SEAGRASS POPULATION CONNECTIVITY
IN THE SOUTH CHINA SEA

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ABSTRACT

Seagrass plays important ecological roles and ecosystem services, yet degrading alarmingly in the South China Sea (SCS), one of the largest marginal seas of the Western Pacific. As connectivity is a vital component in population persistence, understanding of connectivity is of importance for effective seagrass conservation management. In the South China Sea, our understanding of connectivity is mainly based on studies in fishes and invertebrates. Connectivity in seagrass populations, on the other hand, is still poorly investigated. In this review, I predict that genetically structured population of seagrass is likely to occur in the SCS. Future research on seagrass connectivity should include (i) investigation on the pattern of connectivity at a local and broader-regional scale, and (ii) investigation on processes involved in the seagrass connectivity. These investigations are aimed to improve our knowledge of seagrass connectivity and to contribute in providing a solid framework for seagrass restoration/transplantation and spatial planning of seagrass management.

Keywords: seagrass, connectivity, conservation, South China Sea, resilience

INTRODUCTION

In the marine environment, most populations are not randomly distributed in space and they are geographically separated from each other. These populations are often linked to each other to some degree by the exchange of organisms, genes, and materials (e.g., nutrients, pollutants). Connectivity is basically described as the degree of which exchange of materials links populations and encompasses three main aspects, 1) genetic or evolutionary connectivity (the exchange of genes), 2) demographic connectivity (individual exchanges among populations through dispersal), and 3) oceanographic connectivity (flow of materials, mostly by water circulation and currents) (Kool et al., 2013; Lowe & Allendorf, 2010).

In the face of climate change and increasing anthropogenic pressures on marine ecosystems, there has been growing interest among conservationists and ecologists in understanding connectivity and its impact on the persistence of metapopulation. Studies in connectivity link with many subjects in ecology and conservation, including source-sink population dynamics (Bode et al., 2006), dispersal and migration (Cowen & Sponaugle, 2009), and potential resilience to climate changes (Bernhardt & Leslie, 2013). Importantly, understanding connectivity also provides practical insights on a broad range of conservation management, for example, designation of marine protected areas and unit to conserve/UTC (Green et al., 2014; Magris et al., 2014) restoration/transplantation program (Lipcius et al., 2008) and predicting/controlling outbreaks of diseases or invasive species (Hock et al., 2014).

Seagrasses, angiosperms living in the marine environment, are foundation species that form ecologically critical coastal ecosystems, yet they are globally degrading. In the coastal ecosystems, they play significant roles in food web dynamics (Duffy 2006, Vonk et al., 2008),

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nutrient recycling (McGlathery et al., 2007), carbon sink (Duarte, 2016), and habitat provision for numerous organisms, many of which are commercially important species (Ávila et al., 2015; Gartner et al., 2013; Hutchinson et al., 2014). While providing important functions and services, seagrasses are declining in many parts of the world, including the South China Sea; calling for urgent, effective management actions (Short et al., 2014; Vo et al., 2013; Waycott et al., 2009). With regards to effective management, studies in population connectivity may provide a significant contribution in formulating conservation management of seagrasses, especially in the South China Sea.

The review first presents the findings of a literature review of the extent of seagrass conservation status in the South China Sea. Secondly, focuses on the knowledge gap of seagrass connectivity in the South China Sea and how to measure connectivity. Lastly, provides an outline of a direction for future research needed to fill the knowledge gaps and how conservation managers could benefit from the research.

THE SOUTH CHINA SEA

The South China Sea (SCS) is a semi-enclosed sea surrounded by most ASEAN countries (i.e., Singapore, Brunei, Indonesia, Malaysia, Cambodia, Vietnam, and the Philippines) and

Figure 1. The South China Sea situated in Southeast Asia. Dashed circles show hypothetical genetic clusters of seagrass population: Hainan Cluster, Luzon Cluster, Natuna Cluster, and the Gulf Cluster (Panel A). The seasonally changing pattern of water circulation in winter (December-February, Panel B) and in summer (June-August, Panel C). Arrowed lines indicate water current and its directions. SCWS: South China Sea Warm Current; GCC: Guangdong Coastal Current; LCG: Luzon Cyclonic Gyre; NOC: Natuna Offshelf Current; SCG: South China Sea Cyclonic Gyre; VOC: Vietnam Offshore Current (modified from Hu et al., 2000).
China (Figure 1). It is one of the largest marginal seas of the Western Pacific Ocean, spanning the tropical to subtropical zones and covering about 3.5 million square kilometers with an average depth of 1,212 m. The southern limit of the SCS is adjoined with the Java Sea, while the northern limit borders with the East China Sea. On the eastern side, the SCS neighbors with the Sulu Sea and the Pacific Ocean. The SCS connects with the Indian Ocean through the Malacca Strait and the Karimata Strait (Liu, 2013). The coastal borders of the SCS are home to 270 million people, many of whom are dependent on the ecosystem services provided by the sea, e.g., food and livelihood (Vo et al., 2013).

The SCS is generally characterized by eddies and seasonal circulation which reverses its direction in winter (cyclonic) and summer (anticyclonic) (Figure 1). The circulation pattern at the surface layer is mostly driven by the combination of monsoon winds and water exchange between the SCS, the Kuroshio (through the Luzon Strait), and the East China Sea (through the Taiwan Strait). Seabed topography could also contribute to the pattern. Those factors result in at least two prominent eddies: the Luzon Cyclonic Gyre (LCG) in the west side on Luzon and the South China Sea (Anti-) Cyclonic Gyre (SCG) in the Southern part of the SCS (Hu et al., 2000).

Although it occupies less than 2% of Earth’s surface covered by oceans, the SCS harbors diverse assemblages of ecosystems ranging from coral reefs, rocky and sandy shores, seagrasses, mangroves, estuaries, and mudflats to open waters, and has rich reserves of marine biodiversity supporting millions of livelihoods. Species richness in this region averaged 247 species per 100km coastline (Liu, 2013; Ng & Tan, 2000). Being at the western border of the Coral Triangle, the center of maximum marine biodiversity, at least 3,365 species of fishes have been recorded from this region (Arai, 2015; Randall & Lim, 2000). With only 4.7% of the world’s total reef surface area, the SCS is home to 571 species of coral reef, rivaling the Coral Triangle that has 605 species (Huang et al., 2015). Of the 60 seagrass species found worldwide, 18 species were reported to occur in the South China Sea. Mangrove forests (45 mangrove species out of a global total of 51) were estimated to cover about 1,770,000 ha (11.4% of the world’s mangrove forests) in the coastal region of the SCS (Morton & Blackmore, 2001; Vo et al., 2013). Further, in the context of ecosystem services, the SCS has contributed significantly to global fisheries production where about 10% of the global annual fisheries catch was reported from the SCS, and countries bordering the SCS are among the top producers of shrimps and tunas (Song, 2011; UNEP, 2007).

**SEAGRASS CONSERVATION IN THE SOUTH CHINA SEA**

With rapid development and industrialization, the SCS is one of the world’s most over-exploited and degraded ecosystem. Seagrass habitats have been experiencing degradation with decadal loss rates (30% in 2006). More than half of the original mangrove habitats had been lost during the last century. However, coral reefs, a biologically diverse ecosystem, is degrading (16% in 2007) (Vo et al., 2013). Stocks of many economically important species have been reported to be depleted or collapsed due to over-fishing. Illegal, unreported, and unregulated (IUU) fishing is common in the region (Li & Amer, 2015; Vo et al., 2013). Main threats identified on these ecosystems are anthropogenic activities, such as coastal development, pollution, destructive fishing, coastal aquaculture and mariculture, unsustainable tourism, coastal construction, and deforestation upland (Vo et al., 2013). Ecosystem degradation requires more effective measures in fisheries management and marine biodiversity conservation as these interventions are yet to eliminate the threats and to improve the ecosystem status (Zou, 2015).

Despite their important ecosystem services and critical roles in coastal ecosystems, seagrasses have been degrading increasingly at both a global (Waycott et al., 2009) and regional scale: such as the South China Sea (Vo et al., 2013). Vietnam had lost 50% of seagrass meadows within the last decade (Luong et al., 2012). The status of seagrass beds in Indonesia is poorly known, but one source (UNEP, 2008) reported at least 30% of habitat loss in Indonesian seagrass since 1966. About 45% of seagrass habitats have been lost within the last five decades in Singapore (Yaakub et al., 2014). In Thailand, seagrass habitat...
had degraded 20-30%, and in the Philippines, the habitat loss is about 30-50%. Seagrass degradation is mainly driven by anthropogenic factors, particularly destructive fishing, overfishing, sedimentation from coastal development, wastewater effluent, nutrients inputs, severe coastal storms and coastal infrastructure (UNEP, 2008; Vo et al., 2013).

The decline of seagrass ecosystems has necessitated implementation of effective management practices for seagrass restoration and conservation. About 16.5% of the total known area of seagrass in the South China Sea is currently under some form of management, yet most of the management sites do not have any specific legal status. Further, the effectiveness of the conservation management was generally medium to low (Vo et al., 2013). This low success rate of seagrass management was also experienced in many parts of the world (Cunha et al., 2012). Although factors responsible for the management failure vary spatially and temporally at multiple scales, two important factors were highlighted: (i) understanding of population connectivity so that the appropriate spatial scales of the conservation management are considered, and (ii) the critical roles of selecting appropriate donor and restoration sites (Cunha et al., 2012; van Katwijk et al., 2009).

MEASURING POPULATION CONNECTIVITY

Connectivity can have profound consequences in metapopulation dynamics and population persistence. In the context of genetic connectivity, movement of individuals allows gene flow to occur. However, a certain level of gene flow (immigrant) is required to spread advantageous alleles and to avoid harmful effect local inbreeding (Lowe & Allendorf, 2010). Furthermore, as populations need to adapt to environmental changes (e.g., climate change), connectivity ensures species’ adaptive potential to be spread across a metapopulation (Frankham, 2005).

In the context of demographic connectivity, in which population growth (or specific vital rate, e.g., survival) is affected by immigration or emigration, a population can benefit from the supply of immigrants from other populations as a subsidy to compensate low survival or birth rates. In source-sink dynamics, immigrants from source populations can be critical for the persistence of sink populations that have low local recruitment. If sink populations are strongly dependent on the source populations, the diminished supply of immigrants due to, for example, extinction in the sources and changes in the pattern of oceanographic connectivity resulting in dispersal limitation, may pose a risk of extinction for the sink populations (Lowe & Allendorf, 2010).

Measuring Connectivity with the Genetic Approach

Direct tracking may be the most powerful tool to examine connectivity over demographic timescales, yet this tool is not representative over longer timescales (e.g., evolutionary) (Kool et al., 2013). Furthermore, given the vast size of the ocean and the minute size of seagrass propagules (fruit, seeds, and pollen), examining patterns of connectivity by direct tracking is not feasible; thus a different approach is needed. Here, the genetic approach can be used to estimate connectivity indirectly. As successful migrants carry genetic traits of their natal site, the pattern of connectivity over a broad range of spatial and temporal scale can be inferred from the gene flow among populations. Varying levels of gene flow among populations leads in spatially distributed genetic variation that reflects the structure of the metapopulation (Lowe & Allendorf, 2010).

Depending on the objectives and scales of various genetic markers (e.g., microsatellites, single nucleotide polymorphisms/SNP, mitochondrial DNA, etc.) these can be used for estimating connectivity. Microsatellite can be used to assess contemporary connectivity as the mutation rate is relatively high (10-2 to 10-6 mutations per locus per generation). The microsatellite is characterized by highly polymorphic loci, thus very informative to detect change at both the finer spatial scale and the more recent time scale (Selkoe & Toonen, 2006). Sequences of mitochondrial or chloroplastic DNA might be used for examining historical connectivity; however these markers are known to have small variations, thus might not be able to detect changes among populations (Aires et al., 2011; Olsen et al., 2004). In case of failing to detect variation using the sequence markers,
The Pattern of Seagrass Connectivity

Our understanding of seagrass population connectivity in the SCS is yet to develop as connectivity studies in the region are still limited. Studies have mostly focused on marine animals (fishes and invertebrates) using a broader spatial context that includes the neighboring regions, for example, the Coral Triangle and the western Pacific Ocean. Several patterns emerged from these studies. For example, a genetic study on the big eye tuna (Thunnus obesus) showed strong connectivity among the tuna populations in the SCS, Philippine Sea, and the western Pacific Ocean, suggesting that the fish populations over the sampling regions constitute a single panmictic population (Chiang et al., 2006). Furthermore, sub-population structure within the SCS was revealed on other fish species, for example, the six bar wrasse (Thalassoma hardwickii) (Chen et al., 2004) and the mottled spinefoot Siganus fuscescens (Ravago-Gotanco & Juinio-Meñez, 2010). Fine-scale population structure within the SCS system was also revealed in the blue starfish Linckia laevigata and the giant clam Tridacna crocea (Juinio-Meñez et al., 2003). By contrast, the sea urchin (Tripneustes gratilla) did not show any significant genetic differentiation in this region (Casilagan et al., 2013).

Our knowledge of seagrass connectivity in the SCS may be limited and based on Cymodocea rotundata (Arriesgado et al., 2016), C. serrulata (Arriesgado et al., 2015), Enhalus acoroides (Nakajima et al., 2014), and Thalassia hemprichii (Hernawan et al., 2017). The pattern of seagrass connectivity varies among species, and population may be genetically structured at different spatial scales, from a few meters (within meadows) to hundreds of kilometers (among regions). Seagrass panmictic populations can be spatially very large in size, from hundreds to thousands of kilometers as indicated in C. rotundata, C. serrulata, E. acoroides, and Thalassia hemprichii (Arriesgado et al., 2015, 2016; Hemawan et al., 2017; Nakajima et al., 2014). However, the structured population may also occur at finer scales (tens of kilometers; within meadows and among meadows), for example in E. acoroides in the Guimaras Strait, Philippines (Nakajima et al., 2017).

Although the spatial context of those studies was not necessarily located in the SCS, the studies suggested that a single panmictic seagrass population may not occur in the SCS. The seagrass E. acoroides showed limited seagrass connectivity between the Hainan island populations (northern SCS) and the Philippine populations (Nakajima et al., 2014), while the seagrass C. serrulata in the western seaboard of Luzon (on the SCS coast) were genetically clustered with the other populations in the Philippines (Arriesgado et al., 2015). On the other hand, C. rotundata showed limited connectivity among populations in the Hainan island, the Philippine, and Ryukyu island (Arriesgado et al., 2016). In addition, seagrass in Natuna islands, particularly T. hemprichii, was reported to be genetically connected with other populations in the Java Sea and Karimata Strait (Hernawan et al., 2017).

The pattern of population connectivity in seagrass can be significantly influenced by abiotic factors, such as water currents (Hernawan et al., 2017; McMahon et al., 2014). Based on the water circulation pattern (Figure 1B and 1C), it is predicted that seagrass populations in the SCS are structured into four genetic clusters (Figure 1A). Seagrass around the Hainan islands and the Vietnamese coast would be clustered into a single genetic population (Hainan Cluster). The Guangdong Coastal Current (GCC) may facilitate connectivity among seagrass meadows within this genetic population. The LCG that occurs on the western side of Luzon would likely form a connectivity barrier between the Hainan Cluster and the Luzon Cluster. These two clusters were evidently indicated in C. rotundata (Arriesgado et al., 2016). Seagrass around Natuna islands would form single a single genetic cluster (Natuna Cluster) since the SCG might prevent seagrass dispersal beyond the region affected by that gyre. Additionally, seasonal eddies occurring in the Gulf of Thailand might drive seagrasses in the gulf forming the Gulf Cluster separated from populations in the other regions. It is important to note that the patterns mentioned above are hypothetical, and empirical studies are needed to test this prediction.
RESEARCH DIRECTION

As data are insufficient to draw complete patterns of seagrass connectivity at any spatial and temporal scale in the SCS, future research should aim to address the following topics:

The Pattern of Connectivity

The general prediction of a pattern of seagrass connectivity in the SCS has been highlighted (Figure 1) and can be used as a framework to investigate seagrass connectivity in the region empirically. In the observed patterns of connectivity of most marine mammals, these are partially driven by their dispersal potential mainly associated with the species mobility characteristic and the larval duration (Bradbury et al., 2008; Cowen & Sponaugle, 2009). Because seagrasses passively disperse via: (i) propagules (seeds or fruits), (ii) clonal propagation, and (iii) vegetative fragment (unrooted shoots), ranging from a few meters to several hundreds of kilometers over different time scale (days to millennia) (McMahon et al., 2014), different patterns of connectivity might be expected in seagrass populations.

Investigation on this topic encompasses many relevant research questions. Is there any population structure? How many panmictic populations are there? If there is any pattern of population structure, to what extent are the populations connected to each other? Considering the connectivity strength and directionality, is the connectivity among populations symmetrical or asymmetrical? Which populations do act as the sources or sinks? Is there any barrier to connectivity?

Examinining connectivity at a broader spatial scale, are seagrass populations within the SCS clustered together and connected with the other populations of the neighboring regions, for example, the Coral Triangle? If so, what proportion of seagrass recruits is originated from the local meadows, and what proportion comes from outside the SCS? As recent biophysical studies showed a strong connection between the SCS (particularly the Spratly Islands) with the Coral Triangle (Treml et al., 2015) and the SCS acts as important sources of larvae and genetic diversity for the Coral Triangle (Kool et al., 2011), can we expect the same pattern in seagrass population? To what degree the regional connectivity is supporting population recovery of degraded meadows within the SCS and the neighboring regions?

Processes Controlling Connectivity

There are gaps of knowledge in understanding processes that control connectivity in the SCS. Conceptually, connectivity in seagrass population occurs via dispersal of pollen, sexual propagules, and vegetative fragments, mainly by the water current. Seagrasses also expand and colonize available habitat by the individual spread of clonal growth (McMahon et al., 2014). Previous studies have indicated the potential dispersal distance of E. acoroides and T. hemprichii (Lacap et al., 2002) and the influence of the Kuroshio Current in determining the pattern of seagrass connectivity. Several populations show strong genetic connectivity although they have geographically separated far away (>1000 km) (Arriesgado et al., 2015; Hernawan et al., 2017; Nakajima et al., 2014).

To improve our understanding of seagrass connectivity in the SCS, we need to investigate how the interaction between the plants, dispersal vectors (e.g., water current) and the local environmental state determines the seagrass connectivity. How far can the local water current disperse seagrass propagules? What is the probability of successful movement (migrants settle and contribute to the local recruitment) for sexual and vegetative propagules? What is the significance of successful movement to the local population? What is the extent of clonal growth and its significance? Are there any biotic vectors for moving seagrass in the SCS?

SEAGRASS CONSERVATION MANAGEMENT

Comprehensive understanding of connectivity contributes in providing a solid framework for seagrass restoration, transplantation and spatial planning of seagrass management. In a rapidly changing environment, one of the major conservation goals is to maintain species population resilience by representatively protecting the population. Connectivity is crucial in population resilience as it enhances ecosystem capacity for recovery and self-organization after
disturbances. The exchange of propagules, larvae and adults among populations may maintain genetic diversity and also reduce the risk of local extinction because it allows continuous recruitment from outside sites (Bernhardt & Leslie, 2013; Lowe & Allendorf, 2010). For this reason, research on seagrass connectivity provides insight about: (i) the spatial size of management unit, (ii) design of marine reserve network, (iii) which population should be prioritized for the management (based on source-sink populations), and (iv) which population should be selected as a donor population in the case of seagrass transplantation.

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