E, F and G at higher levels of similarity are not shown.

(F), Cebu-Bohol channel (G) and a main group in the Bohol Sea (H). A slight increase in similarity, from 70 to 73% (Figures 4.3, 4.4d), indicated that the main Bohol Sea group (consisting of 42 sites) was further subdivided into two overlapping eastern and western subgroups. The eastern subgroup was composed of 13 sites situated in Leyte and Bohol islands (I), while the western subgroup was composed of 29 sites located in Bohol, Siquijor and Negros islands and NW Mindanao (J). At levels of similarity > 73%, further subdivisions of the two Bohol Sea subgroups resulted in clusters of sites that are situated within 2 to 25 km from each other (Figure 4.3).

The groups of sites formed at increasing levels of similarity of the species assemblage (from > 40 to 70%) showed an increasing trend in average species richness (Appendix 4.1). The sites in group A, which were the first ones to separate from all other sites, had the lowest average species richness with only 37 species site^{-1}. Sites in groups B, B-C, C and E had considerably higher average species richness than group A, ranging from 69 to 72 species site^{-1}. Sites in groups F and G had slightly higher average species richness than the preceding groups, with 85 and 88 species site^{-1}, respectively. The main Bohol Sea group (H) had the highest average species richness (94 species site^{-1}), but it also had >10-20 times the number of sites than any of the other groups (Appendix 4.1). Of the two subgroups of the main Bohol Sea group, subgroup I had a lower average species richness (87 species site^{-1}) than subgroup J (98 species site^{-1}).

4.3.A.2 Fish species assemblage patterns vs. environmental variables

Analysis using BIO-ENV indicated that the grouping of sites could be partly explained by a combination of three environmental variables: degree of embayment, % cover of sand and % cover of rubble. The combination of these environmental variables resulted in a weak correlation ($\rho_w = 0.42$) between the species resemblance matrix and the habitat matrix. Individually, patterns in the degree of embayment of sites had the strongest correlation with the species assemblage patterns ($\rho_w = 0.33$), followed by % cover of sand (0.19) and then by % cover of rubble (0.13). A PCA plot of normalised environmental data from the 61 sampling sites showed considerable overlap between geographic locations (major islands) in terms of habitat types (Figure 4.5a). Overlaying each of the fish groups formed at increasing levels of species assemblage similarity showed that the main Bohol Sea group (H, which later separates into I and J) encompassed the broadest possible range of habitat types, from live hard coral-, sand-, rock-, or macroalgae/seagrass-dominated habitats (Figures 4.5b-c). The types of habitat

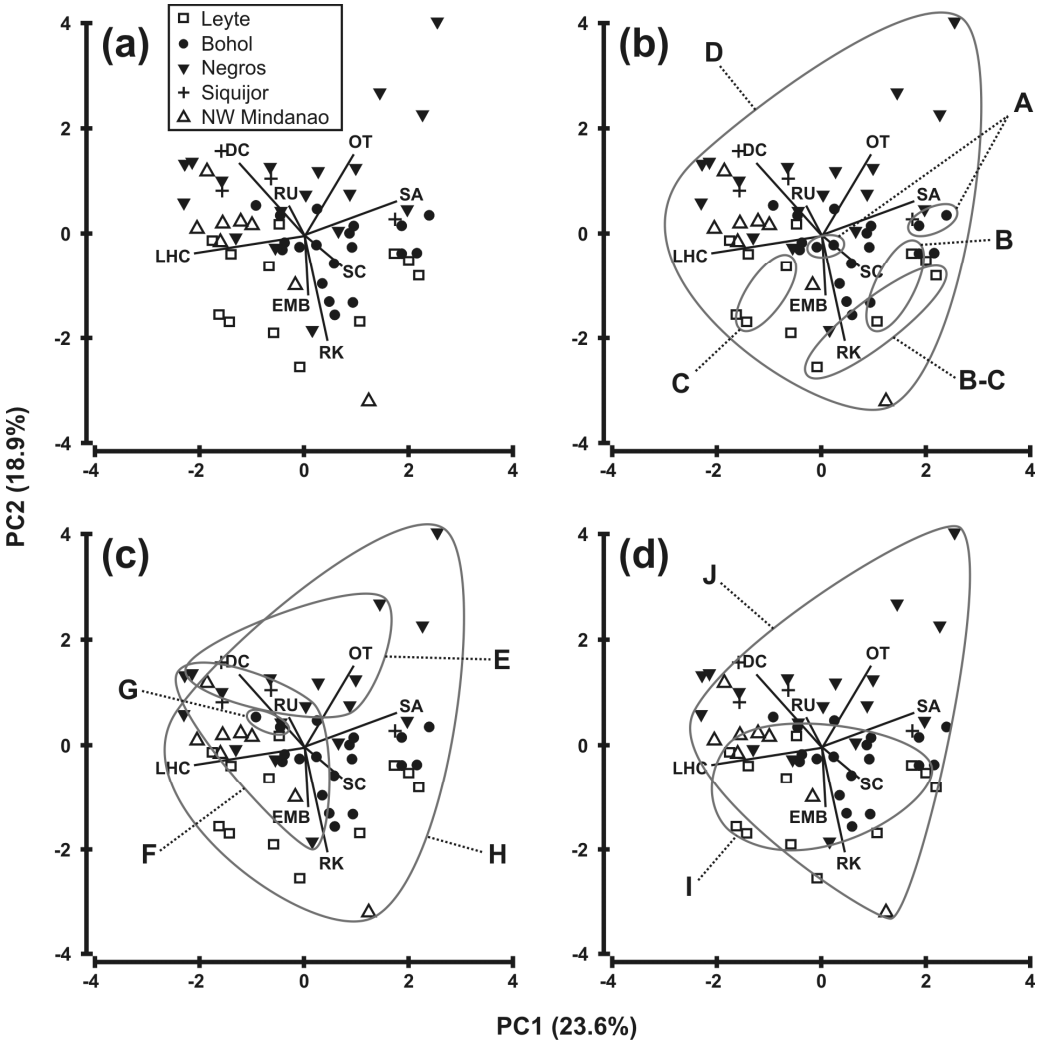


Figure 4.5 Principal Components Analysis (PCA) plot of normalised environmental data from 61 sampling sites (a). Eigenvectors are based on % cover of live hard coral (LHC), dead coral (DC), soft coral (SC), rock (RK), rubble (RU), sand (SA), 'others' (OT, i.e. other invertebrates and macroalgae) and degree of embayment (EMB). PC1 and PC2, combined, accounted for 42.5% of variability in the data. In the succeeding plots (b-d), the groups of sites suggested by hierarchical clustering of fish species assemblages at Bray-Curtis similarity levels of 60 (b), 70 (c) and 73 (d) are enclosed by ellipses and labelled by letters A to J (refer to Figures 4.3 and 4.4). Legend indicates the major islands where sites are situated. For clarity, further subdivisions of groups A, B, C, E, F and G at higher levels of similarity are not shown.

associated with all other groups were subsets of this range. The groups that were first to separate from the rest of the sites at 60% similarity were distinguished by their higher degrees of embayment (i.e., groups B, C and B-C which are in Sogod and Cabalian bays) and, for some sites, by their higher % cover of sand (2 of the 4 sites that belong to group A) (Figure 4.5b). The PCA plot showed that sites belonging to at least one group (G) may be strongly associated with higher % cover of rubble (Figure 4.5c).

4.3.A.3 Patterns of larval dispersal predicted by biophysical models

Results of the three sets of simulations of larval dispersal (15-, 30- and 45-day PLD) indicated that the highest probabilities of settlement to any node were always due to self-recruitment (estimated at a spatial scale of 22-30 km) (Figure 4.6). Maximum probabilities of self-recruitment were 0.69, 0.65 and 0.59 for 15-, 30- and 45-day PLD simulations, respectively. Probabilities of self-recruitment declined with longer PLD (Figure 4.6a-c). On the other hand, probabilities of connectivity were much lower compared to self-recruitment (Figure 4.6). In almost all instances, probabilities of connectivity were < 0.10. The geographic extent and distance of connectivity increased with longer PLD (Figure 4.6). The average dispersal distance of larvae from almost all nodes (except node 12) also increased with longer PLD (Figure 4.7). The modal range of dispersal distance from all nodes was almost always within 0-25 km (Figure 4.7). Modal range increased to 25-50 km only for two nodes (7 and 10) at higher PLDs. Maximal range ($P_{ij} \geq 0.01$) of dispersal distance was usually between 50-75 and 125-150 km regardless of PLD (Figure 4.7). The simulations showed that the prevalent direction of dispersal of larvae from their source node to their sink node was from east to west, notwithstanding the presence of many mesoscale eddies formed by the dominant current at different times of the year (Figure 4.2). This is indicated by more instances of connectivity in the region below (as opposed to above) the broken diagonal line indicating self-recruitment in the three matrices (Figure 4.6). The westward connectivity was particularly evident between many of the nodes that are situated in the Bohol Sea (nodes 3, 5, 6, 7, 8 and 11 in Figure 4.6). This pattern of larval connectivity is consistent with the general direction of the mainstream current (Figure 4.2).

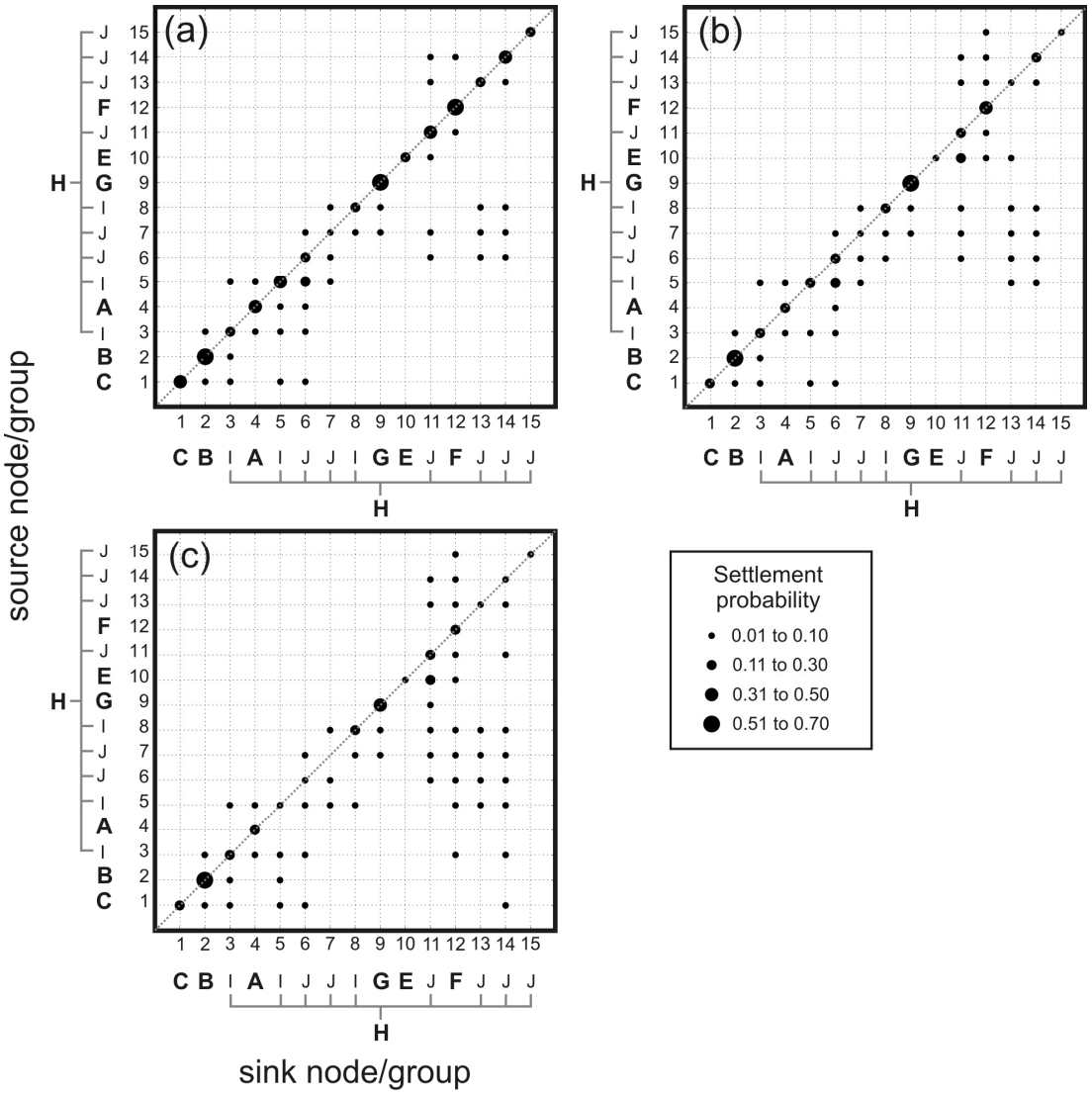


Figure 4.6 Dispersal probability matrices resulting from simulations of larval dispersal using PLD values of 15 (a), 30 (b) and 45 (c) days. The 15 nodes where larvae were spawned in the larval dispersal model are represented both as 'sources' (on the y-axis) and 'sinks' (on the x-axis). Each node corresponds (partly or entirely) to the groups of sites (i.e., groups A, B, C, E, F, G and H; I and J are subgroups of H) that resulted from hierarchical clustering using data on presence/absence of fish species (see Figures 4.3 and 4.4). Probabilities of self-recruitment for each node/group are indicated along the dotted diagonal line. Connectivity in terms of one node/group (source) exporting larvae to other nodes/groups (sinks) can be examined by reading each matrix from left to right parallel to the x-axis. Connectivity in terms of one node/group (sink) receiving larvae from other nodes/groups (sources) can be discerned by reading each matrix from bottom to top parallel to the y-axis. Only $P_{ij} \geq 0.01$ were plotted in the matrices in order to highlight the strongest patterns in the data.

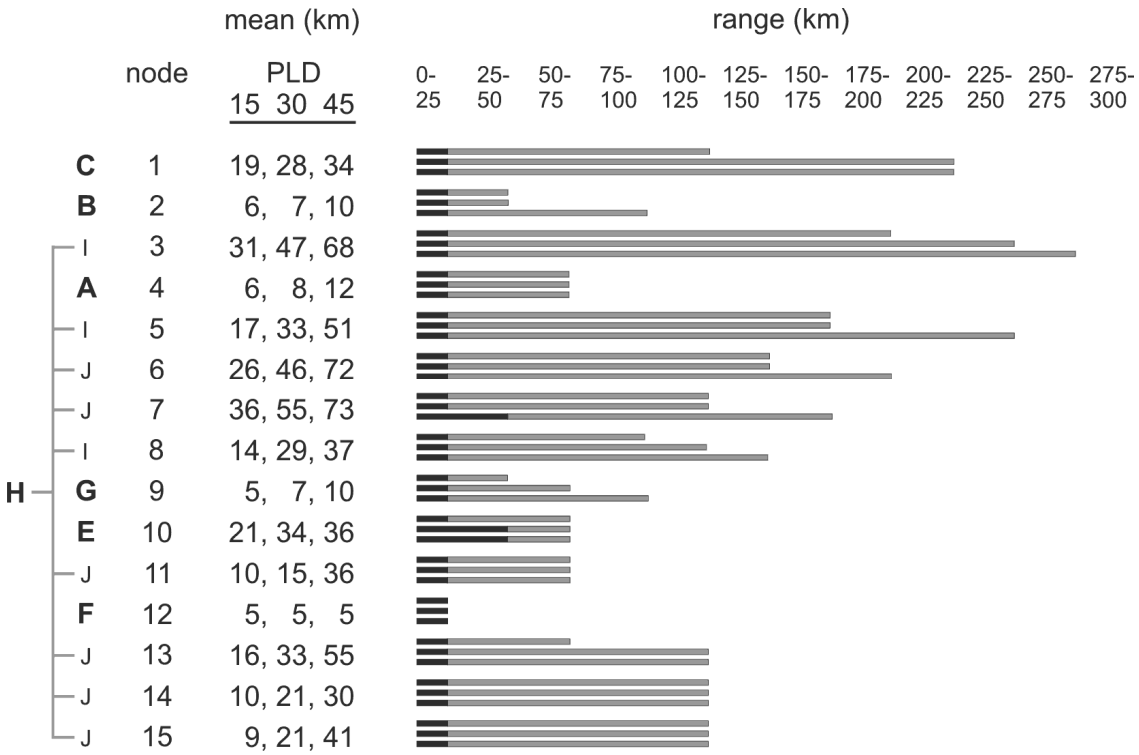


Figure 4.7 Distances of larval dispersal (mean, modal range and maximal range) from each node according to simulations using the biophysical model. Values are given for the range of PLDs (15, 30 and 45 days) used in simulations. Black bars indicate modal range. Grey bars indicate maximal range (P_{ij} ≥ 0.01). For each node, the topmost bars are for 15-day PLD, middle bars for 30-day PLD and bottom bars for 45-day PLD. Each node corresponds (partly or entirely) to the groups of sites (i.e., groups A, B, C, E, F, G and H; I and J are subgroups of H) that resulted from hierarchical clustering using data on presence/absence of fish species (see Figures 4.3 and 4.4).

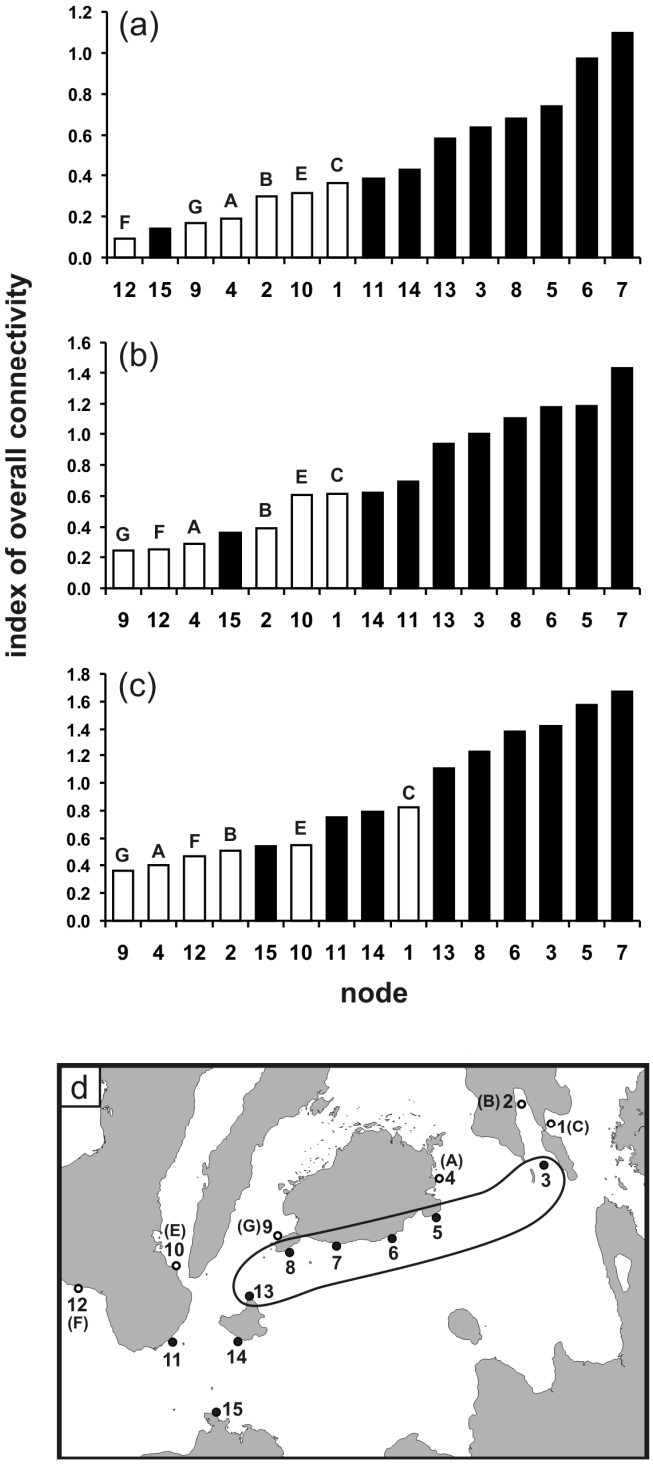


Figure 4.8 Nodes ranked according to index of overall connectivity (see Materials and methods) resulting from simulations using PLD values of 15 (a), 30 (b) and 45 (c) days. The geographic locations of these nodes are shown in the bottom map (d). White bars in (a), (b) and (c) and open circles in (d) indicate nodes that represent groups of sites (A, B, C, E, F and G) that were the least similar to a main Bohol Sea group (H) according to analyses of presence/absence of species of reef fishes (see Results). A, B, C, E, F and G are the same groups specified in the dendrogram, MDS plots and maps in Figures 4.3 and 4.4. Black bars in (a), (b) and (c) and black circles in (d) indicate nodes that constitute the main Bohol Sea group. In (d), an ellipse is drawn around the nodes that consistently showed the strongest connectivity.

4.3.A.4. Fish species assemblage patterns vs. predicted levels of connectivity

Results of simulations that used 15- and 30-day PLD indicated that nodes 1, 2, 4, 9, 10, 12 and 15 had the lowest indices of overall connectivity (Figure 4.8a-b). This pattern only changed slightly in simulations that used 45-day PLD (Figure 4.8c). Except for node 15, the nodes with the weakest overall connectivity represented groups of sites that were least similar to the main Bohol Sea group in terms of reef fish species assemblages (i.e., groups C, B, A, G, E, F, respectively) (Figures 4.4b-c, 4.6). The average distances of larval dispersal from some of these weakly-connected nodes [i.e., nodes 2 (representing group B), 9 (group G) and to a lesser extent, 4 (group A)] were also usually shorter (Table 4.2, Figure 4.7). Note that node 15 represented sites in NW Mindanao that are part of the main Bohol Sea group (H) according to the cluster and MDS analyses of fish species data. On the other hand, a group of 6 nodes that represented the majority of the sites constituting the main Bohol Sea group (H) always had the highest indices of overall connectivity in all simulations (Figure 4.8a-c). Specifically, these were nodes 3, 5, 6, 7, 8 and 13, which are situated in the eastern and central portions of the northern boundary of the Bohol Sea (i.e., southern Leyte, southern Bohol and northern Siquijor (Figure 4.8d). Connectivity (i.e., sum of connectivity indices) among these 6 nodes accounted for about one-third (31, 31 and 28% for 15-, 30-, 45-day PLD, respectively) of the total connectivity between all nodes (Figure 4.6a-c). The remaining nodes that correspond to the western part of the main Bohol Sea group (i.e., nodes 11 and 14, located in southern Negros and southern Siquijor, respectively) were not as strongly connected as the preceding 6 nodes (Figure 4.7).

4.3.B Pair-wise comparisons of groups of sites generated by hierarchical clustering of species assemblage patterns

In the first six pair-wise comparisons, 6 smaller groups of sites (i.e., A, B, C, E, F and G) situated in bodies of water adjacent to the Bohol Sea are each compared to the main Bohol Sea group (H). The sites in the 6 groups had species assemblages that were most dissimilar to those in the main Bohol Sea group (H). Most of the sites in these smaller groups were predicted by the biophysical model to have the weakest larval connectivity to all other sites considered. In contrast, most of the sites in the main Bohol Sea group were predicted to have the strongest larval connectivity to all other

sites considered. In the seventh comparison, two subgroups of the main Bohol Sea group (I and J) are compared. For each of the 7 pair-wise comparisons the information needed to infer the presence (or absence) and potential strength of larval connectivity between groups (e.g., Table 4.1) are reported: predicted strength of larval exchange between groups, the habitat characteristics of the sites within each group, the similarity or dissimilarity of the species assemblages between groups and the habitat preferences of fish species that contributed most to dissimilarity between groups. A summary of information used to predict the presence and probable extent of larval connectivity is given in Table 4.4.

Table 4.2 Predicted levels of connectivity between 6 groups (A, B, C, E, F and G) and the major Bohol Sea group (H) (1. to 6.) and between two subgroups (I vs. J) of the main Bohol Sea group (7.) (see Figures 4.3 and 4.4 for geographic location of the different groups). Index values are also expressed as % of the highest connectivity index recorded in the study for each PLD. Predictions were based on results of simulations using the biophysical model. For the first six comparisons, connectivity indices were summed for all 9 possible connections (indicated in parentheses) between the nodes in the model. Connectivity indices for the seventh comparison were computed for all 20 possible connections between nodes and for the 9 connections that had the highest index values.

	Connectivity Index					
Groups compared	**15-day**		**30-day**		**45-day**	
1. A vs. H (9)	0.18	15%	0.25	12%	0.36	15%
2. B vs. H (9)	0.18	15%	0.27	13%	0.38	16%
3. C vs. H (9)	0.24	20%	0.46	22%	0.65	27%
4. E vs. H (9)	0.30	24%	0.58	28%	0.49	21%
5. F vs. H (9)	0.08	7%	0.23	11%	0.39	16%
6. G vs. H (9)	0.16	13%	0.23	11%	0.34	14%
7. I vs. J (20)	1.23		2.06		2.38	
I vs. J (9 highest)	1.04	85%	1.64	80%	1.72	72%

4.3.B.1 Group A vs. Group H

Group A comprised 4 sites in southeastern Bohol. Two sites were situated on fringing reefs within a small bay (Cogtong Bay) while the other two sites were located on two shoals just outside the mouth of the bay facing the Bohol-Leyte channel (Figure 4.4). The predicted levels of connectivity between groups A and H (regardless of direction) were some of the lowest among all the pairs of groups compared (Table 4.2). Connectivity between groups A and H ($P_{ij} \geq 0.01$) were mostly via export of larvae from group A (node 4) to only two (out of nine) nodes in group H (nodes 5 and 6), and import of larvae to group A from only two nodes in group H (nodes 3 and 5) (Figures 4.1c, 4.4, 4.6). The sites in group A comprised two types of habitat. The first had a moderate degree of embayment and was not dominated by any particular benthic component (i.e., the 2 sites in Cogtong Bay). The second had a high % cover of sand i.e., the 2 sites situated on shoals) (Figure 4.5b). In contrast, the sites in group H comprised a broad range of habitat types, including live hard coral-, sand-, rock-, and macroalgae/seagrass (Figure 4.5c). Analysis using SIMPER indicated that 122 species of reef fish accounted for ~90% of the dissimilarity between groups A and H (Table 4.3; Appendix 4.2). Of this set of species, only 1 species was unique to group A. Sixty species (accounting for 49.5% of dissimilarity) were unique to group H. Sixty-one species were shared by the two groups but most (77%) of these species were more frequently present in group H. A higher proportion of the species associated with group A prefer habitats that are more sheltered from winds and wave action, rocky and/or had more of the substrate types classified as 'others' (i.e., seagrass). In contrast, a higher proportion of the species associated with group H tended to prefer habitats that were more exposed to winds and wave action (Figure 4.9). The habitat preferences of species associated with group H remained consistent across all comparisons and will not be repeated in the succeeding comparisons.

4.3.B.2 Group B vs. Group H

Group B comprised 2 sites in Sogod Bay in southern Leyte (Figure 4.4). The predicted levels of larval connectivity between groups B and H were also among the lowest in the study (Table 4.2). Connectivity between groups B and H ($P_{ij} \geq 0.01$) were mostly through export of larvae from group B (node 2) to only two nodes located in the eastern portion of group H (nodes 3 and 5), and import to group B from only one node

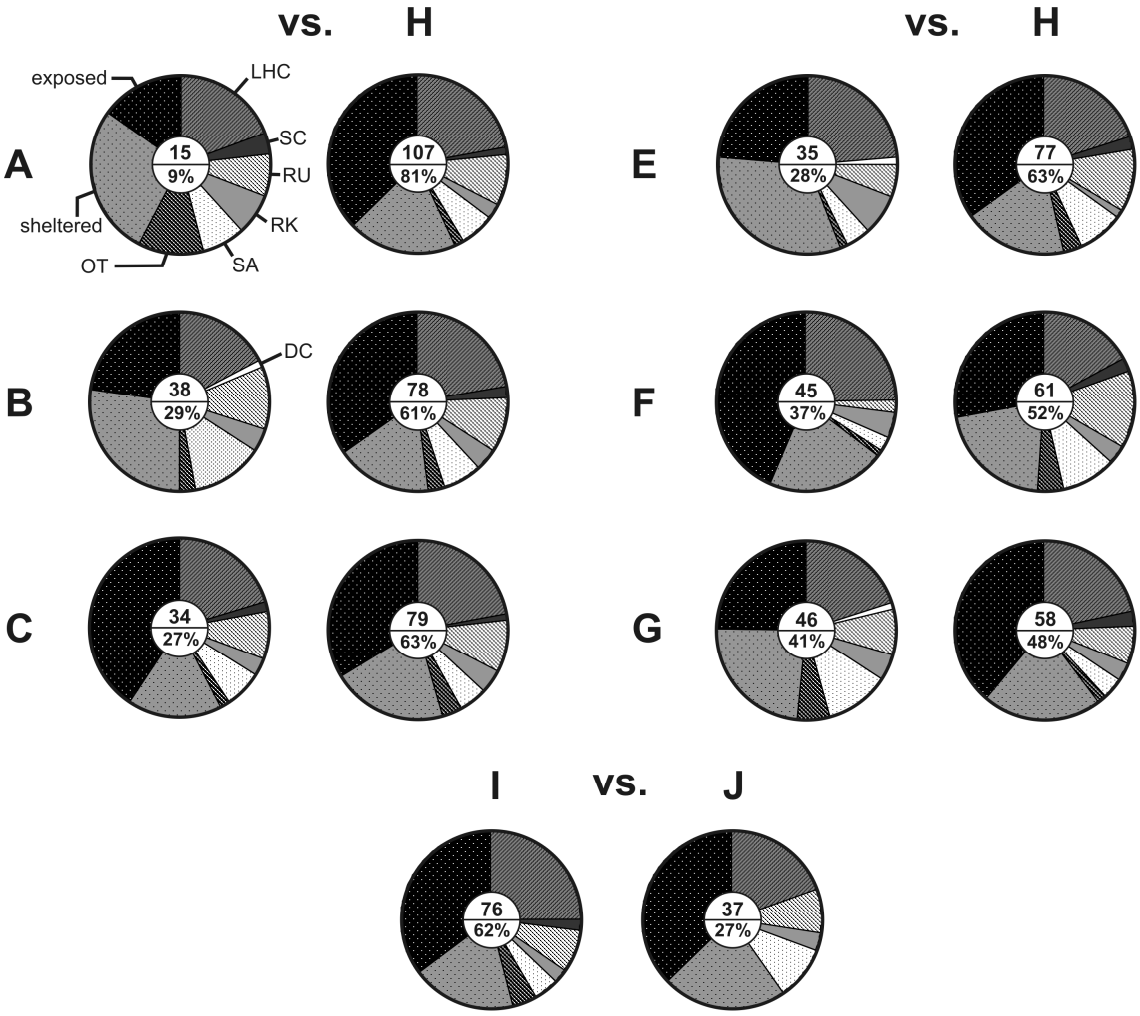


Figure 4.9 Habitat preferences of the species of reef fish that contributed most to the dissimilarity between groups of sites formed by hierarchical clustering (see Figures 4.3 and 4.4). Data from comparisons between 7 pairs of groups are presented. Species that accounted for most (~90%) of dissimilarity between groups were identified using SIMPER analysis. For each pair compared, the numbers at the centre of each pie chart indicate the number of species that are unique to or more frequently present in that group (upper numbers) and the % of dissimilarity accounted for by those species (lower numbers). A legend indicating the 9 categories of habitat is shown by the pie chart on the upper-left side of the figure ('exposed' – reefs that are more exposed; 'sheltered' – reefs that are more sheltered; LHC – live hard coral; DC – dead coral; SC – soft coral; RU – rubble; RK – rock, SA – sand; OT – 'others' (e.g. sponges, macroalgae and seagrass). Species that accounted for 90% of cumulative dissimilarity between groups are listed in Appendices 4.2 to 4.8.

Table 4.3 Summary of results of SIMPER analysis. For each comparison, the number of species that accounted for most (~90%) of the dissimilarity between groups is shown in the first column. Succeeding columns to the right indicate the numbers of species that are unique to the first group, shared between the two groups and unique to the second group. For the set of species that are shared between groups, the number of species that were more frequently present in either the first group or the second group are also shown. Numbers in parentheses are the % dissimilarity accounted for by these sets of species.

Groups compared (Group 1 vs. Group 2)	Species accounting for most of dissimilarity	Present in Group 1 only	Shared between groups	Present in Group 2 only
1. A vs. H	122	1 (1.0)	61 (39.8) A – 14 (8.0) H – 47 (31.8)	60 (49.5)
2. B vs. H	116	11 (8.3)	49 (35.6) B – 27 (20.5) H – 22 (15.1)	56 (46.2)
3. C vs. H	113	4 (2.8)	60 (46.7) C – 30 (24.2) H – 30 (22.5)	49 (40.0)
4. E vs. H	112	3 (4.4)	71 (54.9) E – 32 (23.7) H – 39 (31.2)	38 (30.9)
5. F vs. H	106	3 (2.5)	84 (69.1) F – 42 (34.8) H – 42 (34.3)	19 (18.0)
6. G vs. H	104	6 (7.3)	54 (45.3) G – 40 (33.9) H – 14 (11.4)	44 (36.8)
7. I vs. J	113	10 (5.9)	101 (81.0) I – 66 (55.7) J – 35 (25.3)	2 (1.3)

in group H (node 3) (Figure 4.1c, 4.4, 4.6). Sites in group B encompassed a relatively narrow range of habitat types characterised by high degree of embayment and high % cover of soft coral, rock or sand (Figure 4.5b). Analysis using SIMPER indicated that 116 species of reef fish accounted for ~90% of the dissimilarity between groups B and H (Table 4.3; Appendix 4.3). Of this set of species, 11 species (accounting for 8.3% of dissimilarity) were unique to group B. Fifty-six species (accounting for 46.2% of dissimilarity) were unique to group H. Forty-nine species were shared by the two groups, 55% of which were more frequently present in group B. A higher proportion of the species associated with group B prefer more sheltered and/or rocky habitats (Figure 4.9).

4.3.B.3 Group C vs. Group H

Group C comprised 2 sites in Cabalian Bay, also in southern Leyte (Figure 4.4). The predicted levels of larval connectivity between groups C and H were low for larvae with a PLD of 15 days and moderate for larvae with PLD of 30 to 45 days (Table 4.2). Most of the larval exchange between groups C and H ($P_{ij} \geq 0.01$) were exclusively via export from group C (node 1) to only 3-4 nodes found mostly in the eastern part of group H (nodes 3, 5 and 6 for 15- and 30-day PLD; nodes 3, 5, 6 and 14 for 45-day PLD) (Figure 4.1c, 4.4, 4.6). Sites in group C encompassed a relatively narrow range of habitat types characterised by a high degree of embayment and moderate to high % cover of live hard coral (Figure 4.5b). Analysis using SIMPER indicated that 113 species of reef fish accounted for ~90% of the dissimilarity between groups C and H (Table 4.3; Appendix 4.4). Of these species, 34 (accounting for 29% of dissimilarity) were unique to or more frequently present in group C. The rest (79 species that accounted for 63% of dissimilarity) were unique to or more frequently present in group H. Only 4 species (which accounted for 2.8% of dissimilarity) were unique to group C. Forty-nine species (accounting for 40.0% of dissimilarity) were unique to group H. Sixty species were shared by the two groups, 50% of which were more frequently present in group C and the other 50% more frequently present in group H. The habitat preferences of species associated with group C did not markedly differ from that of species associated with group H (Figure 4.9).

4.3.B.4 Group E vs. Group H

Group E comprised 3 sites in southeastern Negros, facing Tañon Strait (Figure 4.4). The predicted levels of connectivity between groups E and H were weak (Table 4.2). Larval connectivity between groups E and H ($P_{ij} \geq 0.01$) was exclusively via larval export from group E (node 10) to just 1-2 nodes located in the western part of group H (node 11 for 15- and 45-day PLD; nodes 11 and 13 for 30-day PLD) (Figure 4.1c, 4.4, 4.6). Sites within group E had a broad range of habitat types, including reefs with high % cover of live hard coral, dead coral, rubble and/or substrate types classified as 'others' (i.e., macroalgae and seagrass) (Figure 4.5c). Analysis using SIMPER indicated that 112 species of reef fish accounted for ~90% of the dissimilarity between groups E and H (Table 4.3; Appendix 4.5). Of this set of species, only 3 species (accounting for 4.4% of dissimilarity) were unique to group E. Thirty-eight species (accounting for 31.1% of dissimilarity) were unique to group H. Seventy-one species were shared by the two groups, 55% of which were more frequently present in group H. A higher proportion of the species associated with group E prefer more sheltered and/or rocky habitats (Figure 4.9).

4.3.B.5 Group F vs. Group H

Group F comprised 4 sites. Two sites are situated in southern Negros, facing Negros-Mindanao strait, which connects the Bohol Sea to the Sulu Sea (Figure 4.4). The two other sites are situated in southwestern Negros, facing the Sulu Sea (Figure 4.4). The predicted levels of larval connectivity between groups F and H were among the lowest recorded in this study (Table 4.2). Connectivity between groups F and H ($P_{ij} \geq 0.01$) were exclusively via import of larvae to group F (node 12) from 2 to all of the 9 nodes within group H (nodes 11 and 14 for 15-day PLD; nodes 11, 13, 14, 15 for 30-day PLD; and nodes 3, 5, 6, 7, 8, 11, 13, 14, 15 for 45-day PLD). Sites within group F had a broad range of habitat types, which included reefs that are not embayed, with moderate degrees of embayment, higher % cover of live hard coral, dead coral and/or rock (Figure 4.5c). Analysis using SIMPER indicated that 106 species of reef fish accounted for ~90% of the dissimilarity between groups F and H (Table 4.3; Appendix 4.6). Of this set of species, only 3 species (accounting for 2.5% of dissimilarity) were unique to group F. Only 19 species (accounting for 18.0% of dissimilarity) were unique to group H. Eighty-four species were shared by the two groups, 50% of which were

more frequently present in group F and the other 50% more frequently present in group H. A higher proportion of the species associated with group F prefer habitats that are more exposed and/or have live hard coral (Figure 4.9). The proportion of species that prefer more sheltered habitats did not differ between groups F and H (Figure 4.9).

4.3.B.6 Group G vs. Group H

Group G comprised 2 sites on fringing reefs in southeastern Bohol (northern Panglao Is.), facing the Cebu-Bohol channel (Figure 4.4). The predicted levels of connectivity between groups G and H were among the lowest recorded in this study (Table 4.2). Larval connectivity between groups G and H ($P_{ij} \geq 0.01$) was almost exclusively via import of larvae to group G (node 9) from two nodes in group H (nodes 7 and 8 for all PLD values) (Figure 4.6). The only potentially significant export of larvae by group G to group H was to node 11 (45-day PLD), which is situated in the western part of group H (Figure 4.6). Sites within group G had a very narrow range of habitat types characterised by higher % cover of rubble and moderate % cover of live hard coral (Figure 4.5c). Analysis using SIMPER indicated that 104 species of reef fish accounted for ~90% of the dissimilarity between groups G and H (Table 4.3; Appendix 4.7). Of this set of species, only 6 species (accounting for 7.3% of dissimilarity) were unique to group G. Forty-four species (accounting for 36.8% of dissimilarity) were unique to group H. Fifty-four species were shared by the two groups, most (77%) of which were more frequently present in group G. A lower proportion of the species associated with group G prefer habitats that are more exposed but a greater proportion prefer sandy or seagrass-dominated habitats (the latter was classified as 'others' in Figure 4.9). The proportion of species that prefer more sheltered habitats did not differ between groups G and H (Figure 4.9).

4.3.B.7 Group I vs. Group J

Groups I and J are the two overlapping subgroups of the main Bohol Sea group (H) that separate at 73% similarity (Figures 4.3, 4.4). Most of the sites in group I are situated on the eastern side of the Bohol Sea (13 sites in Leyte and Bohol), while most of the sites in group J are on the western side (29 sites in Bohol, Siquijor, Negros and NW Mindanao) (Figure 4.4). The general direction of predicted larval exchange among the nodes situated in the Bohol Sea is from east to west (see Section *4.3.A.3*). The

simulations indicated that export of larvae from group I to group J was more frequent than vice-versa (Figure 4.6). The predicted levels of larval connectivity between groups I and J were the highest among all the pairs of groups compared in this study (Table 4.2). Considering all of the possible connections (20) between the nodes that represent groups I and J, larval connectivity between groups I and J were 1.9 to 15.5 times higher (depending on PLD) than connectivity between any of the 6 smaller groups and the main Bohol Sea group (H in Table 4.2). Limiting it to the same number of potential connections between nodes as in the previous comparisons (9 nodes with highest index values), the levels of connectivity between groups I and J were still 1.6 to 13.1 times higher (Table 4.2). The sites within group I had a wide range of habitat types, including reefs that are not embayed, with moderate degrees of embayment, higher % cover of live hard coral, rock and/or sand (Figure 4.5c). The sites in group J, on the other hand, had the broadest possible range of habitat types (similar to group H). Analysis using SIMPER indicated that 113 species of reef fish accounted for ~90% of the dissimilarity between groups I and J (Table 4.3; Appendix 4.8). The majority of these species (101 species or 89%) were shared between the two groups. However, 65% of the species that were common to the two groups (66 species accounting for 55.7% of dissimilarity) were more frequently present in the eastern group (I). Ten species were unique to the eastern group (I), while only 2 species were exclusive to the western group (J). The habitat preferences of species associated with group I and group J did not greatly differ in terms of preference for exposed and sheltered habitats (Figure 4.9).

4.4 Discussion

The objective of this study was to determine the extent of potential larval connectivity among local populations of coral reef fishes by examining species assemblage patterns across multiple sites and modelling the probabilities of larval exchange between these sites. The spatial patterns of species assemblages and predicted larval exchange were complementary. Taken together, the results from the two approaches suggested the presence of significant larval connectivity among populations situated in an area of the Bohol Sea that is influenced by a westward mainstream current for 6 months of the year. These results also indicated that populations spatially isolated from this dominant current are not strongly connected by larval exchange to the populations in the main Bohol Sea. The larval dispersal simulations showed that the

Table 4.4 Summary of information required to infer the presence and probable extent of larval connectivity between sampling sites. Information on predicted levels of larval exchange, measured habitat characteristics, measured species assemblage structure and habitat preferences of species for each of 7 pairs of site groups are summarised. Conclusions about larval connectivity and the ideas supporting these conclusions are found in the last column.

Groups compared	Predicted level of larval exchange	Measured habitat characteristics	Measured species assemblage structure/ Habitat preferences of species	Conclusions and supporting ideas
A vs. H	*Weak* - A exporting to or importing from only 2 (of 9) nodes in H	*Different* - A = high % cover of sand or slightly embayed; H = broad range of habitat types	*Dissimilar* - Groups distinguished at ~45% similarity - More species associated with A prefer sheltered (e.g. embayed) habitats	*Connectivity likely to be weak* - Currents in the vicinity of A (Bohol-Leyte channel) are weaker and isolated from dominant current in the main Bohol Sea - Habitats in A different from most habitats in H - Species assemblages in A could also be influenced by populations in adjacent internal seas (Visayan/Camotes seas)
B vs. H	*Weak* - B exporting to only 2 nodes or importing from only 1 node in H	*Different* - B = highly embayed, high % cover of sand, soft coral or rock; H = broad range of habitat types	*Dissimilar* - Groups distinguished at ~56% similarity - More species associated with B prefer sheltered (e.g. embayed) habitats	*Connectivity likely to be weak* - Currents in the vicinity of B (within Sogod Bay) are weaker and isolated from dominant current in the main Bohol Sea - Habitats in B different from most habitats in H
C vs. H	*Weak for shorter PLD, moderate for longer PLD* - Unidirectional larval supply: C exporting mostly to 3-4 nodes in eastern part of H	*Different* - C = highly embayed, moderate to high % cover of live hard coral, similar to many sites in H	*Dissimilar* - Groups distinguished at ~59% similarity - Habitat preferences of species associated with C were not very different from those associated with H	*Connectivity likely to be weak* - Currents in the vicinity of C (within Cabalian Bay) are weaker and isolated from dominant current in the main Bohol Sea - Degree of larval exchange may also be limited by strong (unidirectional) current entering Bohol Sea through Surigao Strait - Species assemblages in C may also be influenced by Pacific (eastern Philippine) populations

Table 4.4. Continued.

E vs. H	*Weak* - Unidirectional larval supply: E exporting mostly to 1-2 nodes in western part of H	*More similarities (larger overlap) in habitat types between the two groups* - E = high % cover of live hard coral, dead coral, rubble and/or macroalgae and seagrass), similar to many H sites	*Dissimilar* - Groups distinguished at ~64% similarity - More species associated with E prefer sheltered (e.g. embayed) habitats	*Connectivity likely to be weak and limited to only a few sites in western part of H* - Degree of larval exchange may also be limited by strong (unidirectional) southward current passing through Tañon Strait - Species assemblages in E could also be influenced by populations in an adjacent internal sea (i.e., Visayan Sea)
F vs. H	*Weak* - Unidirectional larval supply: 2 to 9 nodes in H (depending on PLD) exporting to F	*More similarities (larger overlap) in habitat types between the two groups* - F = higher % cover of live hard coral, dead coral and/or rock, similar to many H sites	*Dissimilar* - Groups distinguished at ~66% similarity - More species associated with F prefer exposed habitats but proportion of species that prefer sheltered habitats did not differ between two groups	*Connectivity likely to be weak* - Degree of larval exchange may be limited by strong (unidirectional) current exiting Bohol Sea through Negros-Mindanao Strait - Species assemblages in F may also be influenced by populations in the Sulu Sea
G vs. H	*Weak* - Larval supply almost exclusively unidirectional; only 2 neighbouring nodes in H exporting larvae to G	*Different* - G = high % cover of rubble and moderate % cover of live hard coral; H = broad range of habitat types	*Dissimilar* - Groups distinguished at ~68% similarity - Fewer species associated with G prefer exposed habitats but more species prefer sandy or seagrass-dominated habitats	*Connectivity likely to be weak* - Currents in the vicinity of G (Cebu-Bohol channel) are weaker and isolated from dominant current in the Bohol Sea - Habitats in G different from most habitats in H - Species assemblages in G could also be influenced by populations in adjacent internal seas (i.e., Camotes and Visayan seas)
I vs. J	*Strong* - Mostly via export from I to J (westward) than the opposite	*More similarities (larger overlap) in habitat types between the two groups* - I = higher % cover of live hard coral, rock and/or sand, similar to many sites in J	*Similar* - Groups distinguished at ~73% similarity - Habitat preferences of species associated with each group did not greatly differ	*Connectivity likely to be strong* - Presence of dominant westward current and high degree of similarity in habitat types between the two groups - Previous work by Ablan (2005, 2006) suggesting east to west genetic sub-structuring in 2 species of reef fish within Bohol Sea

direction of potential larval connectivity within the Bohol Sea is predominantly westward. This is consistent with the known general direction of the mainstream current throughout the year.

The assessment of the potential effects of larval supply and local habitat on the species assemblage patterns reinforced the notion of significant population connectivity within the Bohol Sea (Table 4.4). Among all the comparisons between groups of sites, the probable presence of high levels of connectivity can be concluded only for the eastern and western subgroups of the Bohol Sea (i.e., Table 4.4, I vs. J tend to reflect Case 1 in Table 4.1). Compared to other pairs of groups, these two subgroups were predicted to have the highest rates of larval exchange and had substantial overlap in the types of habitat they encompassed. The combination of these two factors may contribute significantly to the higher level of species assemblage similarity (~68-73%) of the two subgroups. Similar types of habitat between the two subgroups would facilitate recruitment of larvae dispersing from eastern to western populations. Further support for the conclusion that populations in the Bohol Sea are likely to be more strongly connected by dispersal and recruitment of larvae is indicated by the set of species that differentiated the two subgroups. The majority (89%) of this set of species was shared by the two subgroups. However, most (65%) of the shared species were more frequently present in the eastern subgroup (I) than in the western subgroup (J). This was the case despite the narrower range of habitat types and fewer sampling sites that were included in the eastern subgroup. Also, there were more species unique to the eastern subgroup (10 species) than the western subgroup (2 species). Such patterns are consistent with the westward direction of potential larval connectivity between the subgroups, i.e., for individual species, the probability of connectivity is expected to decrease downstream of the dominant current. The habitat preferences of the species associated with each subgroup did not greatly differ, which is to be expected if the two subgroups have many types of habitat in common.

Ablan (2005, 2006) used microsatellite DNA markers to determine potential patterns of connectivity among several populations of two species of reef fish (*Dascyllus trimaculatus* and *Pterocaesio pisang*) across the Bohol Sea. The results of her study suggested eastern and western groups of reef fish populations in this area, roughly similar to the two subgroups (I and J) of the main Bohol Sea group that were found in the present study. However, caution must be exercised when comparing the results of the two studies. Ablan (2006) suggested that the eastern and western groups

she found were not strongly connected to each other by larval dispersal, which contradicts the conclusions of the present study. The contrasting conclusions of the two studies about potential connectivity in the Bohol Sea were probably due to differences in the spatial scales at which populations of reef fishes were sampled and the locations of these populations. The study by Ablan had a very limited number of sites (7 at most) to provide a clear picture of probable ecological-scale larval connectivity across a 300 km wide area. Furthermore, the sites she sampled were mostly offshore islands (e.g. Apo, Sumilon, Balicasag, Selinog, Mantigue; see Figure 4.1b), which were not included in the present study. More importantly, two of the sites she sampled are situated outside of the area that was sampled in the present study (i.e., Dinagat Is. and Mantigue Is.; Figure 4.1b). A possible explanation for weak connectivity between the eastern and western regions of the Bohol Sea for some species or sites is the presence of mesoscale eddies that form at different times of the year (Figure 4.2). Such eddies may limit the westward dispersal of larvae. Nevertheless, Ablan (2005, 2006) showed that ecological-scale larval connectivity may be present in the Bohol Sea within spatial scales of 10's of km for the sites that she sampled (e.g., between Apo, Sumilon, and Balicasag islands; Figure 4.1b). Significant self-recruitment at very small spatial scales (< 1 km) may also be present at these sites (Ablan 2005, 2006).

The results of the present study suggested that the species assemblage patterns could be partly explained by a combination of several habitat variables, particularly degree of embayment, % cover of sand and % cover of rubble. These habitat variables could be more important in differentiating the species assemblages of sites situated within bays and two channels (i.e., Bohol-Leyte and Cebu-Bohol channels) from those found in other sites, especially the many sites that comprised the main Bohol Sea group. Two of the sites in group A and all of the sites in groups B and C (including group B-C) were all situated within bays (i.e., Cogtong, Sogod and Cabalian bays, respectively). Fish assemblages on reefs that are sheltered within bays tend to differ in community structure and have lower species richness and diversity compared to assemblages found on more exposed reefs outside of bays (Friedlander et al. 2003). A probable effect of embayment was also indicated by the greater proportion of the species associated with groups A and B (but, interestingly, not the species associated with C) preferring more sheltered habitats compared to the species associated with the Bohol Sea group. The main Bohol Sea group, in contrast, had a higher proportion of species that preferred more exposed habitats probably because the sites that composed this group are mostly

found along coastlines exposed to winds (i.e., southwest and northeast monsoons) and wave action. High % cover of sand could be an important factor in differentiating the species assemblages in two other sites that composed group A, which are situated on shoals in the Bohol-Leyte channel. Higher % cover of sand usually correlates with lower structural complexity of reefs in the region that was studied (Abesamis et al. 2006b). Lower structural complexity, in turn, is commonly associated with lower species richness and abundance of coral reef fishes (e.g., Carpenter et al. 1981). Note, however, that the two sites in group A with sandy habitat were more similar in species assemblage to the two other sites in the same group situated in Cogtong Bay, than any other site in the Bohol Sea group with sandy habitat (Figures 4.3 and 4.5). Lastly, the results suggested that higher % cover of rubble could be important in differentiating the species assemblages of the two sites in group G, which are situated in the Cebu-Bohol channel. However, the set of species associated with group G did not show a strong preference for rubble-dominated habitats. Also, among the three potentially influential habitat variables, % cover of rubble had the lowest correlation to the species assemblage patterns.

Differentiation of the species assemblages in the sites belonging to groups A, B, C and G could be driven to some extent by dissimilarities in habitat, but the larval dispersal simulations indicated low levels of larval exchange between these groups and the Bohol Sea group. Results of comparisons of groups A-C and G with group H (Table 4.4) reflect Case 4 in Table 4.1. Thus it is likely that groups A-C and G are weakly connected by larval exchange to the populations in the Bohol Sea. No other studies are available to independently validate the results of the larval dispersal simulations. However, the results of the simulations with respect to groups A-C and G are plausible representations of potential larval exchange based on the sea surface circulation patterns indicated by the NLOM (Figure 4.2). Throughout the year, all of the sites in these weakly-connected groups are situated in areas that appear to be isolated from the mainstream flow that probably connects populations within the main Bohol Sea (Figure 4.2). The data from NLOM also suggest that the currents in these areas are much weaker compared to the mainstream current (Figure 4.2). Such conditions would significantly decrease the probabilities of population connectivity between groups A-C and G and the main Bohol Sea group. The simulations indicated that the predicted connectivity between these groups and the Bohol Sea group were usually weaker or mostly limited to areas that are relatively close (more frequently within 25-125 km)

even for the longest PLD tested (45 days) (Table 4.2, Figures 4.6, 4.7). It should be noted that for the sites situated within bays, the effect of embayment as a habitat factor is likely to be confounded by its effect as a physical feature. Degree of embayment could also limit larval exchange due to potential differences in circulation patterns inside and outside of bays.

Habitat dissimilarity was unlikely to be the most influential factor in differentiating the species assemblages of the sites in group E in the Tañon Strait and group F in or close to the Sulu Sea from the species assemblages in the main Bohol Sea group. Groups E and F included many types of habitat that were similar to the main Bohol Sea group (Figure 4.5). A more likely reason for the differentiation of the species assemblages of the sites in groups E and F is limitation of larval exchange with populations in the Bohol Sea due to the local geographic (or oceanographic) setting. Results of simulations indicated that the larval connections of groups E and F with the Bohol Sea group are weak. These potential connections predominantly occur in one direction only, due to the strong southward current flowing through the Tañon Strait for group E (towards the Bohol Sea) and the westward current flowing through the Negros-Mindanao Strait for group F (from Bohol Sea to the Sulu Sea) almost throughout the year (Figure 4.2). The data from the NLOM suggest that dispersal of larvae in the directions opposite to the general flow of these strong currents is limited, since it may occur only during the relatively brief flow reversals associated with the tides. The results of the comparisons of groups E and F with the Bohol Sea group (H) (Table 4.4) are more similar to Case 3 in Table 4.1. Thus, it is likely that populations in groups E and F are only weakly connected by larval exchange to the populations in the main Bohol Sea. In addition, the local geographic setting suggests that differentiation of the species assemblages of groups E and F could also be partly due to potential connections of the populations within these two groups with other populations outside of the Bohol Sea (i.e., Visayan Sea populations for group E; Sulu Sea populations for group F). Such a consequence of the local geographic setting may also be partially responsible for the differentiation of species assemblages in group C (i.e., potential connections with Pacific populations) and groups A and G (i.e., potential connections with Visayan Sea and/or Camotes Sea populations).

The findings of this study improve the current understanding of larval connectivity of fish populations on coral reefs within the Bohol Sea, in particular, and also in archipelagic regions, in general. For populations in the Bohol Sea, higher levels

of ecologically-relevant larval connectivity may occur more often within ~25 km of their potential source populations (Figures 4.6, 4.7). Lower levels of connectivity may be expected at greater distances, up to 100-275 km away from potential source populations, depending on geographic location (Figure 4.7). These spatial scales of potential demographic connectivity in reef fishes are consistent with the findings of previous work by Ablan (2005, 2006) in the Bohol Sea and others elsewhere (James et al. 2002; Bode et al. 2006; Cowen et al. 2006; Jones et al. 2009; Planes et al. 2009; Christie et al. 2010; Saenz-Agudelo et al. 2011). In the absence of detailed empirical measurements of population connectivity between reserves and non-reserves across the entire Bohol Sea region, these initial estimates of distances of demographically-significant larval dispersal can be used as 'rules of thumb' in efforts to optimise reserve network design. The limited distances for significant levels of larval exchange between populations also indicate a greater chance for older reserves to subsidise recruitment to nearby fished areas (< 25 km away) and for many neighbouring reserves to interact, potentially resulting in synergistic positive effects (Chapter 5). These possibilities place the small (< 1 km^2) but numerous and closely-spaced (mostly within 1-5 km of each other) reserves in the Bohol Sea in a more positive light given the concern that the majority of these reserves are not protecting sufficient areas of coral reef to achieve conservation goals (McClanahan 1999; Roberts et al. 2002; Weeks et al. 2010a). Weeks et al. (2010a) also pointed out that ecologically-relevant larval connectivity between existing reserves in the Philippines is likely because, on average, many of these reserves are situated within 10's of km of each other.

This study showed that broad-scale species assemblage patterns of coral reef fish may indicate potential larval connectivity within the spatial scales expected for ecologically-relevant larval dispersal. The spatial scales at which the presence or absence of larval connectivity inferred from species assemblage patterns in this study were smaller compared to the study done by Roberts (1991) in the Red Sea but similar to the study done by Williams et al. (1986) across the continental shelf of the Great Barrier Reef. Patterns of larval connectivity among population on coral reefs are likely to be strongly influenced by the local geographic setting (Jones et al. 2009). In the case of the Bohol Sea region, patterns of larval connectivity among reef fish populations are probably heavily influenced by the local hydrodynamic regime, including how current patterns are modified by many islands, the coastline features of larger islands (e.g., bays), bathymetric features and monsoon winds. However, the results of this study

indicate that the insights on probable larval connectivity gained from species assemblage patterns will only be meaningful if the effects of local habitat on species assemblage patterns and the probable patterns of larval exchange are also assessed.

The main contribution of this study was the creation of a working framework for testing hypotheses about population connectivity at the regional (100's of km, inter-island) scale. Such a framework would be invaluable for the application of more direct but also more expensive and labour-intensive methods (e.g. parentage analysis or tagging of larval otoliths) to empirically test larval connectivity between specific local populations of reef fishes in the region. Results of this study also indicate that the most significant levels of demographically-relevant connectivity occur within more limited spatial scales (a few 10's of km). In the final study (Chapter 5), two of the most critical expectations from reserve networks are tested in some of the oldest and most studied reserves in the Bohol Sea: recruitment subsidy by reserves to surrounding fished areas and reserve to reserve connectivity.

Chapter 5

Potential recruitment subsidy and connectivity of small no-take marine reserves in the central Philippines

Abstract. Recruitment subsidy (net larval export) from no-take marine reserves is widely expected to enhance fisheries but remains highly controversial. Its development, magnitude and spatial extent will depend upon the patterns of connectivity (larval exchange) among populations inside and outside reserves. In this study, potential recruitment subsidy and connectivity of 39 small (< 1 km^2) community-based reserves situated on heavily fished coral reefs in the central Philippines were investigated using a simple exponential model of population recovery and larval production inside reserves, coupled with an individual-based larval dispersal model. The 39 reserves protect only 6% of total reef area. Simulations indicated that a 3.5-fold (~250%) increase in recruitment to fished areas can result from a 55-fold increase in larval production by large predatory reef fishes inside reserves if all reserves were continuously and effectively protected for 20 years. Lower larval production differentials (3- and 7-fold increases) within the first decade of reserve protection will bring about much smaller increases (< 21% change) in recruitment. These lower larval subsidies are likely to at least replace losses in yield due to reserve creation but they are difficult to detect because of substantial temporal and spatial variation in recruitment. Results also showed that for the same larval dispersal potential (30-day larval life), the spatial pattern of recruitment subsidy, the probability of net larval export from reserves and the probabilities of larval exchange among reserves are influenced more strongly by local geography and current patterns rather than larval production levels within individual reserves. Probabilities of self-recruitment within and connectivity between the small reserves were extremely low (always < 0.03) but the absolute magnitudes of larval exchange between reserves increased dramatically (up to ~20-fold) with higher larval production. These findings underscore the importance of protecting reserves over the long-term (decades) and establishing networks of reserves that are connected by larval dispersal in order for reserves to provide meaningful recruitment subsidy to fisheries.

5.1 Introduction

It is now well-established that the abundance of organisms targeted by fisheries can build up inside no-take marine reserves (Roberts and Polunin 1993; Russ 2002; Gell and Roberts 2003; Halpern and Warner 2003; Lester et al. 2009; Molloy et al 2009; Babcock et al. 2010). However, the effects of reserves beyond their boundaries remain open to question. Reserves may positively affect surrounding fisheries through net export of mobile adults (i.e.,'spillover'). Such effects have been demonstrated (e.g., Russ et al. 2004; Abesamis and Russ 2005; Halpern et al. 2010). A much larger potential benefit to fisheries may come from the net export of pelagic larvae (i.e., 'recruitment subsidy') (Carr and Reed 1993; Sale et al 2005). However, it is still unclear if recruitment subsidy benefits are realised (Russ 2002; Sale et al 2005). Also, there is concern about whether such larval subsidies to fisheries will ever be enough to more than compensate for the losses in yield that may result from the creation of reserves because of decreased fishing area (Halpern and Warner 2003; Hilborn et al. 2004). At present, the evidence for reserves affecting larval settlement to fished areas is sparse and limited mainly to sessile invertebrates (Gell and Roberts 2003; Sale et al. 2005; Cudney-Bueno et al. 2009; Pelc et al. 2009, 2010; Christie et al. 2010). Demonstrating recruitment subsidy from reserves for the multitude of targeted marine species remains a challenge that is hindered by the same difficulties inherent in the study of marine larval dispersal, recruitment variation and population connectivity.

Most reserves are smaller than the mean larval dispersal range of the majority of marine species (Roberts and Hawkins 1997; Shanks et al. 2003; Palumbi 2004; Jones et al. 2009; Weeks et al. 2010a). Thus, any increase in larval production inside reserves will almost certainly lead to a proportional increase in recruitment to fished areas (and other reserves) within the range of larval dispersal (Halpern et al. 2004). Such larval subsidies are potentially very important in sustaining fisheries especially when most spawners are found within reserves as opposed to fished areas (Davis 1977, Pelc et al. 2010). Even if larval export from reserves is highly likely, theoretical studies indicate that large reserves (10's of km long) with exceptionally high levels of larval production relative to fished areas may be necessary before recruitment subsidy can be detected against the noise of natural recruitment fluctuations (Halpern et al. 2004; Pelc et al. 2010). In reality, however, the conversion of large proportions of fishing grounds into reserves and the successful maintenance of large reserves are more difficult to achieve,

particularly in developing countries (Roberts and Hawkins 1997; Russ and Alcala 1999; Alcala and Russ 2006).

Reserves must be situated in 'source' sites in order to effectively enhance fisheries through recruitment subsidy (Crowder et al. 2000; Russ 2002). This means that reserves should be established in good quality habitats where the potential for population growth is higher, resulting in greater build-up of spawning biomass. This also means that reserves should be located in sites where the probability of export of larvae far outweighs that of import. Conversely, reserves will be less effective contributors of larvae if they are situated in 'sink' sites where poorer-quality habitat limits population growth and larval import is greater than export. The potential for source-sink population dynamics (Pulliam 1998) is likely to be high in coral reefs because of considerable habitat heterogeneity (Crowder et al. 2000). Furthermore, reef populations will likely differ in their tendencies to export and import larvae because of complex hydrodynamic patterns that are typical of coral reef environments (Roberts 1997; James et al. 2002; Bode et al. 2006; Cowen et al. 2006). The implications of source-sink dynamics to reef populations suggest that situating reserves at source sites is of utmost importance, while haphazard or random placement of reserves should be avoided (Crowder et al. 2000). However, the process of establishing reserves is often more strongly driven by socio-economic considerations and opportunism rather than scientific understanding of source-sink dynamics (Roberts 2000; Roberts et al. 2003; Alcala and Russ 2006; McCook et al. 2009). Identifying source and sink sites is time-consuming or simply not feasible in many situations. On the other hand, there is a view that sources may be created simply by establishing reserves, with little or no consideration of source-sink relationships, because spawning biomass inside reserves is likely to become much greater than fished areas (Roberts 1998, 2000). This possibility remains largely unexamined.

Field studies of larval dispersal of reef fishes at ecologically relevant scales have demonstrated significant self-recruitment at the scale of small islands, individual reefs or reserves (i.e., less than a few kilometres) (Jones et al. 1999; Swearer et al. 1999; Jones et al. 2005; Almany et al. 2007; Planes et al. 2009). While these studies indicate the potential for populations within reserves to be self-sustaining, the recovery and persistence of reserve populations may also greatly depend upon larval supply from elsewhere, either from fished areas or other reserves (Jennings 2000; Roberts 2000; Planes et al. 2009). In situations where fished areas are heavily exploited, a network of

reserves that interact via larval exchange may be necessary in order to facilitate the build-up of spawning stocks within reserves and eventually result in meaningful recruitment subsidy (Man et al. 1995; Sladek-Nowlis and Roberts 1999; Roberts 2000). Building networks of reserves that are connected by larval exchange is also proposed as a key strategy to enhance the resilience of reef ecosystems against anthropogenic and natural disturbances (Hughes et al. 2003; Almany et al. 2009; McCook et al. 2009).

In this study, potential recruitment subsidy and connectivity of 39 marine reserves situated within the most heavily fished region in the Philippines were investigated. These reserves are some of the smallest in the world. They also represent just a tiny fraction of the total reserves in the Philippines, the vast majority of which are small (total of 985 in 2008 with and average size of 0.12 km^2 according to Weeks et al. 2010a; also refer to Aliño et al. 2002 and Arceo et al. 2008). Most Philippine reserves were established by local communities, with high expectations of fisheries enhancement (initially from local spillover) but with very little consideration of potential source-sink population relationships or connectivity (Aliño et al. 2002, Alcala and Russ 2006, Arceo et al. 2008, McCook et al. 2009). Furthermore, the success of management of community-based Philippine reserves varies considerably (Pajaro et al. 1999; White et al. 2002, 2006; Alcala and Russ 2006). When and to what magnitude and spatial extent can these small reserves significantly affect recruitment to surrounding fisheries? How difficult would it be to detect larval subsidies from such reserves? Are these reserves situated in probable source sites? If they are situated in probable sink sites, could substantial increases in larval production transform them into sources? To what degree are these reserves self-recruiting or connected to each other by larval dispersal? These questions were explored using a simple model for population recovery and larval production, coupled with a spatially explicit individual-based larval dispersal model developed for the geographic region where the reserves in question are situated.

5.2 Materials and methods

5.2.1 Background and physical setting of the study area

Recruitment subsidy was examined in a 135 x 70 km (about 9,450 km^2) area on the western side of the Bohol Sea in the central Visayas, Philippines (Figure 5.1). The central Visayas is one of the most heavily fished regions in the Philippines (Carpenter

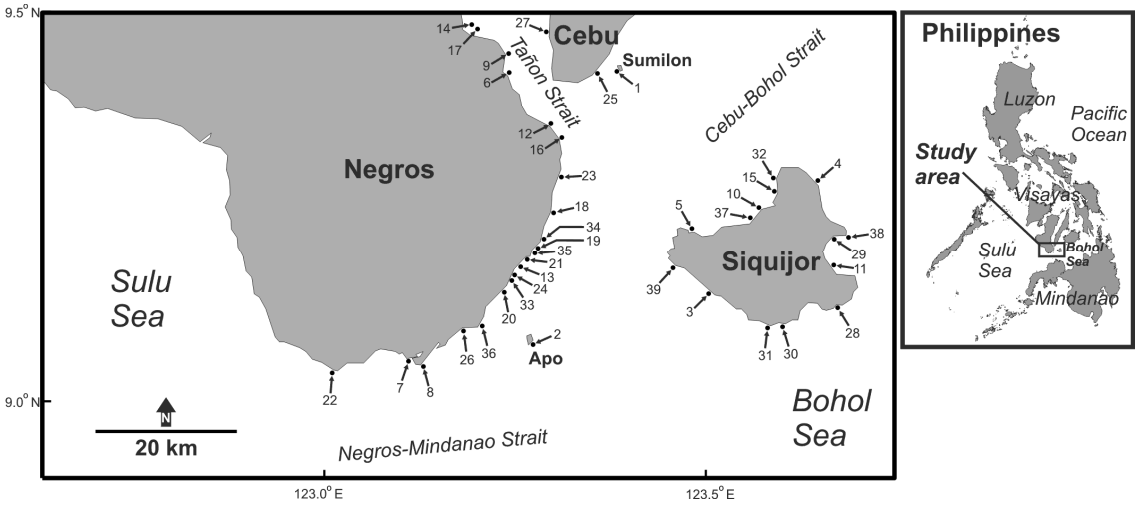


Figure 5.1 Map of the study area showing the 39 no-take marine reserves. The reserves are numbered according to year of establishment (oldest to newest, see Table 5.1).

and Alcala 1977; Burke et al. 2002; Alcala and Russ 2002; Green et al. 2003, 2004; Lavides et al. 2009; Nañola et al. 2010). The area that was studied included coastlines of southern Negros and Cebu islands, the entire island of Siquijor and two smaller islands (<1 km^2 in area), namely Apo and Sumilon (Figure 5.1). The total length of these coastlines is approximately 279 km. Most of the coastlines have coral reefs but detailed data on the extent of reef and other shallow-water habitats for reef fishes (e.g., mangrove, seagrass, rocky and soft-bottom habitats) are lacking. Due to the absence of fine-scale habitat data, the term 'reef' as it is used here broadly refers to coral reefs and other habitat associated with reefs that are suitable for the breeding of adult reef fishes and settlement of their larvae.

The study area is bounded by the Tañon Strait to the north, the Bohol Sea and Cebu-Bohol Strait to the east, the Negros-Mindanao Strait to the south and the Sulu Sea to the west (Figure 5.1). Data from the U.S. Navy Layered Ocean Model (NLOM) indicate that the general direction of surface currents in this area is towards the south/south-west (www7320.nrlssc.navy.mil/global_nlom). These currents are driven mainly by the southward flow of water through Tañon Strait and westward flow from the Bohol Sea to the Sulu Sea, exiting through the Negros-Mindanao Strait. However, actual current patterns are highly complex spatially and exhibit seasonal variation due to the reversing monsoon winds (Chapter 4; Figure 4.2).

5.2.2 No-take marine reserves

Thirty-nine small (all but one were < 0.5 km^2 in area) marine reserves situated mainly on reef habitat occur within the study area according to a recent census done by Alcala et al. (2008) (Figure 5.1, Table 5.1). These reserves were established by local fishing communities with support from their local government units and non-governmental organisations (Russ and Alcala 1999; White and Vogt 2000; Yambao et al. 2001; Alcala and Russ 2006; Alcala et al. 2008). For the most part, the placement of these reserves was not guided by an explicit networking strategy incorporating connectivity (McCook et al. 2009) but there was some consideration of placing reserves on good reef habitat (not necessarily prime fishing ground). The reserves vary in size (0.02 to 0.76 km^2), extent of reef habitat, duration of protection (DOP) and effectiveness of management by the local stakeholders (Table 5.1). Alcala et al. (2008) found that only 22 of the 39 reserves were functional in ca. 2008, i.e., protection was reasonably effective since the establishment of the reserve or after a certain point in

time. Ten were found to be non-functional, i.e., protection was ineffective or totally absent. Seven of the reserves were newly-established, i.e., DOP was ≤ 3 years. The two oldest (since initial establishment) and most studied of these reserves are situated at Sumilon and Apo islands, which were created in 1974 and 1982, respectively (Table 5.1; Russ 1985; Alcala 1988; White 1988; White and Vogt 2000; Alcala and Russ 2006; Russ and Alcala 2010).

5.2.3 Larval dispersal model

A Lagrangian (particle-tracking) model was developed to simulate dispersal of reef fish larvae for the entire Bohol Sea (Chapter 4). This model was used in the present study to examine potential larval exchange between reserves and fished areas that are found within the study area (Figure 5.1). A detailed description of the spatial domain, hydrodynamic forcing and larval behavioural parameters of the model are provided in Chapter 4. However, three key points about how the model was configured for the present study need to be mentioned. Firstly, it was assumed that reefs were uniformly distributed along the coastlines encompassed by the study area (Figure 5.1). Secondly, the reefs found along these coastlines were the only ones designated as sources of larvae (spawning areas) in the model. Thirdly, the size of each grid cell in the model was 2.2 x 2.2 km (4.8 km^2). This grid cell size is much larger than the individual size of any of the 39 reserves, which is a limitation of the model due to the very small size of the reserves (Table 5.1). A reserve may therefore share a grid cell with fished areas and other reserves. In all, there were 32 reef grid cells that contained reserves. Five of these had 2 or 3 neighbouring reserves.

5.2.4 Larval production from and recruitment to reserves and fished areas

The reefs in the model were treated as units of reef slope 0.4 km long, parallel to the coast, and 0.1 km wide, seaward. One unit of reef therefore had a virtual reef slope area of 0.04 km^2 or 40,000 m^2. It was then assumed that each reserve occupied only one unit of reef. The remaining units were fished areas. The resulting ratio between total reserve and fished area units was 1:17. This meant that only about 6% of the total hypothetical reef area in the model was occupied by reserves and 94% was open to fishing. The assumption that an individual reserve protected only 0.04 km^2 of reef can be justified for the majority (34 or 87%) of the 39 reserves, i.e., those reserves that are

Table 5.1 List of the 39 reserves situated on reefs within the study area. Types of habitat within reserves include coral reef (R), seagrass (S), mangrove (M) and soft or sandy bottoms (SB). Some reserves were re-established at least once. Years of re-establishment are enclosed in parentheses. Assessments of fish abundance (density or biomass), coral cover and management status were based on Alcala et al. (2008). The last column indicates the estimated larval production, i.e., equivalent to a fished area, 5, 10 or 20-year-old reserve; see Table 5.2 and Materials and methods).

Reserve, Island	Area (km^2)	Habitat	Year Established	DOP until ca. 2008	Fish Abundance	Coral Cover	Management Status	Equivalent larval production (DOP)
1. Sumilon Island	0.13	R	1974 (1987) (1995)	13	Medium	Fair	Functional since 1995	10
2. Apo Island	0.15	R	1982	26	Very high	Good	Functional	20
3. Tubod, Siquijor	0.09	R	1986 (2004)	4	High	Good	Functional since 2004	5
4. Tulapos, Siquijor	0.25	R, M, S	1987	21	High	Fair	Functional	20
5. Caticugan, Siquijor	0.14	R, SB	1989 (2003)	5	Low	Poor	Functional since 2003	5
6. Poblacion San Jose, Negros	0.05	R, S	1994	14	Low	Poor	Non-functional	= fished
7. Bonbonon, Negros	0.09	R	1995	13	Low	Fair	Non-functional	= fished
8. Andulay, Negros	0.06	R	1996	12	Medium	Fair	Functional	10
9. Tandayag, Negros	0.06	R	1996	12	High	Fair	Functional	10
10. Nonoc, Siquijor	0.04	R, SB	1996 (2003)	5	Low	Poor	Non-functional	= fished
11. Candaping B, Siquijor	0.24	R	1996 (2003)	5	Low	Fair	Functional since 2003	5
12. Cangmating, Negros	0.06	R	1997	11	Very low	Fair	Non-functional	= fished
13. Masaplod Norte, Negros	0.06	R, S	1997	11	Very high	Poor	Functional	10
14. Polo, Negros	0.02	R, M, S	1998	10	Low	Poor	Non-functional	= fished
15. Taculing/Cangma-lalag, Siquijor	0.13	R, M, S	1998 (2003)	5	Low	Poor	Non-functional	= fished
16. Agan-an, Negros	0.06	R, S	1999	9	Low (2002)	Fair	Functional	10
17. Bio-os, Negros	0.09	R	1999	9	Medium	Good	Functional	10
18. Buntis, Negros	0.06	R	2000	8	Low	Poor	Non-functional	= fished
19. North Lipayo, Negros	0.02	R	2000	8	Low	Good	Functional, but low biomass	5

Table 5.1 continued.

20. Maayong Tubig, Negros	0.07	R	2000	8	Medium	Poor	Functional	10
21. Poblacion 1, Negros	0.09	R, S	2000	8	High	Good	Functional	10
22. Salag, Negros	0.10	R	2001	7	Low	Poor	Non-functional	= fished
23. Banilad, Negros	0.76	R, S	2001	7	Medium	Poor	Functional	5
24. Masaplod Sur, Negros	0.06	R	2001	7	Very high	Poor	Functional	10
25. Pasil, Cebu	0.10	R	2002	6	Very high	Fair	Functional	5
26. Lutoban, Negros	0.10	R	2002	6	Low	Fair to Poor	Functional	5
27. Colase, Cebu	0.16	R	2002	6	High	Fair	Functional	5
28. Minalulan, Siquijor	0.12	R, SB	2003	5	Very low	Fair	Non-functional	= fished
29. Olang, Siquijor	0.21	R, M	2003	5	Low	Poor	Non-functional	= fished
30. Talayong, Siquijor	0.07	R	2003	5	Low	Good	Functional	5
31. Lalag Bato-Lower Cabangcalan, Siquijor	0.08	R, S	2003	5	Low	Poor	Functional	5
32. Sandugan, Siquijor	0.10	R, M, S, SB	2003	5	Medium	Poor	Functional	5
33. Bahura, Negros	0.04	R	2005	3	Low	Poor	Newly-established	= fished
34. Bulak, Negros	0.07	R	2005	3	*no data*	*no data*	Newly-established	= fished
35. South Lipayo, Negros	0.08	R	2005	3	Low (2005)	*no data*	Newly-established	= fished
36. Basak, Negros	0.08	R	2006	2	Medium	Fair	Newly-established	= fished
37. Banban-Luyang, Siquijor	0.05	R, S	2007	1	*no data*	*no data*	Newly-established	= fished
38. Bogo, Siquijor	0.21	R, M, S	2007	1	Medium	Fair	Newly-established	= fished
39. Paliton, Siquijor	0.07	R	2008	<1	Low	Fair to Poor	Newly-established	= fished

≤ 0.16 km^2 in area. This is because reef slope areas along most coastlines within the study area are usually narrow and the seaward boundary of reserves often extends beyond the reef slope.

Larval production from reserves and fished areas was estimated for a hypothetical gonochoristic species of large predatory reef fish, e.g. a snapper (Lutjanidae). The build-up of adult biomass of this model species inside reserves was assumed to be exponential during the first 20 years of reserve protection. This assumption is consistent with the pattern of increase of large predatory fish biomass inside Sumilon and Apo reserves in the central Philippines based on repeated, almost annual, measurements made on the reef slope of the two reserves over more than two decades (Russ and Alcala 1996, 2003, 2004; Russ et al. 2005; Russ and Alcala 2010). An intrinsic rate of increase in biomass of 0.20 year^{-1} was used, which is comparable to the rate measured at Sumilon reserve and inferred from 13 coastal reserves (as a group) in the central Philippines, but higher than that measured at Apo reserve (Russ et al. 2005). Adult biomass per unit area of the model species inside reserves before protection, or within one unit of fished area, was set at 0.30 kg 1000 m^{-2}. This value is comparable to the biomass per unit area of large predatory reef fishes on heavily fished coastal reefs (as opposed to small islands) and newly-established coastal reserves [< 1 yr duration of protection (DOP)] in the central Visayas region (Russ et al. 2005) and elsewhere in the Philippines (Nañola et al. 2002).

Total egg output per spawning (E) of the virtual snapper population in a reserve or a unit of fished area was given by:

$$E = \left[(A \cdot M)e^{rt}\right]b \qquad \text{(Equation 5.1);}$$

where A is the total reef area of the reserve or unit of fished area (i.e., 40,000 m^2); M is the number of female spawners per unit area derived from the adult biomass per unit area of a newly-established reserve or a fished area (see below); r is the intrinsic rate of increase of biomass (0.20 year^{-1}); t is the DOP in years (the DOP for a newly-established reserve or a fished area = 0); and b is the batch fecundity of a single female of the model species. To obtain M, the adult biomass value for a newly-established reserve or a fished area (i.e., 0.30 kg 1000 m^{-2}) was first multiplied by 0.5, assuming

that the male to female sex ratio of the model species was 1:1. The resulting value was then divided by 3 kg, which was the assumed average weight of an individual spawning female. The term *b* was given a value of 1 x 10^6 eggs per 3 kg female, which is within the range of the batch fecundity of *Lutjanus argentimaculatus* measured from individual females (specimens from the Philippines) ranging from 2.2-4.5 kg in weight (Emata 2003). Estimated total adult biomass, female biomass, *M* and *E* for one unit of fished area or a newly-established reserve and for reserves with different DOP are given in Table 5.2. Note that these estimates of *E* ignore any potential size-fecundity relationships in the hypothetical species (Evans et al. 2008; Taylor and McIlwain 2010), and thus may underestimate egg production in old reserves with bigger (> 3 kg) fish.

Virtual larvae were given a pelagic larval duration (PLD) of 30 days, similar to that of other *Lutjanus* spp. (e.g., Paris et al. 2005). A larval mortality rate of 0.25 day^{-1} was applied to values of *E* before running simulations. This level of larval mortality is within the range indicated by Houde (1989) for tropical fish larvae. Applying larval mortality resulted in lower effective larval output per unit of reserve or fished area during simulations, greatly reducing the computational load of the model (Table 5.2). As in the original model, virtual larvae were given swimming and sensory abilities that are governed by a fixed ontogenetic schedule (see Chapter 4 for behavioural parameters). A virtual larva is considered settled or recruited to a particular reef grid cell when it is located within that cell during the last 10% of its PLD (i.e., the last 3 days). The terms recruitment and settlement are used in this study interchangeably and simply mean addition of new individuals to a population. To measure recruitment to reserves and fished areas, the total recruitment to each reef grid cell was proportioned according to the percent of coastline in that cell occupied by reserve or fished area units (measured from digitised maps using ArcGIS).

5.2.5 Model simulations

Five cases of larval production from reefs were examined. The first case assumed that all reefs were open to fishing, i.e., reserves were absent. This case provided the hypothetical baseline levels of recruitment to fished areas to which all succeeding cases were compared. In the second, third and fourth cases, the DOP of the 39 reserves were uniformly set at 5, 10 and 20 years, respectively, corresponding to a 3-, 7- and 55-fold increase in larval production for each reserve (Table 5.2). Total

Table 5.2 Estimated total adult biomass, spawning female biomass, number of female spawners (*M*) and egg output (*E*) and effective larval output for one unit (i.e., 40,000 m^2) of fished area, a newly-established reserve and for reserves with different durations of protection (DOP).

	Newly-established reserve or 1 unit of fished area	Reserve DOP = 5 yr	Reserve DOP = 10 yr	Reserve DOP = 20 yr
Total adult biomass (kg 40 x 10^3 m^{-2})	12.0	32.6	88.7	655.2
Spawning female biomass (assuming sex ratio is 1:1)	6.0	16.3	44.3	327.6
M (assuming each spawner is about 3.0 kg on average)	2.0	5.4	14.7	109.2
E (assuming average batch fecundity of 1 x 10^6 eggs $spawning^{-1}$)	2 x 10^6	5.4 x 10^6	14.7 x 10^6	109.2 x 10^6
Effective larval output (assuming larval mortality rate of 0.25 day^{-1} for 30-day PLD)	1,106	3,007	8,174	60,395

(system-wide) larval production for each of these three cases was also 10, 36 and 300% higher, respectively, than the total larval production of the first case (no reserves).

In the fifth case, the potential contribution by the 39 reserves to recruitment in ca. 2008 was examined. For this case, a rough calibration of *E* from each reserve was made in accordance with the assessment of Alcala et al. (2008). Functional reserves were given values of *E* that were equivalent to that of reserves at 5, 10 or 20 yr DOP, whichever was deemed most appropriate for the reserve based on its history of management and estimated total fish abundance (Table 5.1). Non-functional and newly-established reserves were given an *E* value equivalent to that of a unit of fished area.

Simulations of larval dispersal were made for two monthly system-wide spawning events per year for three years (2006-2008), resulting in six temporal replicates of larval dispersal simulations for each of the five cases of larval production. Spawning was timed during the early and latter part of the southwest monsoon season, around the new moon (staggered over a four-day period) in June and September/October. The annual pattern of spawning that was built into the model was based on the broad spawning period of *L. argentimaculatus* in the Philippines which starts in March/May and lasts until November/December, with peaks around June and

October (Emata 2003). However, the annual pattern of spawning in other species of reef fish that are targeted by local fisheries in the Philippines may be very different from this pattern (Chapter 2).

5.2.6 Data analysis

Larvae that successfully settled to reefs within the study area were first classified into those that were: 1) spawned from reserves that recruited to reserves ($L_{r\to r}$); 2) spawned from reserves that recruited to fished areas, i.e., recruitment subsidy ($L_{r\to f}$); 3) spawned from fished areas that recruited to reserves ($L_{f\to r}$); and 4) spawned from fished areas that recruited to fished areas ($L_{f\to f}$). System-wide total recruitment to fished areas (R_f) was then given by the sum of $L_{r\to f}$ and $L_{f\to f}$. Average monthly values of R_f (n = 6 months over 3 years) were computed for each of the five cases of larval production and then compared. To examine any changes in the geographic extent of recruitment subsidy by reserves, values of $L_{r\to f}$ per grid cell per year were plotted on maps of the study area.

Net larval export or import by each reserve was determined by calculating the ratio of the total recruits successfully exported by the reserve ($L_{r\to r} + L_{r\to f}$) with the total recruits successfully imported into the reserve ($L_{r\to r} + L_{f\to r}$). Export-to-import ratios were log-transformed to highlight order of magnitude changes that resulted from varying larval production from reserves.

Probabilities of connectivity between, and self-recruitment within, reserves were estimated using a transition probability matrix where the reserves were represented both as 'sources' (on the y-axis) or 'sinks' (on the x-axis) for virtual larvae. Each element of the matrix was given by the expression:

$$P_{ij} = L_{i\to j} / S_i \qquad \text{(Equation 5.2)},$$

where P_{ij} is the probability of larvae from reserve *i* settling to reserve *j*, $L_{i\to j}$ is the number of larvae that originated in reserve *i* (on the y-axis) and settled in reserve *j* (on the x-axis), and S_i is the total number of larvae spawned from reserve *i*. Probabilities of self-recruitment are represented by the elements of the matrix where reserve *i* is the

same as reserve *j*. Dispersal probability matrices were constructed for each of the five cases of larval output using average probabilities of connectivity and self-recruitment calculated from n = 6 temporal replicates over 3 years.

5.3 Results

Simulations of the first four cases that assumed uniform larval production across reserves (i.e., equivalent to fished, 5, 10 or 20 years DOP) showed that, on average, 79-80% of the larvae originating from reefs within the study area failed to make it back to reef habitat after a PLD of 30 days (dead) or were carried away to the Sulu Sea (presumed dead). This was due to eddies that can retain larvae in the open sea and the strong westward current that exits the Bohol Sea. About 4-5% of the larvae recruited to reefs found within the model domain but outside of the study area. The remaining 15-17% of the larvae settled to the reefs within the study area. On the other hand, simulations for the fifth case, which approximated larval production from reserves in ca. 2008, indicated that only 4% of larvae settle to reefs within the study area. About 95% fail to settle or are advected to the Sulu Sea. The difference in the percent of larvae retained after 30 days between the four cases that assumed uniform larval production across reserves and the ca. 2008 case was due mainly to the location of older reserves in the latter case. Older reserves in the ca. 2008 case were situated in areas where larvae had greater chances of being advected out of the study region.

The monthly total recruitment to fished reefs within the entire study area was highly variable (Figure 5.2). The coefficients of variation (CV) of average monthly recruitment (n = 6 months) in the first four cases ranged from 59-79%, increasing with greater larval production from reserves. Recruitment to fished areas was always higher when reserves were present (Figure 5.2). Recruitment to fished areas increased, on average, by 5, 21 or 252% assuming that all 39 reserves were protected simultaneously for 5, 10 or 20 years, respectively. For these hypothetical scenarios, the reserves, on average, accounted for 12, 27 or 71% of the total recruitment to fished areas. Note that, on average, about 7% of the recruitment contributed by fished areas was replaced by the reserves (Figure 5.2).

Potential recruitment subsidy by reserves in ca. 2008 increased total recruitment to fished areas by 15%, on average, with reserves accounting for 21% of the recruitment (Figure 5.2). Mean recruitment had a CV of 67%. These results are most

Figure 5.2 Average recruitment to fished areas within the entire study area for five cases of larval production (see Table 5.2 and Materials and methods) from reserves and fished areas. Larval output from reserves with 5, 10, and 20 years duration of protection (DOP) are 3, 7 and 55 times greater per unit area than larval output from fished areas, newly-established reserves or non-functional reserves (see Table 5.2 and Materials and methods). Larval output in ca. 2008 was estimated using the management status of reserves according to Alcala et al. (2008) (see Table 5.1 and Materials and methods). Error bars are ± SD.

similar to the case where larval production of each marine reserve was equivalent to that of a 10-year-old reserve.

Greater larval production from reserves increased levels of recruitment to most reefs but resulted only in a very slight, almost negligible, expansion of the geographic extent of recruitment subsidy within the area considered (Figure 5.3). The geographic distribution of recruitment subsidy was highly variable in time and in space at different spatial scales. Recruitment subsidies were not higher in the fished areas closer to concentrations of reserves. Instead, there were areas (10's of km wide) that had a greater tendency to receive larvae, in particular the southern/south-western coast of Negros and Siquijor (Figure 5.3). Within identical periods, the spatial pattern of recruitment subsidy in terms of the relative magnitudes of recruitment from place to place did not differ considerably between different levels of larval production from reserves (Figure 5.3).

Net export of larvae by individual reserves was found to be more strongly influenced by the monthly variability of currents and the geographic location of the

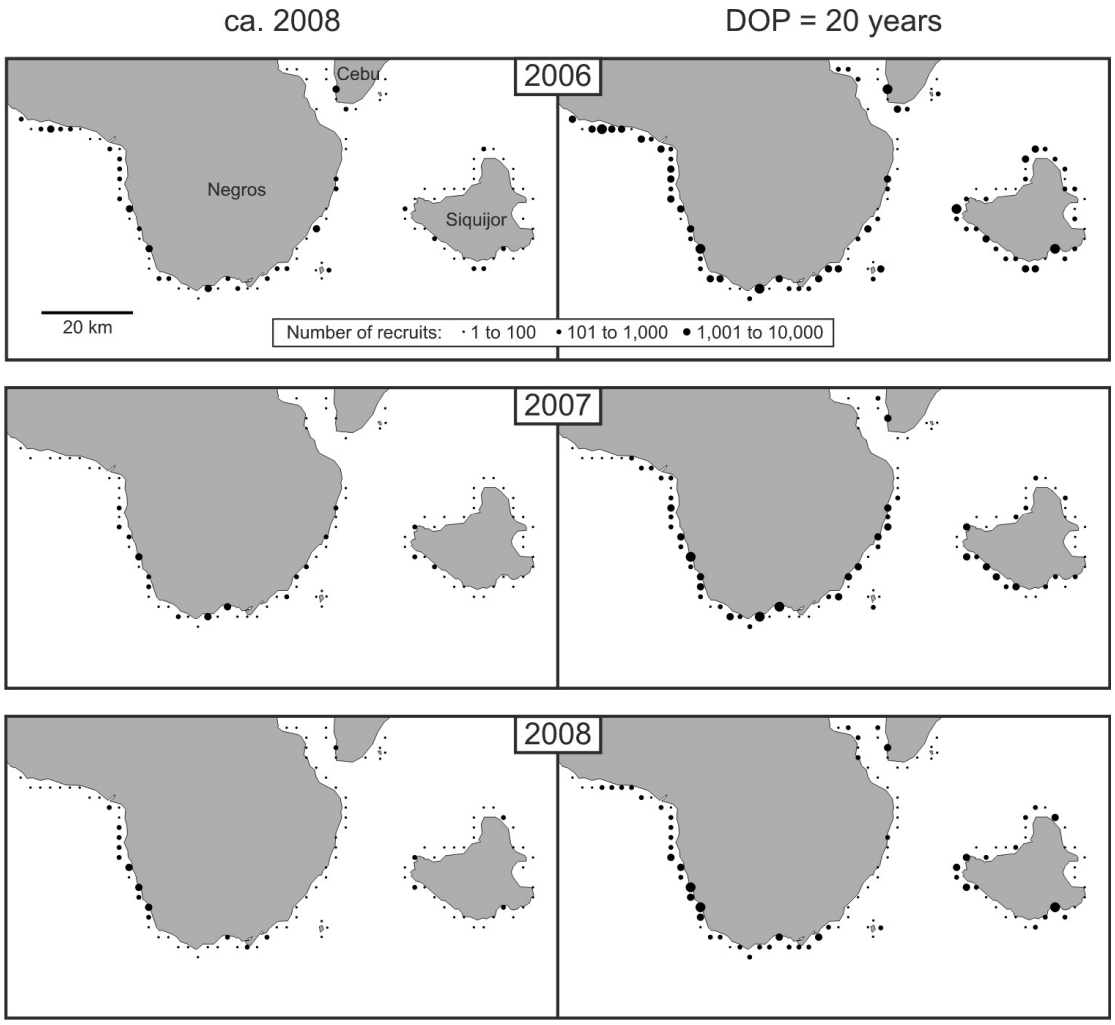


Figure 5.3 Spatial distribution of recruitment subsidy from reserves to fished areas. Results from two cases of larval production (lower – ca. 2008 vs. higher – 20 years duration of protection (DOP); see Table 5.2 and Materials and methods) are shown for contrast. Values plotted are the sum of two months of recruitment (June and September/October) for three years (2006, 2007 and 2008).

reserve rather than by larval production inside reserves (Figure 5.4). Most of the 39 reserves were more often net exporters than net importers of larvae, even when larval production was low (e.g., equivalent to that of a 5-year-old reserve) or equivalent to a fished area (Figure 5.4). Increasing larval production inevitably resulted in significantly higher export to import ratios, often up to about 2 orders of magnitude greater. However, a shift from being a net importer to a net exporter as a consequence of increased larval production occurred only in some reserves and only in relatively few instances.

The direction of larval dispersal between reserves was towards the south/south-west (Figure 5.5), which is consistent with the spatial pattern of recruitment subsidy (Figure 5.3) and the general current patterns in the study area (Figure 4.2). Probabilities of self-recruitment within reserves and connectivity between reserves were always very low regardless of the magnitude of larval production. Probabilities of self-recruitment were negligible (< 0.0001) or zero for the majority (~70%) of reserves. Probabilities of connectivity were typically < 0.001. The highest probability for any inter-reserve larval connection was just 0.03. However, the absolute magnitudes of connectivity between reserves (i.e., number of successfully recruiting larvae) increased dramatically with greater larval production (Figure 5.5). The total number of larvae that were exchanged between reserves increased by 160% (2.6-fold) when larval production was increased from 3- to 7-fold (5 to 10 year old reserves) and by 660% (7.6-fold) when larval production was increased from 7- to 55-fold (10 to 20 year old reserves). The increase in total number of larvae exchanged between reserves, when larval production was increased from 3- to 55-fold, was 1890% (19.9-fold). The average number of connections a reserve had with other reserves also increased with greater larval production (i.e., 47, 57 and 72% of the 31 possible inter-reserve connections at the grid cell level for the 3-, 7- and 55-fold larval production differentials, respectively) (Figure 5.5).

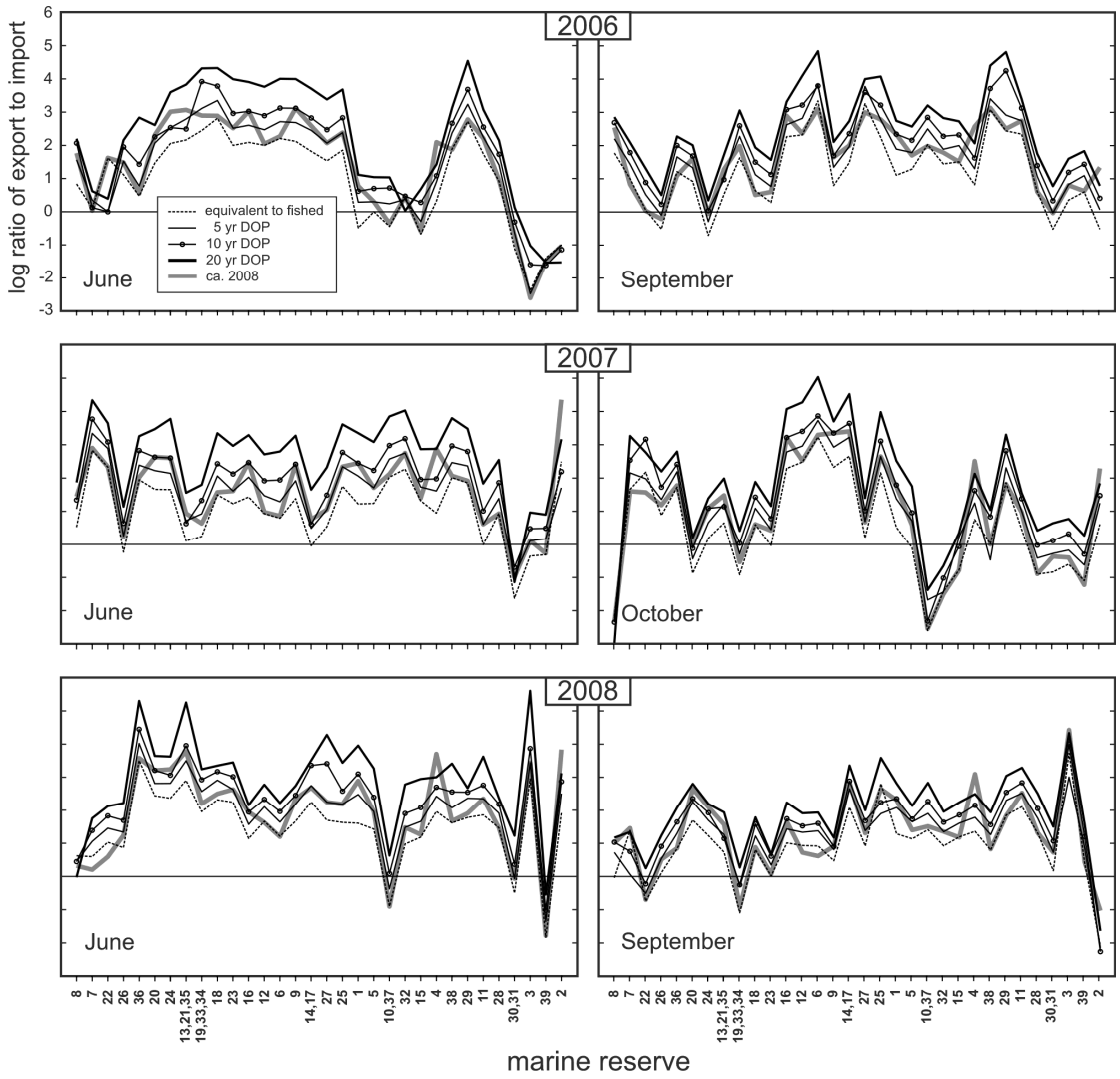


Figure 5.4 Monthly ratio of larval export to import (log-transformed) for each reserve. Results of simulations using different levels of larval production from reserves are distinguished from each other (see legend near upper left-hand side). Larval output from reserves with 5, 10, and 20 years duration of protection (DOP) are 3, 7 and 55 times greater per unit area than larval output from fished areas, newly-established reserves or non-functional reserves (refer to Table 5.2 and Materials and methods). Larval output in ca. 2008 was estimated using the management status of reserves according to Alcala et al. (2008) (see Table 5.1 and Materials and methods). The reserves on x-axis (numbered from 1-39) are ordered based on geography (refer Figures 5.1 and 5.5).

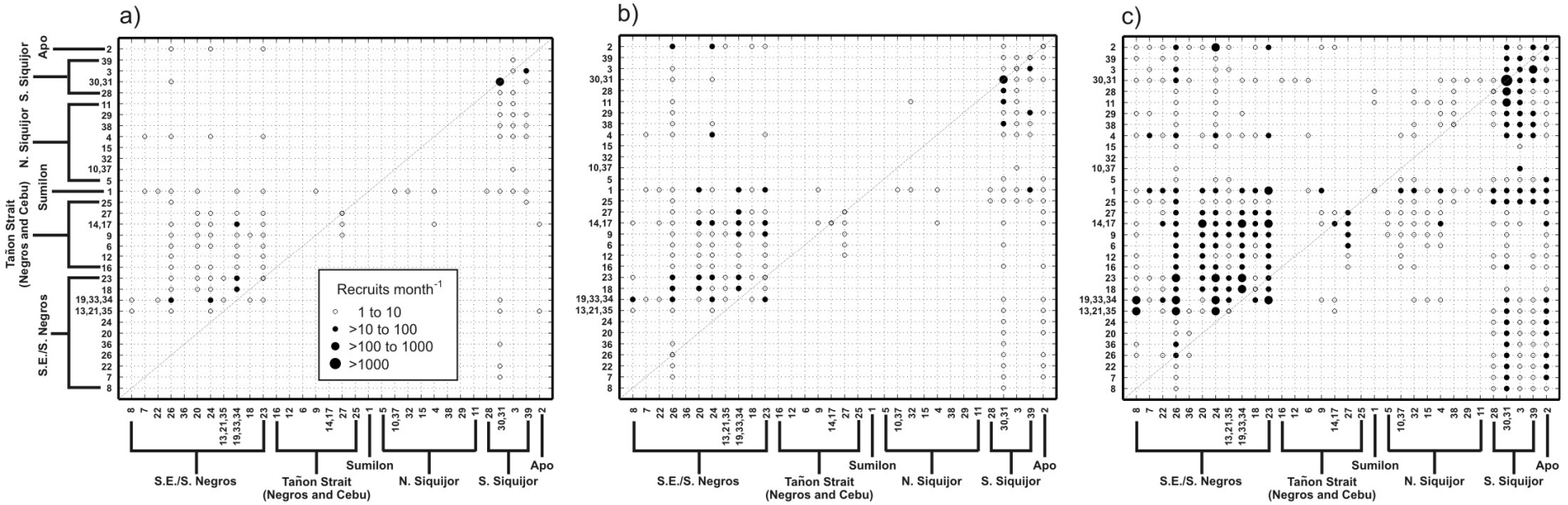


Figure 5.5 Matrices showing connectivity between reserves when reserves are uniformly protected for 5 years (a), 10 years (b) and 20 years (c). The 39 reserves where larvae were spawned in the larval dispersal model are represented by 32 reef grid cells in the model. Geographic locations are indicated on the x and y axes (refer to Figure 5.1). Self-recruitment to reserves is indicated along the dotted diagonal line. Connectivity in terms of a reserve exporting larvae to other reserves can be examined by reading each matrix from left to right parallel to the x-axis. Connectivity in terms of a reserve receiving larvae from other reserves can be discerned by reading each matrix from bottom to top parallel to the y-axis. Values plotted are the average number of recruits over n = 6 months over 3 years (refer to legend on the leftmost matrix).

5.4 Discussion

This study investigated the potential recruitment subsidy from and connectivity among small community-based reserves in the Philippines. The results showed considerable potential for such reserves to benefit surrounding reef fisheries at the predicted spatial scales of ecologically-significant larval connectivity, i.e., within 10's of kilometres (Cowen et al. 2006; Jones et al. 2009; Planes et al. 2009; Christie et al. 2010; Saenz-Agudel et al. 2011). However, large recruitment subsidies from these small reserves are to be expected only after most of them have been continuously and effectively protected for long periods (i.e., > 10 years), when substantial spawning biomass has accumulated inside reserves. The model predicted a ~250% (3.5-fold) increase in total recruitment to fished areas assuming that larval production inside all 39 reserves were to reach a level that is 55 times greater, per unit area, than fished areas after 20 years of protection. Such a huge larval production differential, and a considerable period of time to reach it, are likely for large predatory fishes (e.g., snappers and groupers) on Philippine reefs given the high rates of fishing mortality on these reefs, very low fish biomass on intensely fished reefs and the known rates of build up and attainable levels of biomass inside well-enforced reserves (McManus 1996, 1997; Russ and Alcala 1996, 2003, 2004, 2010; Nañola et al. 2002; Russ et al. 2005; Nañola et al. 2010).

Recruitment subsidies resulting from less significant larval production differentials may still benefit highly exploited fisheries. However, these smaller subsidies will be very difficult to detect in the field because of large temporal and spatial variations in recruitment (Russ 2002; Halpern et al. 2004; Pelc et al. 2010). For instance, the model predicted average increases in recruitment to fished areas of only 5 and 21% assuming 3- and 7-fold larval production differentials, respectively. These increases are much smaller than the CVs of average monthly recruitment, which ranged from about 60-80%. Of greater significance to present-day conditions, the estimated increase in recruitment to fished areas given the management status of reserves in ca. 2008 was only 15%. Any recruitment subsidies from reserves were therefore unlikely to have been noticed by fishers in the past two decades because of natural recruitment variation.

Field studies on patterns of recruitment in reef fishes (reviewed by Doherty 1991, 2002) provide additional insights on how challenging it would be to detect

recruitment subsidy to reef fisheries. For example, Abesamis and Russ (2010) monitored the recruitment of 120 species of commonly-occurring reef fishes for almost two years at 11 sites situated within the same geographic area as the present study (see Chapter 3). They found that the CV of average community-wide recruitment can range from 60-126% at the same site over time and from 67-167% during the same month across different sites. Their study indicated that, at the minimum, almost a tripling (200% increase) of average recruitment rates from before reserves were established, or close to what can be expected if all 39 reserves were protected for 20 years or their larval production was 55 times greater (per unit area) than fished areas, would be required before recruitment subsidy can be detected by field surveys or by fishers.

Recruitment subsidy may manifest as a gradient of decreasing larval settlement away from a reserve (Russ 2002; Beukers-Stewart et al. 2004, 2005; Sale et al 2005; Pelc et al. 2009, 2010). This predictable pattern may occur if the spatial scale of larval dispersal is not extremely long relative to the size of the reserve and directional currents play a major role in the advection of larvae (Pelc et al. 2010). In this study, directional currents (e.g., flow to the Sulu Sea) were present but decreasing gradients of recruitment away from individual reserves were not evident (Figure 5.3). This occurred for at least two reasons. Firstly, the sizes of the reserves are orders of magnitude smaller than the potential larval dispersal scale (over a 30-day PLD) of the modelled species. Secondly, the reserves are distributed over a wide area. Many occur within the potential dispersal kernel of other reserves. This would mask any gradient of recruitment within the vicinity of an individual reserve. However, there was some indication of directionality of recruitment subsidy at the scale of the entire study area (Figure 5.3). For instance, in all simulations, larval subsidies were often higher on the south/south-western coast of Negros (Figure 5.3), which was probably a consequence of the spatial distribution of the reserves (biased to the east), the directional current (towards the south/south-west) and mesoscale features (e.g., eddies) associated with this current. This finding underscores the importance of spatially-explicit models of larval dispersal in choosing sites where recruitment will be monitored in Before-After Control Impact Pair (BACIP) studies aimed at detecting recruitment subsidy (Russ 2002; Sale et al. 2005; Babcock et al. 2010; Pelc et al. 2010).

It is very likely that recruitment subsidy from small reserves will be enough to more than offset potential losses in yield resulting from reserve establishment that causes loss of fishing area. Assuming fishing grounds and larval settlement are both

uniformly distributed, the 6% of total fishing area lost to the 39 reserves would result in roughly the same loss in recruitment available to fishers, which translates to losses in future yield. The results suggested that this loss in recruitment can be replaced by a little more than a 3-fold increase in larval production in reserves (providing > 5% net gain in recruitment to fished areas), which can happen, for instance, a few years after all of the reserves have been simultaneously protected for 5 years. Clearly, longer-term protection (> 5 years) of all the reserves will be necessary to greatly exceed the compensation for initial losses in recruitment due to reserve protection. Another potential consequence of reserve establishment is the displacement of fishing effort ('fisheries squeeze') which will increase fishing mortality in fished areas and decrease catch per fisher. In a spatially-implicit theoretical model, Halpern et al. (2004) suggested that a 3-fold increase in larval production from reserves is enough to compensate for displaced fishing effort for up to 50% of fishing area lost to reserves. Using their approach, the required increase in larval production (or 'compensation factor') for the 6% of fishing area lost to reserves in this study will be just slightly higher than 2-fold.

Regarding optimal reserve placement, the results suggested that the majority of the reserves were situated in sites that would allow net export of larvae from reserves most of the time. Thus, it appears that in this particular case, the 'haphazard' or 'opportunistic' placement of reserves (see Alcala and Russ 2006) was unlikely to have been counterproductive in the sense that most reserves are probably not sinks for larvae. Haphazard placement of reserves will also not be entirely ineffective if some reserves are situated on good reef habitat, since better habitat will support higher biomass leading to greater larval production (Crowder et al. 2000). Assessing the effects of varying habitat quality on recruitment subsidy is beyond the scope of this study but the available data on the quality of habitat of the reserves in question indicates that most (~60%) of the reserves include reefs with 'fair' to 'good' coral cover (i.e., equivalent to 25 to 75% live coral cover) (Table 5.1, Alcala et al. 2008). Nonetheless, the simulations suggested that potential larval production is not the most critical factor that determines whether or not reserves will exhibit net export. Instead, local geography and hydrodynamic patterns are likely to have a stronger influence on where and when net export is more probable, regardless of the magnitude of larval output. These findings do not support the view that sources may be created simply by establishing reserves.

However, there is no question that the magnitude of larval export from reserves will be determined by larval production.

The model indicated that self-recruitment within most of the reserves was highly unlikely, which is not surprising because the spatial scale of larval dispersal was many times greater than the size of individual reserves. Although finer-scale models and field studies (e.g., Jones et al. 1999, 2005; Paris and Cowen 2004; Almany et al. 2007; Planes et al. 2009) are required to assess self-recruitment, this result suggested that the recovery of populations within the small reserves is likely to be greatly dependent upon recruitment of larvae coming from other populations, especially from other reserves. A good proportion of the reserves were found to be potentially connected by demographically-relevant larval exchange, which is consistent with the expectation of Weeks et al. (2010a) who analysed distances between existing reserves in the entire Philippines. The probabilities of larval exchange between individual reserves were very low, but even low numbers of successfully-recruiting larvae (relative to larval output) are probably important to sustain local populations (Planes et al. 2009). More significantly, results indicated that any increase in larval production within individual reserves will directly increase recruitment to other reserves that are potentially connected to them by larval dispersal, regardless of how small the probabilities of connectivity are (e.g., Steneck et al. 2009). This indicates that strict protection of individual reserves that interact via larval exchange will likely lead to synergistic effects that may increase the rate of recovery of populations within reserves, and consequently the rate of development of recruitment subsidy.

Substantial recruitment subsidy from networks of reserves will be important to sustaining fisheries because recruitment is clearly a major determinant of fisheries yield (e.g., Hjort 1914, 1926; Morgan et al. 1982; Phillips 1986; Caputi et al. 1995; Shanks and Roegner 2007). Recruitment subsidy becomes all the more important when the majority of spawning biomass is found inside reserves due to high fishing pressure in areas open to fishing. Such a ‘scorched earth’ situation was previously noted by Davis (1977) in lobster populations in Florida and by Pelc et al. (2009) in mussel populations in South Africa. The present study reflects a similar situation because the abundance of the hypothetical reef fish stock outside of reserves in the model approximated overfished levels typical of many Philippine reefs (Russ and Alcala 2002; Russ et al. 2005; Nañola et al. 2002). Recruitment subsidy will most likely be critical to reef fisheries in many parts of the world since overfishing affects the vast majority of reefs

worldwide (mostly in developing countries) (Bryant et al. 1998; Burke et al. 2002; Burke and Maidens 2004) and reserves are increasingly advocated as viable reef management tools (Roberts 2000; Russ 2002; Hughes et al. 2003; Sale et al. 2005; McCook et al. 2010). However, recruitment subsidy cannot sustain fisheries if management of nursery habitats for settling larvae and juveniles outside of reserves is neglected (Steneck et al. 2009).

This study is the first to evaluate potential recruitment subsidy to reef fisheries in the context of existing small, locally-managed reserves situated on heavily fished coral reefs. The findings emphasise two major factors that will determine whether or not and when meaningful larval benefits from reserves can be realised. Firstly, strict protection of existing reserves over the long-term (decades) is essential in order for reserves to significantly accumulate spawning biomass and increase larval production. Secondly, reserves must be established in sites with good quality habitat where protected populations will have a higher chance of attaining high biomass and exchanging larvae with other reserves. While the latter point implies that knowledge of source-sink dynamics is required, the establishment of new reserves cannot wait for perfect data on such dynamics given the first point. Most importantly, the findings of this study demonstrate the clear potential for networks of no-take marine reserves, protected effectively over decades, to contribute significantly to food security for human populations.

Chapter 6

General Discussion

6.1. Synthesis – the importance of the monsoons and local geographic setting to replenishment and connectivity of reef fish populations

A major point that was made at the beginning of this thesis was that we know very little about the patterns of reproduction, recruitment and population connectivity of reef fishes in the Coral Triangle compared to other places, such as the Great Barrier Reef and the Caribbean (Figure 1.2a). Yet, there seems to be tremendous interest to conserve and manage coral reefs and coral reef fisheries resources in the Coral Triangle through the use of networks of no-take marine reserves (e.g., Alcala and Russ 2006; Allen 2008; Clifton 2009; Green et al. 2009; Mills et al. 2010; see Figure 1.2b). A synthesis of the results of this thesis provides an indication of how the Asian monsoons and local geographic setting may affect patterns of reef fish population replenishment and connectivity in the Coral Triangle and how we can assess if existing or future reserve networks can achieve their conservation and fisheries management goals within this important region.

It has long been recognised that the annual patterns of reproduction and recruitment of reef fishes closer to the equator are less seasonal compared to those at higher latitudes. The results of Chapter 2 and 3 of this thesis confirmed this well-known pattern. What has received less attention in the past is the potential for the monsoons to influence the annual patterns of reef fish population replenishment in equatorial regions, including the Coral Triangle (Johannes 1978; Pauly and Navaluna 1983). The results of Chapter 2 suggest that the monsoons will probably affect the timing of reproduction of many species of reef fish differently. Reproduction in different species may show various responses to more localised changes in the environment caused by the monsoons, such as degree of wave action depending on exposure to winds, proximity to localised monsoon-induced upwelling events or regional patterns of rainfall. For the same species, potential monsoonal effects on reproduction may also differ geographically because rainfall and wind patterns vary with longitude and latitude within the Coral Triangle (Wang et al. 2001; Wahl and Morrill 2010).

On the other hand, the potential effects of the monsoons on recruitment patterns seemed more predictable. Chapter 3 and the only other study in the Coral Triangle that compared reef fish recruitment data against environmental data (i.e., Srinivasan and Jones 2006) showed that rainfall and wind strength (the latter causing turbulence or advection at the sea surface) are two monsoonal factors that can negatively affect larval survival and recruitment of many species. However, the effects of these two factors probably also vary geographically within the Coral Triangle and between some taxonomic groups. For instance, as discussed in Chapter 3, heavy rainfall at Kimbe Bay, Papua New Guinea was detrimental to recruitment of damselfishes but not to recruitment of wrasses (Srinivasan and Jones 2006). In contrast, lower rainfall levels did not have a noticeable effect on the recruitment of either damselfishes or wrasses in the central Philippines (Chapter 3). As for the effects of wind, different wind exposures in many archipelagic areas of the Coral Triangle may result in temporal patterns of recruitment that vary between regions at the scale of 100's of km encompassing many islands because of different directions of prevailing monsoon winds (e.g., north-east/south-west in the Philippines; north-west/south-east in Papua New Guinea and Indonesia). Variable temporal patterns of recruitment may also occur at more limited spatial scales within these regions, such as amongst smaller islands and locations within larger islands.

It is still difficult to predict the annual patterns of population replenishment of various species of reef fishes at different places within the Coral Triangle. What has become clearer in this thesis is that the degree of monsoonal effects at a particular place can influence the timing and shape of replenishment peaks within the year. Several characteristic annual patterns of reef fish replenishment may be present within the Coral Triangle. These characteristic annual patterns of replenishment may also dictate the strength of density-dependent post-settlement processes (e.g., competition, predation and mortality) at different times of the year, potentially affecting the structure of local reef fish populations. The importance of the monsoons in influencing patterns of replenishment in reef fishes can be further tested by comparing sites that differ in their exposures to monsoon winds or have different rainfall patterns. With regards to the potential effects of wind stress on larval survival, data from sites that are not exposed to monsoon winds (e.g., bays that are surrounded by high mountains) may provide valuable insights.

Patterns of dispersal of reef fish larvae in the Coral Triangle may also vary considerably according to the monsoons, depending on how winds affect ocean circulation patterns (reviewed by Cowen 2002). For instance, McManus (1994) showed that potential large-scale (100's of km) trajectories of larval transport from spawning populations on reefs in the South China Sea (Spratly Islands) can vary significantly within a year because the monsoons have a strong influence on the surface current patterns of that region. However, dramatic changes in potential patterns of larval connectivity between local populations caused by the monsoons were not so evident in Chapter 4 because of the hydrodynamic characteristics of the Bohol Sea, particularly the persistent unidirectional (westward) current that passes within the vicinity of the sites that were studied. Nonetheless, potential patterns of larval connectivity between other local populations also situated within the Bohol Sea may be influenced strongly by mesoscale (10's of km), monsoon-induced, changes in surface current patterns (Ablan 2005, 2006). These preceding examples, that suggest different patterns of larval dispersal between two areas (South China Sea vs. Bohol Sea) and within the same area (Bohol Sea), emphasise how the local oceanographic setting can greatly influence potential patterns of larval connectivity. The development of high-resolution (< 10 km) models of monthly sea surface circulation patterns at the relevant spatial scales (10's to 100's of km) and the validation of these models with empirical data (e.g., oceanographic surveys, drifter tracking data, etc.) should therefore be given some priority. Such models probably do not yet exist for many parts of the Coral Triangle. On the other hand, there are no studies available to date that demonstrate any relationship between monsoon winds and smaller-scale (within 10's of km) circulation patterns that may promote retention of reef fish larvae near their natal populations. Present evidence suggests that wind is probably more important for transport mechanisms that promote successful settlement of late-stage larvae and not necessarily for retention mechanisms that may be crucial during earlier stages of larval development (Cowen 2002). Some of the important physical mechanisms that could promote larval retention occur 10's of m below the surface (e.g., onshore flow), which swimming larvae can take advantage of through vertical migration in order to avoid offshore flow due to prevailing winds (Cowen et al. 2000; Paris and Cowen 2004).

Finally, the approach that was taken in Chapter 5 provides an indication of what may be required to determine if new or existing reserve networks have the potential to achieve their conservation and fisheries management objectives for targeted reef fish

species in some of the most heavily exploited regions of the Coral Triangle. Firstly, models of reef fish larval dispersal that incorporate the best data available on local oceanographic patterns and larval biology (swimming and sensory behaviour, larval mortality) must be developed. Secondly, these models should take into account any major variations in current patterns caused by the monsoons. Thirdly, estimates of the present population density, biomass and size structure of the target species inside reserves, or proposed reserves, and outside reserves must be obtained through field surveys. Fourthly, models of population recovery of the targeted species in response to reserve protection must be coupled to the larval dispersal model. These models of population recovery can be based on time-series data obtained from one reserve over the long-term (decades) with the appropriate control sites (fished areas) (e.g., Russ and Alcala 2010). Alternatively, these models can be based on comparisons of many reserves that have habitats that are as similar as possible but with different durations of protection (spanning decades) against appropriate control sites (McClanahan and Graham 2005; Russ et al. 2005; McClanahan et al. 2007; Stockwell et al. 2009). Fifthly, basic information on the life histories of the targeted species must be obtained in the field and incorporated into the larval dispersal and population recovery models. This includes size and age at sexual maturity inside and outside reserves (e.g., Taylor and McIlwain 2010), body size and batch fecundity relationships, spawning frequency and spawning output per unit area, the best temporal 'windows' for spawning and recruitment which are likely to be related to the monsoons (Chapter 2 and 3), spatial patterns of spawning (if the species undergoes spawning migrations) and distribution of settlement habitats for larvae or nursery habitats for juveniles. The collection of basic life history data on key groups of targeted reef fish species (groupers, snappers, emperors, parrotfishes and surgeonfishes) is extremely important and should be given a high priority. For instance, a major limitation of the model that was used in Chapter 5 is the lack of detailed information on the spatial distribution of critical settlement and juvenile habitats for the model species (i.e., snappers, which may use non-reef settlement or nursery habitats). Better information on the distribution of these habitats will probably affect the conclusions about the spatial patterns of recruitment subsidy and inter-reserve connectivity to some extent.

6.2 Climate change and the influence of the monsoons on reef fish population dynamics

The preceding section discussed the potential of the monsoons to profoundly affect the patterns of replenishment and population connectivity of reef fishes in the Coral Triangle. The variability of the Asian monsoons is somehow linked to the El Niño-Southern Oscillation (ENSO) (Webster 1995; Hu et al. 2000; Cook et al. 2010). Models of climate change also suggest that the frequency of warm ENSO events (El Niño), which are sometimes followed by cold ENSO events (La Niña), is expected to increase for many years into the future if 'greenhouse' gas concentrations in the atmosphere continue to increase (e.g., Trenberth and Hoar 1997; Timmerman et al. 1999; Hu et al. 2000). Thus, how climate change may affect the dynamics of reef fish populations in the Coral Triangle is of considerable significance. Although the dynamic processes that govern the spatial and temporal variability of the Asian monsoons and their complex relationships with the ENSO are still not well-understood (Webster and Palmer 1997; Wu and Chan 2005; Wahl and Morrill 2010), some possible consequences of climate change for the monsoons and, in turn, the dynamics of reef fish populations are worth exploring.

Weaker summer monsoon winds in some areas of the Coral Triangle (e.g., south-west monsoon in the Philippines) are associated with El Niño decaying years (Chou et al. 2003). El Niño is also usually characterised by decreased rainfall levels in the western Pacific, including the Coral Triangle (e.g., Philippines and Indonesia), leading to severe drought (Webster and Palmer 1997). Weaker winds may be favourable to the survival of larvae in the pelagic environment (Chapter 3) while decreased rainfall probably has no effect on larval survival or recruitment (Srinivasan and Jones 2006). Thus, higher levels of recruitment may be expected for many species during El Niño decaying years. However, weaker winds and higher sea surface temperatures associated with the El Niño usually result in widespread coral bleaching in many areas of the Coral Triangle (Brown and Suharsono 1990; Arceo et al. 2001; Raymundo and Maypa 2002; Jones et al. 2004). Mass mortality of corals due to bleaching may work against potential gains in recruitment for species that are dependent on live corals as habitat for new settlers and juveniles (Booth and Berretta 2002; Bonin et al. 2009). Moreover, the loss of live coral habitats can impair the recruitment of many reef fish species over many years (e.g., Jones et al. 2004; Garpe et

al. 2006; Wilson et al. 2006; Graham et al. 2007). On the other hand, the La Niña is usually characterised by higher annual rates of rainfall in the western Pacific, including the Coral Triangle region (Webster and Palmer 1997). In places where rainfall becomes exceptionally heavy during the La Niña, the recruitment of some species (e.g., damselfishes) could be negatively affected (Srinivasan and Jones 2006).

Any alterations of ocean circulation patterns as a result of climate change may also have direct consequences for patterns of larval dispersal and connectivity between local populations of reef fishes. As mentioned above, the summer monsoon winds in some areas of the Coral Triangle may weaken during the El Niño, potentially altering large-scale hydrodynamic patterns and thus the patterns of reef fish population connectivity. With regards to how climate change can influence other oceanographic processes that may be important to reef fish reproduction and larval survival, at least one study within the Coral Triangle has shown that increased precipitation during the La Niña can suppress monsoon-driven upwelling in a coastal area (Villanoy et al. 2011). Failure of upwelling events in the vicinity of reefs may have implications for reproduction of reef fishes that are 'cuing-in' to upwelling signals (McIlwain et al. 2006) or to the survival of reef fish larvae at first-feeding.

No studies to date have examined how potential relationships between the monsoons and the ENSO may influence patterns of reef fish replenishment or connectivity. In fact, recent reviews of the potential effects of climate change on individual performance, population or community dynamics of reef fishes (e.g., Wilson et al. 2006; Munday et al. 2008) had little to say about the possible consequences of alterations in environmental factors that characterise the monsoons (i.e., wind and rainfall). The effects of climate change on the monsoons and their potential implications for the dynamics and management of reef fish populations in the Coral Triangle should be given more attention in future studies.

6.3 Reserve network goals and the future of *ad hoc* reserve networks in the Philippines

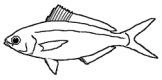
The results of Chapter 5 suggest that even no-take reserves that were established with very little consideration of optimum size, spacing and placement can still provide some of the most important larval benefits that are expected from marine reserve networks. The Philippine reserves that were studied clearly had the potential to

significantly subsidise recruitment to fished areas within their vicinity (within 10's of km) and to interact with each other through larval exchange. This is an important positive message because the *ad hoc* establishment of hundreds of small marine reserves in that country has evidently fallen short of achieving conservation targets, such as sufficient reserve coverage of critical habitats and biodiversity representation (Weeks et al. 2010a). The establishment of larger reserves that protect more substantial areas of critical marine habitats and the consideration of larval connectivity between these reserves should still be strongly encouraged (Weeks et al. 2010a, b). Furthermore, if systematic conservation planning is undertaken to design new or improve existing reserve networks, then incorporating reliable information on patterns of larval connectivity for a range of important species should be given priority. However, the results of Chapter 5 indicate that the effective and continuous protection of reserves from any form of extractive or destructive activity is the most crucial factor that will determine the success of reserve networks. No reserve network will be effective without the long-term support from local stakeholders. If considerable fisheries enhancement is the main expectation from protecting reserves, then local stakeholders must be convinced that reserves will eventually provide substantial recruitment benefits. Also note that some local spillover and tourism benefits from reserves may also help convince stakeholders to continue reserve protection indefinitely (e.g. Abesamis et al 2006a, Alcala and Russ 2006). Most importantly, local stakeholders also must eventually 'feel' these benefits.

There are at least two potential ways in which scientists can help convince local stakeholders to protect reserves over the long-term. First is to plan and assist in the implementation of a before-after-control-impact (BACIP) type experiment (Russ 2002; Sale et al. 2005; Babcock et al. 2010; Pelc et al. 2010) to test recruitment subsidy from reserves. This must involve the participation of local fishing communities. Predictions on the locations of 'control' sites (reefs that are not likely to receive larval subsidies from reserves) and 'impact' sites (reefs that are likely to receive larval subsidies from reserves) can come from more sophisticated models of population recovery of the chosen target species inside reserves, potential larval output from reserves and fished populations, and spatial and temporal estimates of larval connectivity (discussed in Section 6.1). Measurements of recruitment subsidy can be done through monitoring of catch-per-unit effort of fishers at control and impact sites that are open to fishing (standardised across sites according to fisher population) and visual surveys of

recruitment at the appropriate habitats within the same sites, as well as inside reserves that are 'impacted' by larval subsidies. Note that the choice of target reef fish species will be critical to this experiment. The most appropriate species for the experiment are probably those that: 1) are highly important to local fisheries; 2) are relatively short-lived and fast-growing; 3) have relatively fast rates of population recovery in response to reserve protection; and 4) have recruits that are relatively easy to monitor. Species that are very important to local fisheries and are quicker to develop net larval export from reserves may help convince local stakeholders within shorter periods. In the context of reef fisheries and recovery of target species inside reserves in the Philippines, parrotfishes (Scaridae) are probably some of the best species to use for such an experiment (Stockwell et al. 2009; Chapter 3 and Abesamis and Russ 2010).

The second manner by which scientists can help convince local stakeholders to support the long-term protection of reserves is by empirically validating the presence of larval connections from reserves to fished areas and from reserves to other reserves. Larval connectivity between two places can be convincingly demonstrated through parentage analysis using multiple microsatellite DNA markers, which can be done in combination with larval mark-recapture experiments via chemical tagging of larval otoliths (e.g., Jones et al. 2005; Almany et al. 2007; Planes et al. 2009; Williamson et al. 2009; Christie et al. 2010; Saenz-Agudelo et al. 2011). For instance, validation experiments can be performed between sites that are suspected to be strongly connected by larval dispersal based on the findings of Chapter 4 and 5. Validation studies can also be designed to complement the BACIP fisheries experiment described above. Needless to say, it is crucial that the basic principles behind sophisticated methods of predicting and validating reef fish larval connectivity are explained to local stakeholders using concepts that they can easily grasp. The same undoubtedly applies to the results of the BACIP and validation studies. Stakeholders who are sufficiently informed about how their reef fishery resources function can mean the difference between failure and success of reserve networks.



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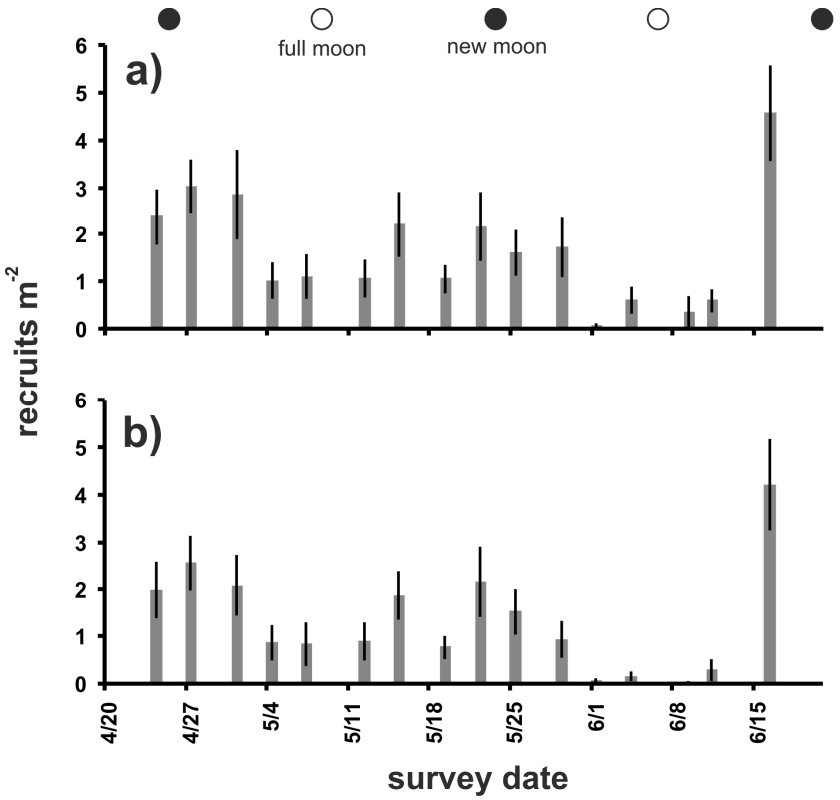
Appendices



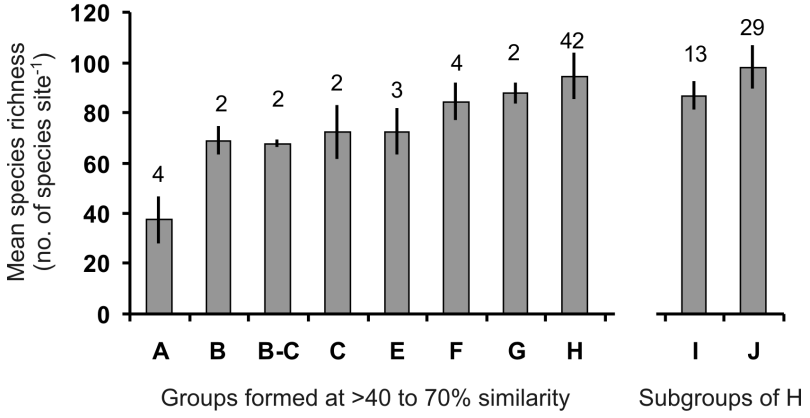
Appendix 3.1 Lunar patterns of settlement of juvenile reef fishes measured at one site (Dauin- see Figure 3.1). Data presented for recruits of all species that were encountered (a) and for *Pomacentrus moluccensis* only (b), which dominated recruit counts. Sampling units were15 individually-marked branching coral colonies (*Acropora* spp.). Colony sizes ranged from 0.3 to 10.5 m^2. Newly-settled recruits were monitored every 2-3 days over 2 lunar cycles. Error bars are ± SE.

Appendix 3.2 Summary of recruitment patterns of the most abundant species (i.e. cumulative abundance of ≥ 50 recruits recorded from all sites). The data used for each species were obtained only from the site/s and depth/s where that particular species was most abundant. Site/depth code: A = northeast Sumilon, 3-4 m; B = northeast Sumilon, 10-12 m; C = southwest Sumilon, 3-4 m; D = southwest Sumilon, 10-12 m; E = southeastern Apo, 3-4 m; F = southeastern Apo, 10-12 m; G = southwest Apo, 3-4 m; H = southwest Apo, 10-12 m; I = Dauin, 3-4 m; J = Dauin, 8-12 m; K = Dumaguete, 3-4 m. ATA is the adjusted total abundance in one year (see Materials and methods of Chapter 3). Average density was expressed as recruits 100 m^{-2}. Length of the recruitment period of each species was estimated using two thresholds: ≥ 1 % and ≥ 5 % of ATA. Months when % ATA was ≥ 1 % but < 5% are marked by +. Months when % ATA was ≥ 5 % are marked by ±. Peak months are denoted by the % of ATA they contributed. Major peaks are underscored to distinguish them from minor peaks. NE = northeast monsoon; SW = monsoon; INT = inter-monsoon. *Identification of recruits of the Apogonidae to the species level was difficult hence data for several species (probably 3-4) were pooled.

					Length of recruitment period (months)		Season/Months												
							NE			INT			SW			INT	NE		Total % ATA of peak months
Family/Species	Rank	Sites	ATA	Average density	≥ 5%	≥ 1%	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
I. Serranidae, subfamily Anthiinae (anthiases)																			
Pseudanthias huchti	7	D	1020	30.0 ± 5.0	5	11		+	+	+	±	+	25.3	±	+	19.4	+	15.6	60.3
Pseudanthias tuka	3	D	1595	48.3 ± 8.7	6	10		+		±	±	+	30.7	±	±	17.4	+	15.4	63.4
II. Apogonidae* (cardinalfishes)																			
Apogon spp./Cheilodipterus spp.	6	D	992	6.1 ± 3.7	4	7			+		±	+	51.0	+	±	26.2			77.3
III. Chaetodontidae (butterflyfishes)																			
Chaetodon baronessa	27	I	70	0.9 ± 0.2	6	12	±	+	+	+	+	+	+	±	18.7	15.8	17.3	18.7	70.5
IV. Pomacentridae (damselfishes)																			
Amblyglyphidodon curacao	13	C,E,G	515	5.4 ± 0.9	8	11		+	+	15.8	±	±	14.8	+	±	20.2	±	±	50.8
Amblyglyphidodon leucogaster	8	D,F,H	931	9.8 ± 1.2	9	11		±	±	13.9	±	+	14.2	±	±	13.6	±	+	41.8
Chromis amboinensis	14	D,J	442	3.7 ± 1.1	3	5							±	±	+	75.2		+	75.2
Chromis retrofasciata	5	D	1215	33.3 ± 7.3	5	8		+			+		19.3	17.9	±	39.3	±	+	76.5
Chromis ternatensis	2	D	1777	51.2 ± 8.6	7	10			+	±	±	+	±	17.5	±	32.0	±	+	49.5
Chromis viridis	4	D,I	1615	17.2 ± 2.9	9	11		±	+	±	+	±	16.3	±	±	23.2	±	±	39.6
Chrysiptera rollandi	24	J	90	1.4 ± 0.3	6	11	±		+	±	+	+	±	±	+	45.6	+	±	45.6
Chrysiptera springeri	15	J	257	4.1 ± 1.5	7	9	±		+			+	±	20.3	±	31.2	±	±	51.5
Chrysiptera talboti	23	J	97	1.5 ± 0.3	5	11	+	+		+	+	±	±	±	+	43.5	±	+	43.5
Dascyllus aruanus	28	K	54	1.5 ± 0.3	7	9	+			+	±		±	26.2	±	29.9	±	±	56.1
Dascyllus reticulatus	16	J	264	4.0 ± 1.4	5	10	+	±			+	+	+	17.6	+	24.3	21.3	±	63.2

Appendix 3.2 continued.

Dascyllus trimaculatus	25	A,B,D	74	0.7 ± 0.2	3	6				+			+	21.1	±	54.4	+		75.5
Neoglyphidodon thoracotaeniatus	35	J	21	0.4 ± 0.1	6	6				14.6		22.0	36.6	±	±	±			73.2
Neopomacentrus anabatoides	10	I	572	11.6 ± 3.8	4	6						±	52.5	±	+	17.7		+	70.2
Neopomacentrus azysron	12	I	541	10.6 ± 3.6	4	6	+					28.2	33.5	±		23.7		+	85.4
Pomacentrus adelus	21	I, K	88	1.2 ± 0.3	3	9	+			+	+	±	53.7	±	+	+		+	53.7
Pomacentrus alexanderae	17	J	181	3.1 ± 0.6	7	9	+			±		±	22.1	±	±	33.7	±	+	55.8
Pomacentrus amboinensis	20	B	104	3.4 ± 0.5	10	10			±	±	±	±	18.8	±	24.2	±	±	±	43.0
Pomacentrus brachialis	11	D,J	532	6.7 ± 0.8	6	11	+	+		15.1	+	±	37.8	±	±	±	+	+	52.9
Pomacentrus coelistis	30	A	45	1.3 ± 0.4	6	8		26.7	±	+	±	27.8	+	±		17.8			72.2
Pomacentrus lepidogenys	19	I, K	93	1.3 ± 0.3	5	7				±	±	±	59.1	±	+	+			59.1
Pomacentrus moluccensis	1	I, K	2563	31.1 ± 4.4	7	11	+	+		+	±	±	35.4	±	±	14.7	+	±	50.2
Pomacentrus smithii	33	J	31	0.7 ± 0.4	3	4						+	80.3	±	±				80.3
V. Labridae (wrasses)																			
Cirrhilabrus cyanopleura	18	D,F	119	1.9 ± 0.3	8	10			+	+	18.5	24.8	±	±	±	±	±	±	43.3
Halichoeres podostigma	37	A,C	19	0.3 ± 0.1	6	9			+	18.4	±	+	±	±	+	21.1		21.1	60.5
Labrichthys unilineatus	29	I, K	44	0.5 ± 0.1	5	8		+				+	22.7	29.5	±	±	18.2	+	70.5
Labroides dimidiatus	32	F,I,J	35	0.3 ± 0.04	9	9			15.9	±	±	±	18.8	±	±	11.6	±		46.4
Thalassoma hardwicke	22	I, K	98	1.1 ± 0.1	7	11	+		+	±	±	±	20.9	±	±	35.7	+	+	56.6
Thalassoma lunare	9	A,D,I,K	694	4.8 ± 0.5	6	9				+	±	±	19.0	21.3	±	18.7	+	+	59.1
VI. Scaridae (parrotfishes)																			
Chlorurus sordidus	26	E,K	50	0.9 ± 0.3	5	8			+		30.0	+	±	29.0	±	14.0		+	73.0
Scarus dimidiatus	34	E,G	34	0.6 ± 0.2	8	9			±	14.7	14.7	±	±	20.6		+	±	±	50.0
Scarus niger	31	E,G	44	0.6 ± 0.1	6	10		±		+	13.6	±	±	15.9	+	36.4	+	+	65.9
VII. Acanthuridae (surgeonfishes)																			
Ctenochaetus binotatus	36	E,G,J	26	0.2 ± 0.04	6	10	±	23.5	±	±	+	+	+		±		+	19.6	43.1



Appendix 4.1 Average species richness of each group of sites formed at increasing levels of species assemblage similarity (> 40-70%). The average species richness values of the two subgroups (I and J) of the main group in the Bohol Sea (H) are also shown. Numbers above bars indicate the number of sites within each group. Error bars are ± SD.

Appendix 4.2 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group A vs. group H (see Materials and methods of Chapter 4). The average presence/absence of each species in groups A and H, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group A	Group H	Diss.	% Cont.	Cum. %
1	*Centropyge vroliki*	0	1	0.76	1.29	1.29
2	*Chaetodon lunulatus*	0	1	0.76	1.29	2.59
3	*Pomacentrus vaiuli*	0	1	0.76	1.29	3.88
4	*Halichoeres podostigma*	0	0.98	0.74	1.26	5.15
5	*Pygoplites diacanthus*	0	0.98	0.74	1.26	6.41
6	*Thalassoma hardwicke*	0	0.98	0.74	1.26	7.67
7	*Amblyglyphidodon aureus*	0	0.98	0.74	1.26	8.93
8	*Bodianus diana*	0	0.95	0.72	1.24	10.16
9	*Chromis amboinensis*	0	0.95	0.72	1.24	11.4
10	*Abudefduf vaigiensis*	0	0.95	0.72	1.23	12.63
11	*Chromis margaritifer*	0	0.93	0.7	1.2	13.83
12	*Hemigymnus fasciatus*	0	0.93	0.7	1.2	15.03
13	*Pseudocheilinus hexataenia*	0	0.93	0.7	1.2	16.23
14	*Pomacentrus lepidogenys*	0	0.93	0.7	1.2	17.43
15	*Amphiprion ocellaris*	0	0.86	0.65	1.12	18.54
16	*Halichoeres prosopeion*	0	0.86	0.65	1.12	19.66
17	*Hemigymnus melapterus*	0	0.83	0.63	1.07	20.73
18	*Chaetodon vagabundus*	0	0.83	0.62	1.06	21.79
19	*Coris gaimard*	0	0.81	0.61	1.04	22.84
20	*Halichoeres biocellatus*	0	0.79	0.6	1.02	23.85
21	*Macropharyngodon meleagris*	0	0.76	0.59	1	24.85
22	*Centropyge tibicen*	0.25	1	0.58	0.99	25.84
23	*Chaetodon kleini*	0.25	1	0.58	0.99	26.83
24	*Chromis ternatensis*	0.25	1	0.58	0.99	27.82
25	*Heniochus varius*	0.25	1	0.58	0.99	28.81
26	*Pomacentrus cuneatus*	0.75	0	0.58	0.99	29.8
27	*Gomphosus varius*	0	0.76	0.57	0.98	30.78
28	*Labrichthys unilineatus*	0.25	0.98	0.57	0.97	31.76
29	*Chelmon rostratus*	0.75	0.02	0.54	0.93	32.68
30	*Chromis analis*	0	0.71	0.54	0.92	33.6
31	*Plectroglyphidodon lacrymatus*	0.25	0.9	0.54	0.92	34.52
32	*Cheilinus trilobatus*	0	0.71	0.54	0.92	35.44
33	*Chromis atripectoralis*	0	0.71	0.53	0.91	36.35
34	*Amphiprion perideraion*	0.25	0.83	0.51	0.88	37.23
35	*Centropyge nox*	0.25	0.83	0.51	0.87	38.09
36	*Chaetodon octofasciatus*	1	0.33	0.5	0.86	38.95
37	*Pomacentrus adelus*	0	0.67	0.5	0.85	39.81
38	*Chaetodon rafflesi*	0	0.67	0.5	0.85	40.66
39	*Pomacentrus opisthostigma*	0.25	0.79	0.49	0.84	41.49
40	*Oxycheilinus diagrammus*	0.25	0.76	0.49	0.83	42.33
41	*Centropyge bicolor*	0	0.64	0.47	0.8	43.13
42	*Halichoeres solorensis*	0.25	0.71	0.47	0.8	43.93
43	*Cheilio inermis*	0	0.62	0.46	0.79	44.72
44	*Chaetodon auriga*	0	0.62	0.46	0.79	45.5
45	*Halichoeres chrysus*	0	0.6	0.44	0.76	46.26
46	*Halichoeres richmondi*	0.25	0.67	0.44	0.75	47.01

47	*Chaetodon lunula*	0.25	0.64	0.44	0.75	47.76
48	*Chaetodon ornatissimus*	0	0.6	0.44	0.74	48.5
49	*Amphiprion sandaracinos*	0	0.57	0.43	0.73	49.24
50	*Chaetodon melannotus*	0	0.57	0.42	0.72	49.96
51	*Forcipiger flavissimus*	0	0.57	0.42	0.72	50.67
52	*Chaetodon punctatofasciatus*	0.25	0.62	0.42	0.72	51.39
53	*Chaetodon trifascialis*	0.25	0.6	0.41	0.71	52.1
54	*Halichoeres hortulanus*	0.5	0.95	0.4	0.68	52.78
55	*Pomacentrus bankanensis*	0.25	0.57	0.4	0.68	53.46
56	*Labropsis manabei*	0	0.52	0.4	0.68	54.14
57	*Novaculichthys taeniourus*	0	0.52	0.39	0.67	54.81
58	*Cirrhilabrus lubbocki*	0	0.52	0.39	0.66	55.47
59	*Amblyglyphidodon leucogaster*	0.5	1	0.39	0.66	56.13
60	*Amphiprion clarkii*	0.5	1	0.39	0.66	56.78
61	*Bodianus mesothorax*	0.5	0.98	0.39	0.66	57.44
62	*Pomacentrus alexanderae*	0.5	0.98	0.38	0.66	58.1
63	*Pomacentrus stigma*	0.5	0.95	0.38	0.66	58.75
64	*Anampses geographicus*	0	0.52	0.38	0.66	59.41
65	*Neoglyphidodon nigroris*	0.5	0.93	0.38	0.66	60.06
66	*Pomacentrus philippinus*	0	0.52	0.38	0.66	60.72
67	*Stethojulis bandanensis*	0.25	0.52	0.38	0.65	61.37
68	*Chaetodontoplus mesoleucus*	0.5	0.71	0.38	0.65	62.02
69	*Cheilinus fasciatus*	0.5	0.74	0.38	0.65	62.68
70	*Halichoeres nebulosus*	0.5	0.29	0.38	0.65	63.33
71	*Oxycheilinus bimaculatus*	0.5	0.38	0.38	0.65	63.98
72	*Chrysiptera springeri*	0.25	0.5	0.38	0.65	64.62
73	*Oxycheilinus celebicus*	0.75	0.5	0.38	0.65	65.27
74	*Stethojulis interupta*	0.5	0.64	0.38	0.64	65.92
75	*Halichoeres scapularis*	0.5	0.76	0.38	0.64	66.56
76	*Chromis weberi*	0.5	0.83	0.38	0.64	67.2
77	*Chromis viridis*	0.5	0.86	0.38	0.64	67.84
78	*Macropharyngodon negrosensis*	0.5	0.88	0.38	0.64	68.48
79	*Premnas biaculeatus*	0.5	0.1	0.38	0.64	69.12
80	*Neoglyphidodon melas*	0.5	0.9	0.38	0.64	69.76
81	*Amphiprion frenatus*	0.5	0.95	0.37	0.64	70.4
82	*Pomacentrus coelestis*	0.5	0.95	0.37	0.64	71.04
83	*Chaetodon baronessa*	0.5	1	0.37	0.64	71.67
84	*Dascyllus reticulatus*	0.5	1	0.37	0.64	72.31
85	*Chromis xanthura*	0	0.5	0.37	0.63	72.94
86	*Coradion chrysozonus*	0.5	0.24	0.37	0.63	73.56
87	*Chaetodon ocellicaudus*	0	0.5	0.37	0.62	74.19
88	*Pteragogus cryptus*	0.5	0.14	0.36	0.62	74.81
89	*Hologymnosus annulatus*	0	0.48	0.36	0.61	75.42
90	*Anampses meleagrides*	0	0.48	0.35	0.6	76.02
91	*Neoglyphidodon thoracotaeniatus*	0	0.48	0.35	0.6	76.62
92	*Choerodon anchorago*	0.25	0.43	0.35	0.59	77.21
93	*Hologymnosus doliatus*	0	0.45	0.33	0.57	77.78
94	*Heniochus chrysostomus*	0.25	0.38	0.33	0.56	78.34
95	*Thalassoma amblycephalum*	0	0.45	0.33	0.56	78.91
96	*Abudefduf sexfasciatus*	0	0.43	0.33	0.56	79.47
97	*Chaetodon adiergastos*	0	0.43	0.32	0.55	80.02
98	*Pseudocheilinus evanidus*	0	0.4	0.31	0.52	80.54
99	*Cheilinus chlorourus*	0.75	0.76	0.28	0.48	81.03
100	*Epibulus insidiator*	0.75	0.79	0.28	0.48	81.51

101	*Chromis atripes*	0.25	0.26	0.28	0.48	81.99
102	*Pomacentrus nigromarginatus*	0	0.38	0.28	0.47	82.46
103	*Oxycheilinus unifasciatus*	0	0.36	0.27	0.46	82.93
104	*Cheilinus oxycephalus*	0	0.36	0.27	0.46	83.39
105	*Chaetodon ulietensis*	0.25	0.19	0.27	0.45	83.84
106	*Cheiloprion labiatus*	0.25	0.17	0.25	0.42	84.26
107	*Chromis scotochiloptera*	0	0.31	0.24	0.41	84.68
108	*Oxycheilinus rhodochrous*	0.25	0.14	0.24	0.4	85.08
109	*Halichoeres marginatus*	0	0.31	0.23	0.4	85.48
110	*Cirrhilabrus cyanopleura*	0.75	0.93	0.23	0.4	85.87
111	*Amblyglyphidodon curacao*	0.75	0.93	0.23	0.4	86.27
112	*Chaetodon speculum*	0	0.29	0.22	0.37	86.63
113	*Genicanthus lamarck*	0	0.29	0.21	0.37	87
114	*Neopomacentrus anabatoides*	0	0.29	0.21	0.36	87.36
115	*Heniochus singularis*	0	0.29	0.21	0.36	87.72
116	*Pomacentrus nagasakiensis*	0.25	0.07	0.21	0.36	88.07
117	*Labroides bicolor*	0	0.29	0.21	0.35	88.43
118	*Chromis retrofasciata*	0.75	1	0.21	0.35	88.78
119	*Chrysiptera rollandi*	0.75	1	0.21	0.35	89.13
120	*Chrysiptera talboti*	0.75	1	0.21	0.35	89.49
121	*Halichoeres chloropterus*	0.25	0.02	0.2	0.35	89.84
122	*Halichoeres leucurus*	0.25	0.02	0.2	0.35	90.18

Appendix 4.3 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group B vs. group H (see Materials and methods of Chapter 4). The average presence/absence of each species in groups B and H, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group B	Group H	Diss.	% Cont.	Cum. %
1	*Centropyge vroliki*	0	1	0.61	1.37	1.37
2	*Chaetodon kleini*	0	1	0.61	1.37	2.74
3	*Chrysiptera unimaculata*	1	0	0.61	1.37	4.1
4	*Bodianus mesothorax*	0	0.98	0.6	1.34	5.44
5	*Labrichthys unilineatus*	0	0.98	0.6	1.34	6.78
6	*Halichoeres chloropterus*	1	0.02	0.59	1.33	8.11
7	*Pygoplites diacanthus*	0	0.98	0.59	1.33	9.45
8	*Chromis amboinensis*	0	0.95	0.58	1.31	10.75
9	*Halichoeres hortulanus*	0	0.95	0.58	1.3	12.05
10	*Abudefduf vaigiensis*	0	0.95	0.58	1.3	13.35
11	*Pomacentrus tripunctatus*	1	0.07	0.57	1.27	14.62
12	*Chromis margaritifer*	0	0.93	0.57	1.27	15.89
13	*Hemigymnus fasciatus*	0	0.93	0.57	1.27	17.16
14	*Pomacentrus nagasakiensis*	1	0.07	0.56	1.27	18.43
15	*Chaetodon selene*	1	0.07	0.56	1.27	19.69
16	*Pomacentrus lepidogenys*	0	0.93	0.56	1.27	20.96
17	*Plectroglyphidodon lacrymatus*	0	0.9	0.55	1.23	22.19
18	*Halichoeres argus*	1	0.12	0.54	1.21	23.4
19	*Coris gaimard*	0	0.81	0.49	1.1	24.5
20	*Halichoeres biocellatus*	0	0.79	0.48	1.08	25.58
21	*Pomacentrus chrysurus*	1	0.21	0.48	1.07	26.65
22	*Epibulus insidiator*	0	0.79	0.47	1.07	27.72
23	*Macropharyngodon meleagris*	0	0.76	0.47	1.05	28.77
24	*Gomphosus varius*	0	0.76	0.46	1.03	29.8
25	*Cheilinus trilobatus*	0	0.71	0.43	0.97	30.77
26	*Chromis atripectoralis*	0	0.71	0.43	0.97	31.74
27	*Chaetodon rafflesi*	0	0.67	0.4	0.9	32.64
28	*Halichoeres richmondi*	0	0.67	0.4	0.9	33.54
29	*Centropyge bicolor*	0	0.64	0.38	0.86	34.39
30	*Cheilio inermis*	0	0.62	0.37	0.84	35.23
31	*Chaetodon auriga*	0	0.62	0.37	0.83	36.06
32	*Chaetodon punctatofasciatus*	0	0.62	0.37	0.83	36.89
33	*Chaetodon trifascialis*	0	0.6	0.36	0.8	37.69
34	*Halichoeres chrysus*	0	0.6	0.36	0.8	38.5
35	*Chaetodon ornatissimus*	0	0.6	0.35	0.79	39.29
36	*Forcipiger flavissimus*	0	0.57	0.34	0.76	40.05
37	*Pomacentrus bankanensis*	0	0.57	0.34	0.76	40.81
38	*Labropsis manabei*	0	0.52	0.32	0.72	41.53
39	*Novaculichthys taeniourus*	0	0.52	0.32	0.71	42.24
40	*Stethojulis bandanensis*	0	0.52	0.31	0.7	42.94
41	*Amblyglyphidodon leucogaster*	0.5	1	0.31	0.7	43.65
42	*Amphiprion polymnus*	0.5	0	0.31	0.7	44.35
43	*Coris pictoides*	0.5	0	0.31	0.7	45.05
44	*Halichoeres hartzfeldii*	0.5	0	0.31	0.7	45.75
45	*Halichoeres margaritaceus*	0.5	0	0.31	0.7	46.45

46	*Pomacentrus cuneatus*	0.5	0	0.31	0.7	47.15
47	*Pseudocoris yamashiroi*	0.5	0	0.31	0.7	47.85
48	*Choerodon zosterophorus*	0.5	0.02	0.31	0.7	48.55
49	*Chrysiptera bleekeri*	0.5	0.02	0.31	0.7	49.25
50	*Thalassoma hardwicke*	0.5	0.98	0.31	0.7	49.95
51	*Pseudocheilinus hexataenia*	0.5	0.93	0.31	0.7	50.65
52	*Neoglyphidodon nigroris*	0.5	0.93	0.31	0.7	51.35
53	*Neoglyphidodon melas*	0.5	0.9	0.31	0.7	52.04
54	*Macropharyngodon negrosensis*	0.5	0.88	0.31	0.7	52.74
55	*Pomacentrus philippinus*	0	0.52	0.31	0.7	53.44
56	*Amphiprion perideraion*	0.5	0.83	0.31	0.7	54.13
57	*Hemigymnus melapterus*	0.5	0.83	0.31	0.7	54.83
58	*Pomacentrus opisthostigma*	0.5	0.79	0.31	0.69	55.52
59	*Cheilinus chlorourus*	0.5	0.76	0.31	0.69	56.22
60	*Cheilinus fasciatus*	0.5	0.74	0.31	0.69	56.91
61	*Chaetodontoplus mesoleucus*	0.5	0.71	0.31	0.69	57.6
62	*Genicanthus lamarck*	0.5	0.29	0.31	0.69	58.29
63	*Pomacentrus adelus*	0.5	0.67	0.31	0.69	58.98
64	*Oxycheilinus unifasciatus*	0.5	0.36	0.31	0.69	59.67
65	*Anampses geographicus*	0.5	0.52	0.3	0.68	60.35
66	*Oxycheilinus celebicus*	1	0.5	0.3	0.68	61.04
67	*Chrysiptera springeri*	1	0.5	0.3	0.68	61.72
68	*Chaetodon melannotus*	0.5	0.57	0.3	0.68	62.4
69	*Amphiprion sandaracinos*	0.5	0.57	0.3	0.68	63.08
70	*Pomacentrus nigromarginatus*	0.5	0.38	0.3	0.68	63.76
71	*Chaetodon lunula*	0.5	0.64	0.3	0.68	64.44
72	*Chaetodon octofasciatus*	0.5	0.33	0.3	0.68	65.12
73	*Chromis scotochiloptera*	0.5	0.31	0.3	0.68	65.8
74	*Oxycheilinus diagrammus*	0.5	0.76	0.3	0.67	66.47
75	*Coradion chrysozonus*	0.5	0.24	0.3	0.67	67.15
76	*Chaetodon ulietensis*	0.5	0.19	0.3	0.67	67.82
77	*Centropyge nox*	0.5	0.83	0.3	0.67	68.5
78	*Pomacentrus burroughi*	0.5	0.17	0.3	0.67	69.17
79	*Cheiloprion labiatus*	0.5	0.17	0.3	0.67	69.84
80	*Pomacanthus sexstriatus*	0.5	0.05	0.3	0.67	70.51
81	*Cirrhilabrus lubbocki*	1	0.52	0.3	0.67	71.18
82	*Chaetodon bennetti*	0.5	0.02	0.3	0.67	71.85
83	*Paracheilinus carpenteri*	0.5	0.02	0.3	0.67	72.52
84	*Abudefduf lorenzi*	0.5	0	0.3	0.67	73.18
85	*Chaetodon lunulatus*	0.5	1	0.3	0.67	73.85
86	*Chaetodontoplus caeruleopunctatus*	0.5	0	0.3	0.67	74.52
87	*Cheilinus celebicus*	0.5	0	0.3	0.67	75.19
88	*Chrysiptera oxycephala*	0.5	0	0.3	0.67	75.85
89	*Dascyllus trimaculatus*	0.5	1	0.3	0.67	76.52
90	*Pomacentrus vaiuli*	0.5	1	0.3	0.67	77.19
91	*Chromis xanthura*	0	0.5	0.3	0.67	77.86
92	*Chaetodon ocellicaudus*	0	0.5	0.3	0.66	78.52
93	*Hologymnosus annulatus*	0	0.48	0.29	0.65	79.17
94	*Anampses meleagrides*	0	0.48	0.28	0.64	79.81
95	*Neoglyphidodon thoracotaeniatus*	0	0.48	0.28	0.64	80.45
96	*Hologymnosus doliatus*	0	0.45	0.27	0.6	81.05
97	*Thalassoma amblycephalum*	0	0.45	0.27	0.6	81.65
98	*Abudefduf sexfasciatus*	0	0.43	0.26	0.59	82.24
99	*Chaetodon adiergastos*	0	0.43	0.26	0.58	82.82

100	*Choerodon anchorago*	0	0.43	0.26	0.58	83.4
101	*Pseudocheilinus evanidus*	0	0.4	0.25	0.55	83.96
102	*Oxycheilinus bimaculatus*	0	0.38	0.23	0.52	84.48
103	*Heniochus chrysostomus*	0	0.38	0.22	0.5	84.98
104	*Cheilinus oxycephalus*	0	0.36	0.22	0.49	85.47
105	*Stethojulis interupta*	1	0.64	0.21	0.47	85.94
106	*Halichoeres marginatus*	0	0.31	0.19	0.42	86.36
107	*Chromis analis*	1	0.71	0.18	0.39	86.75
108	*Halichoeres nebulosus*	0	0.29	0.17	0.39	87.14
109	*Halichoeres solorensis*	1	0.71	0.17	0.39	87.53
110	*Chaetodon speculum*	0	0.29	0.17	0.39	87.92
111	*Neopomacentrus anabatoides*	0	0.29	0.17	0.38	88.3
112	*Heniochus singularis*	0	0.29	0.17	0.38	88.69
113	*Labroides bicolor*	0	0.29	0.17	0.38	89.06
114	*Chromis atripes*	0	0.26	0.16	0.35	89.42
115	*Anampses twistii*	0	0.26	0.16	0.35	89.77
116	*Halichoeres scapularis*	1	0.76	0.15	0.33	90.09

Appendix 4.4 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group C vs. group H (see Materials and methods of Chapter 4). The average presence/absence of each species in groups C and H, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group C	Group H	Diss.	% Cont.	Cum. %
1	*Chaetodon baronessa*	0	1	0.6	1.49	1.49
2	*Chromis retrofasciata*	0	1	0.6	1.49	2.99
3	*Dascyllus reticulatus*	0	1	0.6	1.49	4.48
4	*Choerodon zosterophorus*	1	0.02	0.58	1.46	5.94
5	*Plectroglyphidodon leucozonus*	1	0.02	0.58	1.46	7.4
6	*Pomacentrus stigma*	0	0.95	0.57	1.43	8.82
7	*Bodianus diana*	0	0.95	0.57	1.42	10.25
8	*Chromis amboinensis*	0	0.95	0.57	1.42	11.67
9	*Pomacentrus coelestis*	0	0.95	0.57	1.42	13.09
10	*Chrysiptera rex*	1	0.1	0.54	1.36	14.45
11	*Dischistodus melanotus*	1	0.17	0.5	1.25	15.7
12	*Cheiloprion labiatus*	1	0.17	0.5	1.24	16.94
13	*Chromis weberi*	0	0.83	0.5	1.24	18.18
14	*Centropyge nox*	0	0.83	0.49	1.23	19.41
15	*Coris gaimard*	0	0.81	0.48	1.2	20.62
16	*Chaetodon citrinellus*	1	0.21	0.47	1.18	21.8
17	*Plectroglyphidodon dickii*	1	0.24	0.46	1.15	22.95
18	*Halichoeres scapularis*	0	0.76	0.45	1.14	24.09
19	*Chaetodontoplus mesoleucus*	0	0.71	0.43	1.08	25.16
20	*Halichoeres solorensis*	0	0.71	0.43	1.07	26.23
21	*Chromis analis*	0	0.71	0.43	1.06	27.3
22	*Stethojulis interupta*	0	0.64	0.39	0.98	28.28
23	*Chaetodon rafflesi*	0	0.67	0.39	0.98	29.26
24	*Halichoeres richmondi*	0	0.67	0.39	0.98	30.24
25	*Chaetodon lunula*	0	0.64	0.39	0.97	31.21
26	*Cheilio inermis*	0	0.62	0.37	0.91	32.12
27	*Halichoeres chrysus*	0	0.6	0.35	0.87	32.99
28	*Chaetodon ornatissimus*	0	0.6	0.35	0.86	33.86
29	*Thalassoma amblycephalum*	1	0.45	0.34	0.84	34.7
30	*Centropyge tibicen*	0.5	1	0.31	0.78	35.48
31	*Thalassoma lunare*	0.5	1	0.31	0.78	36.26
32	*Chromis lepidolepis*	0.5	0.02	0.31	0.78	37.04
33	*Plectroglyphidodon johnstonianus*	0.5	0.02	0.31	0.78	37.81
34	*Pygoplites diacanthus*	0.5	0.98	0.31	0.78	38.59
35	*Pomacentrus alexanderae*	0.5	0.98	0.31	0.78	39.37
36	*Amblyglyphidodon aureus*	0.5	0.98	0.31	0.78	40.15
37	*Hemigymnus fasciatus*	0.5	0.93	0.31	0.78	40.92
38	*Pomacentrus nagasakiensis*	0.5	0.07	0.31	0.78	41.7
39	*Cirrhilabrus cyanopleura*	0.5	0.93	0.31	0.77	42.48
40	*Neoglyphidodon melas*	0.5	0.9	0.31	0.77	43.25
41	*Halichoeres argus*	0.5	0.12	0.31	0.77	44.02
42	*Halichoeres prosopeion*	0.5	0.86	0.31	0.77	44.79
43	*Amphiprion perideraion*	0.5	0.83	0.31	0.77	45.56
44	*Halichoeres biocellatus*	0.5	0.79	0.31	0.77	46.33
45	*Cirrhilabrus lubbocki*	0	0.52	0.31	0.76	47.09
46	*Cheilinus fasciatus*	0.5	0.74	0.31	0.76	47.85

47	*Pomacentrus philippinus*	0	0.52	0.3	0.76	48.61
48	*Halichoeres marginatus*	0.5	0.31	0.3	0.76	49.37
49	*Centropyge bicolor*	0.5	0.64	0.3	0.75	50.13
50	*Chaetodon auriga*	0.5	0.62	0.3	0.75	50.88
51	*Forcipiger flavissimus*	0.5	0.57	0.3	0.75	51.63
52	*Labropsis manabei*	0.5	0.52	0.3	0.75	52.38
53	*Chrysiptera springeri*	0	0.5	0.3	0.75	53.13
54	*Novaculichthys taeniourus*	0.5	0.52	0.3	0.75	53.88
55	*Oxycheilinus celebicus*	0	0.5	0.3	0.75	54.62
56	*Anampses geographicus*	0.5	0.52	0.3	0.75	55.37
57	*Stethojulis bandanensis*	0.5	0.52	0.3	0.75	56.12
58	*Chromis xanthura*	0.5	0.5	0.3	0.75	56.86
59	*Anampses meleagrides*	0.5	0.48	0.3	0.74	57.61
60	*Amphiprion sandaracinos*	0.5	0.57	0.3	0.74	58.35
61	*Chaetodon trifascialis*	0.5	0.6	0.3	0.74	59.09
62	*Oxycheilinus unifasciatus*	0.5	0.36	0.3	0.74	59.83
63	*Cheilinus oxycephalus*	0.5	0.36	0.29	0.74	60.56
64	*Chromis atripectoralis*	0.5	0.71	0.29	0.73	61.3
65	*Cheilinus trilobatus*	0.5	0.71	0.29	0.73	62.03
66	*Epibulus insidiator*	0.5	0.79	0.29	0.73	62.76
67	*Centropyge bispinosus*	0.5	0.24	0.29	0.73	63.49
68	*Bodianus axillaris*	0.5	0.21	0.29	0.73	64.21
69	*Chaetodon ocellicaudus*	0	0.5	0.29	0.72	64.94
70	*Chromis viridis*	0.5	0.86	0.29	0.72	65.66
71	*Pomacanthus semicirculatus*	0.5	0.12	0.29	0.72	66.38
72	*Chaetodon unimaculatus*	0.5	0.07	0.29	0.72	67.1
73	*Abudefduf vaigiensis*	0.5	0.95	0.29	0.72	67.82
74	*Halichoeres leucurus*	0.5	0.02	0.29	0.71	68.53
75	*Halichoeres podostigma*	0.5	0.98	0.29	0.71	69.25
76	*Dascyllus aruanus*	0.5	0.98	0.29	0.71	69.96
77	*Thalassoma quinquevittatum*	0.5	0.02	0.29	0.71	70.68
78	*Chromis ternatensis*	0.5	1	0.29	0.71	71.39
79	*Chromis xanthochira*	0.5	0	0.29	0.71	72.1
80	*Cirrhilabrus rubripinnis*	0.5	0	0.29	0.71	72.82
81	*Dascyllus trimaculatus*	0.5	1	0.29	0.71	73.53
82	*Labropsis xanthonota*	0.5	0	0.29	0.71	74.24
83	*Thalassoma purpureum*	0.5	0	0.29	0.71	74.96
84	*Hologymnosus annulatus*	0	0.48	0.28	0.71	75.66
85	*Neoglyphidodon thoracotaeniatus*	0	0.48	0.28	0.7	76.36
86	*Pomacentrus bankanensis*	1	0.57	0.26	0.66	77.02
87	*Hologymnosus doliatus*	0	0.45	0.26	0.66	77.68
88	*Chaetodon melannotus*	1	0.57	0.26	0.66	78.34
89	*Abudefduf sexfasciatus*	0	0.43	0.26	0.65	78.98
90	*Chaetodon adiergastos*	0	0.43	0.25	0.64	79.62
91	*Choerodon anchorago*	0	0.43	0.25	0.63	80.25
92	*Pseudocheilinus evanidus*	0	0.4	0.24	0.6	80.86
93	*Chaetodon punctatofasciatus*	1	0.62	0.24	0.59	81.45
94	*Oxycheilinus bimaculatus*	0	0.38	0.23	0.57	82.01
95	*Pomacentrus nigromarginatus*	0	0.38	0.22	0.55	82.56
96	*Heniochus chrysostomus*	0	0.38	0.22	0.55	83.12
97	*Pomacentrus adelus*	1	0.67	0.2	0.51	83.62
98	*Chaetodon octofasciatus*	0	0.33	0.2	0.5	84.12
99	*Chromis scotochiloptera*	0	0.31	0.19	0.47	84.6
100	*Halichoeres nebulosus*	0	0.29	0.17	0.43	85.02

101	*Chaetodon speculum*	0	0.29	0.17	0.42	85.45
102	*Genicanthus lamarck*	0	0.29	0.17	0.42	85.87
103	*Neopomacentrus anabatoides*	0	0.29	0.17	0.42	86.29
104	*Heniochus singularis*	0	0.29	0.17	0.42	86.7
105	*Labroides bicolor*	0	0.29	0.17	0.41	87.12
106	*Chromis atripes*	0	0.26	0.15	0.38	87.5
107	*Anampses twistii*	0	0.26	0.15	0.38	87.88
108	*Gomphosus varius*	1	0.76	0.15	0.36	88.25
109	*Cheilinus chlorourus*	1	0.76	0.14	0.36	88.61
110	*Macropharyngodon meleagris*	1	0.76	0.14	0.34	88.95
111	*Oxycheilinus diagrammus*	1	0.76	0.14	0.34	89.29
112	*Chromis delta*	0	0.24	0.14	0.34	89.64
113	*Coradion chrysozonus*	0	0.24	0.14	0.34	89.98
114	*Pomacanthus imperator*	0	0.24	0.14	0.34	90.32

Appendix 4.5 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group E vs. group H (see Materials and methods of Chapter 4). The average presence/absence of each species in groups E and H, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group E	Group H	Diss.	% Cont.	Cum. %
1	*Pomacentrus cuneatus*	1	0	0.59	1.66	1.66
2	*Pomacentrus smithi*	1	0	0.59	1.66	3.31
3	*Pomacentrus vaiuli*	0	1	0.59	1.66	4.97
4	*Pomacentrus nagasakiensis*	1	0.07	0.54	1.53	6.5
5	*Chaetodon vagabundus*	0	0.83	0.48	1.37	7.87
6	*Halichoeres biocellatus*	0	0.79	0.46	1.3	9.17
7	*Macropharyngodon meleagris*	0	0.76	0.45	1.27	10.44
8	*Gomphosus varius*	0	0.76	0.44	1.25	11.7
9	*Neopomacentrus anabatoides*	1	0.29	0.42	1.19	12.89
10	*Halichoeres solorensis*	0	0.71	0.42	1.18	14.07
11	*Chaetodon lunulatus*	0.33	1	0.4	1.13	15.21
12	*Centropyge tibicen*	0.33	1	0.39	1.11	16.31
13	*Chaetodon octofasciatus*	1	0.33	0.39	1.1	17.41
14	*Chromis margaritifer*	0.33	0.93	0.39	1.09	18.5
15	*Hemigymnus fasciatus*	0.33	0.93	0.39	1.09	19.59
16	*Stethojulis interupta*	0	0.64	0.39	1.09	20.68
17	*Hemiglyphidodon plagiometapon*	0.67	0	0.38	1.07	21.75
18	*Neoglyphidodon melas*	0.33	0.9	0.38	1.07	22.82
19	*Coradion melanopus*	0.67	0.07	0.37	1.04	23.86
20	*Centropyge bicolor*	0	0.64	0.37	1.04	24.9
21	*Amphiprion perideraion*	0.33	0.83	0.37	1.03	25.93
22	*Pomacentrus burroughi*	0.67	0.17	0.37	1.03	26.96
23	*Hemigymnus melapterus*	0.33	0.83	0.36	1.03	27.99
24	*Cheilio inermis*	0	0.62	0.36	1.01	29
25	*Chaetodon auriga*	0	0.62	0.36	1.01	30.01
26	*Chaetodon punctatofasciatus*	0	0.62	0.36	1	31.02
27	*Cheilinus chlorourus*	0.33	0.76	0.35	0.99	32
28	*Coris gaimard*	0.33	0.81	0.35	0.98	32.98
29	*Chaetodon trifascialis*	0	0.6	0.35	0.97	33.95
30	*Halichoeres chrysus*	0	0.6	0.34	0.97	34.92
31	*Chaetodon oxycephalus*	0.67	0.21	0.34	0.97	35.89
32	*Oxycheilinus diagrammus*	0.33	0.76	0.34	0.96	36.85
33	*Chaetodon ornatissimus*	0	0.6	0.34	0.96	37.81
34	*Choerodon anchorago*	1	0.43	0.34	0.96	38.77
35	*Cheilinus trilobatus*	0.33	0.71	0.34	0.95	39.72
36	*Chaetodon speculum*	0.67	0.29	0.33	0.93	40.65
37	*Chromis scotochiloptera*	0.67	0.31	0.33	0.93	41.58
38	*Forcipiger flavissimus*	0	0.57	0.33	0.92	42.51
39	*Pomacentrus bankanensis*	0	0.57	0.33	0.92	43.43
40	*Chaetodon lunula*	0.33	0.64	0.32	0.91	44.34
41	*Pomacentrus adelus*	0.33	0.67	0.32	0.91	45.25
42	*Pomacentrus nigromarginatus*	0.67	0.38	0.32	0.89	46.14
43	*Labropsis manabei*	0	0.52	0.31	0.87	47.01
44	*Hologymnosus doliatus*	0.67	0.45	0.31	0.86	47.88
45	*Chaetodon melannotus*	0.33	0.57	0.31	0.86	48.74

46	*Novaculichthys taeniourus*	0	0.52	0.31	0.86	49.6
47	*Amphiprion sandaracinos*	0.33	0.57	0.31	0.86	50.46
48	*Stethojulis bandanensis*	0	0.52	0.3	0.85	51.31
49	*Anampses geographicus*	0	0.52	0.3	0.85	52.16
50	*Pomacentrus philippinus*	0	0.52	0.3	0.84	53
51	*Chaetodon ocellicaudus*	0.67	0.5	0.3	0.84	53.84
52	*Cirrhilabrus lubbocki*	0.33	0.52	0.3	0.83	54.67
53	*Oxycheilinus celebicus*	0.33	0.5	0.29	0.83	55.5
54	*Chrysiptera springeri*	0.67	0.5	0.29	0.83	56.33
55	*Chromis xanthura*	0.33	0.5	0.29	0.82	57.15
56	*Abudefduf sexfasciatus*	0.33	0.43	0.28	0.8	57.95
57	*Thalassoma amblycephalum*	0.33	0.45	0.28	0.79	58.74
58	*Chaetodon adiergastos*	0.33	0.43	0.28	0.78	59.52
59	*Hologymnosus annulatus*	0	0.48	0.28	0.78	60.3
60	*Pseudocheilinus evanidus*	0.33	0.4	0.27	0.77	61.08
61	*Anampses meleagrides*	0	0.48	0.27	0.77	61.85
62	*Neoglyphidodon thoracotaeniatus*	0	0.48	0.27	0.77	62.63
63	*Oxycheilinus bimaculatus*	0.33	0.38	0.27	0.77	63.4
64	*Chromis atripectoralis*	0.67	0.71	0.26	0.73	64.12
65	*Cheilinus fasciatus*	0.67	0.74	0.25	0.71	64.84
66	*Labroides bicolor*	0.33	0.29	0.25	0.69	65.53
67	*Halichoeres scapularis*	0.67	0.76	0.24	0.68	66.21
68	*Coradion chrysozonus*	0.33	0.24	0.24	0.68	66.89
69	*Diproctacanthus xanthurus*	0.67	0.81	0.24	0.67	67.56
70	*Plectroglyphidodon dickii*	0.33	0.24	0.23	0.66	68.22
71	*Oxycheilinus rhodochrous*	0.33	0.14	0.23	0.65	68.88
72	*Amphiprion ocellaris*	0.67	0.86	0.23	0.65	69.53
73	*Bodianus axillaris*	0.33	0.21	0.23	0.65	70.18
74	*Pseudocheilinus hexataenia*	0.67	0.93	0.22	0.62	70.79
75	*Macropharyngodon negrosensis*	0.67	0.88	0.22	0.61	71.41
76	*Heniochus chrysostomus*	0	0.38	0.22	0.61	72.02
77	*Halichoeres prosopeion*	0.67	0.86	0.22	0.61	72.63
78	*Amblyglyphidodon aureus*	0.67	0.98	0.21	0.6	73.22
79	*Pomacentrus grammorhynchus*	0.33	0.02	0.21	0.59	73.82
80	*Labrichthys unilineatus*	0.67	0.98	0.21	0.59	74.41
81	*Oxycheilinus unifasciatus*	0	0.36	0.21	0.59	75.01
82	*Cheilinus oxycephalus*	0	0.36	0.21	0.59	75.6
83	*Chaetodon baronessa*	0.67	1	0.21	0.58	76.18
84	*Halichoeres richmondi*	1	0.67	0.2	0.57	76.75
85	*Chaetodon rafflesi*	1	0.67	0.2	0.57	77.32
86	*Pomacentrus tripunctatus*	0.33	0.07	0.2	0.57	77.89
87	*Halichoeres leucurus*	0.33	0.02	0.2	0.56	78.45
88	*Halichoeres podostigma*	0.67	0.98	0.2	0.56	79.01
89	*Amphiprion frenatus*	0.67	0.95	0.2	0.55	79.57
90	*Bodianus diana*	0.67	0.95	0.2	0.55	80.12
91	*Cirrhilabrus rubripinnis*	0.33	0	0.19	0.55	80.67
92	*Paracheilinus filamentosus*	0.33	0	0.19	0.55	81.22
93	*Chelmon rostratus*	0.33	0.02	0.19	0.54	81.76
94	*Coris batuensis*	0.67	0.98	0.19	0.54	82.29
95	*Neopomacentrus azysron*	0.33	0.02	0.19	0.54	82.83
96	*Dascyllus aruanus*	0.67	0.98	0.19	0.54	83.37
97	*Abudefduf lorenzi*	0.33	0	0.19	0.52	83.9
98	*Halichoeres marginatus*	0	0.31	0.18	0.51	84.4
99	*Chromis analis*	1	0.71	0.17	0.48	84.88

100	*Halichoeres nebulosus*	0	0.29	0.17	0.47	85.35
101	*Genicanthus lamarck*	0	0.29	0.17	0.47	85.82
102	*Chaetodontoplus mesoleucus*	1	0.71	0.16	0.46	86.29
103	*Heniochus singularis*	0	0.29	0.16	0.46	86.75
104	*Chromis atripes*	0	0.26	0.15	0.43	87.18
105	*Anampses twistii*	0	0.26	0.15	0.42	87.6
106	*Centropyge bispinosus*	0	0.24	0.14	0.38	87.98
107	*Chromis delta*	0	0.24	0.14	0.38	88.36
108	*Pomacanthus imperator*	0	0.24	0.13	0.38	88.74
109	*Epibulus insidiator*	1	0.79	0.13	0.37	89.11
110	*Pomacentrus opisthostigma*	1	0.79	0.13	0.36	89.47
111	*Pomacentrus chrysurus*	0	0.21	0.13	0.36	89.83
112	*Thalassoma jansenii*	0	0.21	0.13	0.36	90.18

Appendix 4.6 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group F vs. group H (see Materials and methods of Chapter 4). The average presence/absence of each species in groups F and H, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group F	Group H	Diss.	% Cont.	Cum. %
1	*Chrysiptera cyanea*	1	0	0.56	1.63	1.63
2	*Chromis ovatiformis*	1	0.02	0.54	1.59	3.21
3	*Chaetodon bennetti*	1	0.02	0.54	1.59	4.8
4	*Chromis caudalis*	1	0.07	0.52	1.51	6.31
5	*Chrysiptera rex*	1	0.1	0.51	1.48	7.79
6	*Neoglyphidodon melas*	0	0.9	0.5	1.47	9.25
7	*Chromis viridis*	0	0.86	0.47	1.38	10.63
8	*Bodianus axillaris*	1	0.21	0.44	1.29	11.92
9	*Chaetodon xanthurus*	1	0.21	0.44	1.29	13.21
10	*Halichoeres biocellatus*	0	0.79	0.44	1.28	14.49
11	*Macropharyngodon meleagris*	0	0.76	0.43	1.25	15.74
12	*Cheilinus chlorourus*	0	0.76	0.42	1.24	16.98
13	*Centropyge tibicen*	0.25	1	0.42	1.22	18.2
14	*Dascyllus aruanus*	0.25	0.98	0.41	1.2	19.4
15	*Bodianus diana*	0.25	0.95	0.41	1.2	20.6
16	*Abudefduf vaigiensis*	0.25	0.95	0.41	1.19	21.78
17	*Halichoeres solorensis*	0	0.71	0.4	1.16	22.95
18	*Chromis atripectoralis*	0	0.71	0.39	1.15	24.1
19	*Macropharyngodon negrosensis*	0.25	0.88	0.39	1.13	25.23
20	*Amphiprion ocellaris*	0.25	0.86	0.38	1.11	26.34
21	*Halichoeres binotopsis*	0.75	0.14	0.38	1.11	27.45
22	*Amphiprion perideraion*	0.25	0.83	0.37	1.09	28.54
23	*Diproctacanthus xanthurus*	0.25	0.81	0.37	1.08	29.61
24	*Coris gaimard*	0.25	0.81	0.37	1.07	30.68
25	*Stethojulis interupta*	0	0.64	0.37	1.07	31.75
26	*Halichoeres scapularis*	0.25	0.76	0.35	1.03	32.78
27	*Pomacentrus nigromarginatus*	1	0.38	0.35	1.03	33.8
28	*Cheilio inermis*	0	0.62	0.34	1	34.8
29	*Chaetodontoplus mesoleucus*	0.25	0.71	0.34	0.99	35.79
30	*Cheilinus trilobatus*	0.25	0.71	0.34	0.99	36.78
31	*Halichoeres chrysus*	0	0.6	0.33	0.95	37.73
32	*Halichoeres richmondi*	0.25	0.67	0.32	0.94	38.67
33	*Chaetodon adiergastos*	0.75	0.43	0.3	0.87	39.54
34	*Novaculichthys taeniourus*	0	0.52	0.29	0.85	40.39
35	*Labropsis manabei*	0.25	0.52	0.29	0.83	41.23
36	*Cirrhilabrus lubbocki*	0	0.52	0.29	0.83	42.06
37	*Chromis xanthura*	1	0.5	0.29	0.83	42.89
38	*Amphiprion clarkii*	0.5	1	0.28	0.83	43.72
39	*Chromis analis*	0.5	0.71	0.28	0.82	44.54
40	*Coris batuensis*	0.5	0.98	0.28	0.82	45.37
41	*Anampses geographicus*	0.25	0.52	0.28	0.82	46.19
42	*Halichoeres melanurus*	0.5	0.88	0.28	0.82	47.01
43	*Hemigymnus melapterus*	0.5	0.83	0.28	0.82	47.83
44	*Thalassoma jansenii*	0.5	0.21	0.28	0.82	48.65
45	*Plectroglyphidodon dickii*	0.5	0.24	0.28	0.82	49.47
46	*Chromis atripes*	0.5	0.26	0.28	0.82	50.28

47	*Chaetodon melannotus*	0.5	0.57	0.28	0.81	51.1
48	*Chrysiptera springeri*	0.25	0.5	0.28	0.81	51.91
49	*Oxycheilinus celebicus*	0.25	0.5	0.28	0.81	52.73
50	*Stethojulis bandanensis*	0.5	0.52	0.28	0.81	53.54
51	*Chaetodon ocellicaudus*	0.5	0.5	0.28	0.81	54.35
52	*Pseudocheilinus evanidus*	0.5	0.4	0.28	0.81	55.16
53	*Chaetodon lunula*	0.5	0.64	0.28	0.81	55.97
54	*Chaetodon octofasciatus*	0.5	0.33	0.28	0.81	56.78
55	*Chaetodon trifascialis*	0.5	0.6	0.28	0.81	57.59
56	*Neopomacentrus anabatoides*	0.5	0.29	0.28	0.81	58.4
57	*Heniochus chrysostomus*	0.5	0.38	0.28	0.81	59.21
58	*Halichoeres marginatus*	0.5	0.31	0.28	0.81	60.02
59	*Halichoeres argus*	0.5	0.12	0.28	0.81	60.82
60	*Chaetodon citrinellus*	0.5	0.21	0.28	0.8	61.63
61	*Chaetodon speculum*	0.5	0.29	0.28	0.8	62.43
62	*Labroides bicolor*	0.5	0.29	0.27	0.8	63.23
63	*Chaetodon ulietensis*	0.5	0.19	0.27	0.8	64.03
64	*Pomacentrus philippinus*	1	0.52	0.27	0.8	64.83
65	*Anampses meleagrides*	0.25	0.48	0.27	0.79	65.62
66	*Neoglyphidodon thoracotaeniatus*	0.25	0.48	0.27	0.79	66.4
67	*Hologymnosus annulatus*	0	0.48	0.26	0.77	67.17
68	*Pomacentrus bankanensis*	0.75	0.57	0.26	0.77	67.94
69	*Hologymnosus doliatus*	0.25	0.45	0.26	0.76	68.7
70	*Thalassoma amblycephalum*	0.25	0.45	0.26	0.76	69.46
71	*Chaetodon ornatissimus*	0.75	0.6	0.26	0.75	70.21
72	*Forcipiger flavissimus*	1	0.57	0.25	0.72	70.93
73	*Amphiprion sandaracinos*	1	0.57	0.24	0.7	71.64
74	*Abudefduf sexfasciatus*	0	0.43	0.24	0.7	72.34
75	*Cheilinus oxycephalus*	0.25	0.36	0.24	0.69	73.03
76	*Choerodon anchorago*	0	0.43	0.24	0.69	73.72
77	*Chaetodon rafflesi*	0.75	0.67	0.23	0.68	74.41
78	*Chaetodon punctatofasciatus*	1	0.62	0.22	0.64	75.05
79	*Cheilinus fasciatus*	0.75	0.74	0.22	0.63	75.68
80	*Halichoeres nebulosus*	0.25	0.29	0.22	0.63	76.31
81	*Chaetodon auriga*	1	0.62	0.22	0.63	76.95
82	*Anampses twistii*	0.25	0.26	0.22	0.63	77.57
83	*Heniochus singularis*	0.25	0.29	0.21	0.63	78.2
84	*Oxycheilinus bimaculatus*	0	0.38	0.21	0.62	78.82
85	*Centropyge bicolor*	1	0.64	0.21	0.61	79.43
86	*Oxycheilinus diagrammus*	0.75	0.76	0.2	0.59	80.02
87	*Oxycheilinus unifasciatus*	0	0.36	0.2	0.58	80.6
88	*Chaetodon oxycephalus*	0.25	0.21	0.2	0.58	81.18
89	*Pomacentrus chrysurus*	0.25	0.21	0.2	0.58	81.76
90	*Labropsis alleni*	0.25	0.21	0.19	0.57	82.33
91	*Dascyllus melanurus*	0.25	0.19	0.19	0.55	82.88
92	*Pomacentrus adelus*	1	0.67	0.19	0.55	83.43
93	*Forcipiger longirostris*	0.25	0.19	0.19	0.55	83.98
94	*Chromis weberi*	0.75	0.83	0.19	0.54	84.52
95	*Pomacentrus burroughi*	0.25	0.17	0.19	0.54	85.06
96	*Chromis scotochiloptera*	0	0.31	0.18	0.52	85.58
97	*Pomacentrus coelestis*	0.75	0.95	0.16	0.47	86.05
98	*Chromis margaritifer*	0.75	0.93	0.16	0.46	86.51
99	*Genicanthus lamarck*	0	0.29	0.16	0.46	86.97
100	*Hemigymnus fasciatus*	0.75	0.93	0.16	0.45	87.42

101	*Amphiprion frenatus*	0.75	0.95	0.15	0.43	87.86
102	*Stethojulis trilineatus*	0.25	0	0.15	0.43	88.29
103	*Amblyglyphidodon aureus*	0.75	0.98	0.15	0.43	88.72
104	*Halichoeres podostigma*	0.75	0.98	0.14	0.42	89.13
105	*Thalassoma quinquevittatum*	0.25	0.02	0.14	0.41	89.54
106	*Gomphosus varius*	1	0.76	0.14	0.4	89.94
107	*Chrysiptera unimaculata*	0.25	0	0.13	0.39	90.33

Appendix 4.7 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group G vs. group H (see Materials and methods of Chapter 4). The average presence/absence of each species in groups G and H, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group G	Group H	Diss.	% Cont.	Cum. %
1	*Hemiglyphidodon plagiometapon*	1	0	0.54	1.62	1.62
2	*Pomacentrus pavo*	1	0	0.54	1.62	3.24
3	*Pomacentrus simsiang*	1	0	0.54	1.62	4.86
4	*Dischistodus pseudochrysopoecilus*	1	0.02	0.53	1.58	6.44
5	*Pygoplites diacanthus*	0	0.98	0.53	1.58	8.02
6	*Thalassoma hardwicke*	0	0.98	0.53	1.58	9.6
7	*Pomacentrus stigma*	0	0.95	0.52	1.55	11.15
8	*Dischistodus perspicillatus*	1	0.1	0.49	1.47	12.62
9	*Dischistodus prosopotaenia*	1	0.1	0.49	1.46	14.08
10	*Neoglyphidodon melas*	0	0.9	0.49	1.46	15.54
11	*Plectroglyphidodon lacrymatus*	0	0.9	0.49	1.46	17
12	*Halichoeres argus*	1	0.12	0.48	1.43	18.43
13	*Macropharyngodon negrosensis*	0	0.88	0.48	1.43	19.86
14	*Amphiprion ocellaris*	0	0.86	0.47	1.4	21.25
15	*Dischistodus melanotus*	1	0.17	0.45	1.36	22.61
16	*Pomacentrus burroughi*	1	0.17	0.45	1.35	23.96
17	*Diproctacanthus xanthurus*	0	0.81	0.44	1.32	25.28
18	*Pomacentrus opisthostigma*	0	0.79	0.42	1.26	26.55
19	*Cheilinus chlorourus*	0	0.76	0.41	1.23	27.78
20	*Halichoeres solorensis*	0	0.71	0.39	1.16	28.94
21	*Halichoeres nebulosus*	1	0.29	0.39	1.16	30.09
22	*Halichoeres marginatus*	1	0.31	0.37	1.12	31.22
23	*Chaetodon octofasciatus*	1	0.33	0.36	1.08	32.29
24	*Pomacentrus adelus*	0	0.67	0.36	1.07	33.37
25	*Chaetodon lunula*	0	0.64	0.35	1.05	34.41
26	*Centropyge bicolor*	0	0.64	0.34	1.02	35.43
27	*Oxycheilinus bimaculatus*	1	0.38	0.33	1	36.44
28	*Chaetodon auriga*	0	0.62	0.33	0.99	37.43
29	*Pseudocheilinus evanidus*	1	0.4	0.32	0.96	38.39
30	*Chaetodon ornatissimus*	0	0.6	0.31	0.94	39.33
31	*Amphiprion sandaracinos*	0	0.57	0.31	0.92	40.25
32	*Chaetodon melannotus*	0	0.57	0.3	0.91	41.16
33	*Forcipiger flavissimus*	0	0.57	0.3	0.91	42.06
34	*Pomacentrus bankanensis*	0	0.57	0.3	0.91	42.97
35	*Neoglyphidodon thoracotaeniatus*	1	0.48	0.29	0.86	43.83
36	*Labropsis manabei*	0	0.52	0.28	0.85	44.68
37	*Stethojulis bandanensis*	0	0.52	0.28	0.83	45.51
38	*Chaetodon ocellicaudus*	1	0.5	0.28	0.83	46.35
39	*Anampses geographicus*	0	0.52	0.28	0.83	47.17
40	*Chromis xanthura*	1	0.5	0.28	0.83	48
41	*Abudefduf lorenzi*	0.5	0	0.27	0.82	48.83
42	*Amphiprion polymnus*	0.5	0	0.27	0.82	49.65
43	*Centropyge vroliki*	0.5	1	0.27	0.82	50.47
44	*Chrysiptera cyanea*	0.5	0	0.27	0.82	51.3
45	*Dascyllus trimaculatus*	0.5	1	0.27	0.82	52.12
46	*Neoglyphidodon nigroris*	0.5	0.93	0.27	0.82	52.94

47	*Premnas biaculeatus*	0.5	0.1	0.27	0.82	53.76
48	*Labropsis alleni*	0.5	0.21	0.27	0.82	54.58
49	*Macropharyngodon meleagris*	0.5	0.76	0.27	0.82	55.4
50	*Chromis atripectoralis*	0.5	0.71	0.27	0.82	56.21
51	*Chaetodon rafflesi*	0.5	0.67	0.27	0.81	57.03
52	*Pomacentrus nigromarginatus*	0.5	0.38	0.27	0.81	57.84
53	*Cheilio inermis*	0.5	0.62	0.27	0.81	58.65
54	*Chaetodon punctatofasciatus*	0.5	0.62	0.27	0.81	59.47
55	*Abudefduf sexfasciatus*	0.5	0.43	0.27	0.81	60.28
56	*Novaculichthys taeniourus*	0.5	0.52	0.27	0.81	61.09
57	*Oxycheilinus celebicus*	1	0.5	0.27	0.81	61.9
58	*Chrysiptera springeri*	1	0.5	0.27	0.81	62.71
59	*Hologymnosus doliatus*	0.5	0.45	0.27	0.81	63.52
60	*Choerodon anchorago*	0.5	0.43	0.27	0.81	64.32
61	*Oxycheilinus unifasciatus*	0.5	0.36	0.27	0.81	65.13
62	*Halichoeres richmondi*	0.5	0.67	0.27	0.81	65.94
63	*Stethojulis interupta*	0.5	0.64	0.27	0.81	66.74
64	*Cheilinus trilobatus*	0.5	0.71	0.27	0.8	67.55
65	*Chromis atripes*	0.5	0.26	0.27	0.8	68.35
66	*Coradion chrysozonus*	0.5	0.24	0.27	0.8	69.15
67	*Thalassoma jansenii*	0.5	0.21	0.27	0.8	69.96
68	*Centropyge nox*	0.5	0.83	0.27	0.8	70.76
69	*Hemitaurichthys polylepis*	0.5	0.14	0.27	0.8	71.56
70	*Pomacanthus navarchus*	0.5	0.05	0.27	0.8	72.36
71	*Centropyge tibicen*	0.5	1	0.27	0.8	73.15
72	*Pomacentrus philippinus*	1	0.52	0.26	0.79	74.74
73	*Cirrhilabrus lubbocki*	1	0.52	0.26	0.79	75.53
74	*Hologymnosus annulatus*	0	0.48	0.26	0.77	76.3
75	*Anampses meleagrides*	0	0.48	0.25	0.76	77.06
76	*Thalassoma amblycephalum*	0	0.45	0.24	0.71	77.77
77	*Chaetodon adiergastos*	0	0.43	0.23	0.69	78.46
78	*Halichoeres chrysus*	1	0.6	0.22	0.67	79.13
79	*Chaetodon trifascialis*	1	0.6	0.22	0.67	79.8
80	*Heniochus chrysostomus*	0	0.38	0.2	0.6	80.4
81	*Cheilinus oxycephalus*	0	0.36	0.19	0.58	80.98
82	*Chromis scotochiloptera*	0	0.31	0.17	0.51	81.49
83	*Chromis analis*	1	0.71	0.16	0.47	81.96
84	*Chaetodon speculum*	0	0.29	0.15	0.46	82.42
85	*Genicanthus lamarck*	0	0.29	0.15	0.46	82.87
86	*Chaetodontoplus mesoleucus*	1	0.71	0.15	0.45	83.33
87	*Neopomacentrus anabatoides*	0	0.29	0.15	0.45	83.78
88	*Heniochus singularis*	0	0.29	0.15	0.45	84.24
89	*Labroides bicolor*	0	0.29	0.15	0.45	84.69
90	*Cheilinus fasciatus*	1	0.74	0.14	0.43	85.12
91	*Anampses twistii*	0	0.26	0.14	0.42	85.53
92	*Gomphosus varius*	1	0.76	0.13	0.39	85.93
93	*Halichoeres scapularis*	1	0.76	0.13	0.39	86.31
94	*Oxycheilinus diagrammus*	1	0.76	0.12	0.37	86.69
95	*Centropyge bispinosus*	0	0.24	0.12	0.37	87.06
96	*Chromis delta*	0	0.24	0.12	0.37	87.44
97	*Plectroglyphidodon dickii*	0	0.24	0.12	0.37	87.81
98	*Pomacanthus imperator*	0	0.24	0.12	0.37	88.18
99	*Epibulus insidiator*	1	0.79	0.12	0.36	88.54
100	*Chaetodon oxycephalus*	0	0.21	0.12	0.35	88.88

101	*Pomacentrus chrysurus*	0	0.21	0.12	0.35	89.23
102	*Halichoeres biocellatus*	1	0.79	0.12	0.35	89.58
103	*Chaetodon citrinellus*	0	0.21	0.11	0.34	89.92
104	*Chaetodon xanthurus*	0	0.21	0.11	0.34	90.26

Appendix 4.8 Results of 'similarity/distance percentage' (SIMPER) analysis in PRIMER for group I vs. group J (see Materials and methods of Chapter 4). The average presence/absence of each species in groups I and J, average dissimilarity between groups (Ave. Diss.), percent contribution to dissimilarity (% Cont.) and cumulative % of dissimilarity (Cum. %) are shown. Data sorted according to increasing cumulative % of dissimilarity.

		Ave. Presence/Absence		Ave.		
	Species	Group I	Group J	Diss.	% Cont.	Cum. %
1	*Chromis scotochiloptera*	0.1	0.77	0.38	1.38	1.38
2	*Anampses geographicus*	0.72	0.08	0.37	1.34	2.73
3	*Pomacentrus philippinus*	0.72	0.08	0.37	1.34	4.06
4	*Forcipiger flavissimus*	0.76	0.15	0.36	1.32	5.38
5	*Centropyge bicolor*	0.83	0.23	0.36	1.31	6.7
6	*Chaetodon punctatofasciatus*	0.79	0.23	0.35	1.27	7.96
7	*Halichoeres richmondi*	0.83	0.31	0.33	1.21	9.18
8	*Chaetodon ornatissimus*	0.72	0.31	0.31	1.14	10.32
9	*Stethojulis bandanensis*	0.66	0.23	0.31	1.13	11.45
10	*Abudefduf sexfasciatus*	0.31	0.69	0.31	1.12	12.57
11	*Chaetodon melannotus*	0.69	0.31	0.31	1.12	13.69
12	*Pomacentrus bankanensis*	0.69	0.31	0.31	1.11	14.81
13	*Chromis xanthura*	0.62	0.23	0.3	1.1	15.9
14	*Chaetodon ocellicaudus*	0.62	0.23	0.3	1.09	16.99
15	*Hologymnosus annulatus*	0.59	0.23	0.29	1.07	18.06
16	*Cirrhilabrus lubbocki*	0.62	0.31	0.29	1.07	19.13
17	*Neoglyphidodon thoracotaeniatus*	0.59	0.23	0.29	1.06	20.19
18	*Centropyge nox*	1	0.46	0.29	1.05	21.24
19	*Chromis atripectoralis*	0.83	0.46	0.28	1.03	22.27
20	*Hologymnosus doliatus*	0.55	0.23	0.28	1.02	23.29
21	*Chaetodon rafflesi*	0.76	0.46	0.28	1.01	24.31
22	*Oxycheilinus unifasciatus*	0.28	0.54	0.28	1.01	25.32
23	*Chaetodon trifascialis*	0.66	0.46	0.28	1.01	26.32
24	*Stethojulis interupta*	0.48	1	0.27	1	27.32
25	*Pomacentrus nigromarginatus*	0.52	0.08	0.27	1	28.32
26	*Choerodon anchorago*	0.52	0.23	0.27	1	29.31
27	*Novaculichthys taeniourus*	0.48	0.62	0.27	0.99	30.3
28	*Labropsis manabei*	0.48	0.62	0.27	0.98	31.29
29	*Chrysiptera springeri*	0.52	0.46	0.27	0.98	32.27
30	*Oxycheilinus celebicus*	0.48	0.54	0.27	0.98	33.25
31	*Anampses meleagrides*	0.48	0.46	0.27	0.97	34.22
32	*Amphiprion sandaracinos*	0.59	0.54	0.27	0.96	35.18
33	*Thalassoma amblycephalum*	0.48	0.38	0.26	0.96	36.15
34	*Chaetodon auriga*	0.66	0.54	0.26	0.96	37.1
35	*Cheilio inermis*	0.66	0.54	0.26	0.95	38.06
36	*Chaetodon adiergastos*	0.45	0.38	0.26	0.95	39.01
37	*Chaetodon lunula*	0.52	0.92	0.26	0.95	39.96
38	*Pomacentrus adelus*	0.72	0.54	0.26	0.95	40.91
39	*Halichoeres chrysus*	0.59	0.62	0.26	0.94	41.86
40	*Heniochus chrysostomus*	0.48	0.15	0.26	0.94	42.8
41	*Pseudocheilinus evanidus*	0.45	0.31	0.26	0.94	43.74
42	*Cheilinus trilobatus*	0.79	0.54	0.26	0.93	44.67
43	*Chaetodon vagabundus*	0.97	0.54	0.25	0.92	45.6
44	*Oxycheilinus bimaculatus*	0.38	0.38	0.25	0.92	46.52
45	*Cheilinus oxycephalus*	0.38	0.31	0.24	0.89	47.41
46	*Halichoeres marginatus*	0.28	0.38	0.24	0.88	48.28

47	*Chaetodon octofasciatus*	0.34	0.31	0.24	0.86	49.15
48	*Halichoeres solorensis*	0.76	0.62	0.24	0.86	50
49	*Genicanthus lamarck*	0.24	0.38	0.24	0.86	50.86
50	*Cheilinus fasciatus*	0.79	0.62	0.23	0.85	51.7
51	*Halichoeres scapularis*	0.83	0.62	0.23	0.83	52.53
52	*Chaetodontoplus mesoleucus*	0.59	1	0.22	0.81	53.34
53	*Neopomacentrus anabatoides*	0.41	0	0.22	0.81	54.15
54	*Chromis analis*	0.72	0.69	0.22	0.81	54.96
55	*Halichoeres biocellatus*	0.86	0.62	0.22	0.8	55.76
56	*Chaetodon ulietensis*	0.1	0.38	0.22	0.79	56.56
57	*Chaetodon speculum*	0.31	0.23	0.21	0.78	57.33
58	*Halichoeres nebulosus*	0.34	0.15	0.21	0.77	58.11
59	*Anampses twistii*	0.24	0.31	0.21	0.77	58.88
60	*Heniochus singularis*	0.38	0.08	0.21	0.77	59.65
61	*Labroides bicolor*	0.38	0.08	0.21	0.77	60.42
62	*Gomphosus varius*	0.79	0.69	0.21	0.76	61.18
63	*Heniochus acuminatus*	0	0.38	0.2	0.74	61.92
64	*Epibulus insidiator*	0.83	0.69	0.2	0.74	62.66
65	*Pomacentrus opisthostigma*	0.83	0.69	0.2	0.74	63.4
66	*Chaetodon oxycephalus*	0.17	0.31	0.2	0.73	64.13
67	*Thalassoma jansenii*	0.17	0.31	0.2	0.73	64.86
68	*Pomacentrus chrysurus*	0.17	0.31	0.2	0.73	65.59
69	*Chromis atripes*	0.34	0.08	0.2	0.72	66.31
70	*Cheilinus chlorourus*	0.76	0.77	0.2	0.71	67.02
71	*Chromis delta*	0.24	0.23	0.19	0.69	67.71
72	*Pomacentrus burroughi*	0.1	0.31	0.19	0.68	68.39
73	*Cheiloprion labiatus*	0.1	0.31	0.19	0.67	69.07
74	*Oxycheilinus diagrammus*	0.66	1	0.18	0.67	69.73
75	*Centropyge bispinosus*	0.34	0	0.18	0.67	70.4
76	*Coradion chrysozonus*	0.28	0.15	0.18	0.66	71.07
77	*Macropharyngodon meleagris*	0.72	0.85	0.18	0.66	71.73
78	*Plectroglyphidodon dickii*	0.34	0	0.18	0.66	72.39
79	*Pomacanthus imperator*	0.34	0	0.18	0.66	73.05
80	*Chromis viridis*	0.93	0.69	0.18	0.66	73.71
81	*Chaetodon citrinellus*	0.21	0.23	0.18	0.66	74.37
82	*Hemigymnus melapterus*	0.86	0.77	0.17	0.61	74.97
83	*Chaetodon xanthurus*	0.31	0	0.16	0.6	75.57
84	*Bodianus axillaris*	0.31	0	0.16	0.6	76.17
85	*Labropsis alleni*	0.31	0	0.16	0.6	76.76
86	*Coris gaimard*	0.79	0.85	0.16	0.59	77.35
87	*Heniochus monoceros*	0	0.31	0.16	0.58	77.94
88	*Dascyllus melanurus*	0.21	0.15	0.16	0.58	78.51
89	*Chromis weberi*	0.83	0.85	0.15	0.54	79.06
90	*Diproctacanthus xanthurus*	0.72	1	0.15	0.53	79.59
91	*Forcipiger longirostris*	0.28	0	0.14	0.52	80.11
92	*Chaetodon ephippium*	0.07	0.23	0.14	0.51	80.62
93	*Plectroglyphidodon lacrymatus*	0.97	0.77	0.14	0.5	81.13
94	*Anampses neoguinaicus*	0.21	0.08	0.14	0.5	81.62
95	*Amphiprion perideraion*	0.79	0.92	0.14	0.5	82.12
96	*Premnas biaculeatus*	0.03	0.23	0.13	0.49	82.61
97	*Dischistodus melanotus*	0.21	0.08	0.13	0.48	83.09
98	*Hemitaurichthys polylepis*	0.14	0.15	0.13	0.48	83.57
99	*Halichoeres prosopeion*	0.86	0.85	0.13	0.48	84.05
100	*Apolemichthys trimaculatus*	0.14	0.15	0.13	0.48	84.53

101	*Pseudocheilinus hexataenia*	1	0.77	0.12	0.44	84.97
102	*Oxycheilinus rhodochrous*	0.17	0.08	0.12	0.43	85.4
103	*Macropharyngodon negrosensis*	0.9	0.85	0.12	0.43	85.83
104	*Amphiprion ocellaris*	0.79	1	0.11	0.4	86.23
105	*Halichoeres binotopsis*	0.21	0	0.11	0.4	86.64
106	*Dischistodus prosopotaenia*	0.07	0.15	0.11	0.4	87.04
107	*Pteragogus cryptus*	0.21	0	0.11	0.4	87.43
108	*Halichoeres argus*	0.14	0.08	0.1	0.37	87.81
109	*Pomacanthus semicirculatus*	0.14	0.08	0.1	0.37	88.18
110	*Neoglyphidodon nigroris*	0.97	0.85	0.1	0.36	88.54
111	*Cirrhilabrus cyanopleura*	0.97	0.85	0.1	0.36	88.89
112	*Pomacentrus nagasakiensis*	0.03	0.15	0.1	0.35	89.24
113	*Chaetodon lineolatus*	0.03	0.15	0.1	0.35	89.59
114	*Pomacentrus lepidogenys*	0.97	0.85	0.09	0.34	89.93
115	*Chromis margaritifer*	0.97	0.85	0.09	0.34	90.27