

# Coral reef social–ecological systems under pressure in Southern Sulawesi

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**Abstract**

*Ecological and social processes of the Spermonde Archipelago, South Sulawesi, Indonesia, have been intensively studied during the Science for the Protection of Indonesian Coastal Ecosystems (SPICE) program. The archipelago is of specific interest to better understand how intensive exploitation of marine resources results in the degradation of reef systems. The projects specifically targeted (1) ecological processes in coral reefs, (2) genetic structure of populations, and (3) social–ecological dynamics relating to resource use, social networks, and governance structures. A modeling component emphasized (4) the integration of different ecological, social, and environmental components. Results indicated that reef resources in the Spermonde Archipelago are intensively exploited and further stressed by pollution effluents from hinterland processes. The lack of alternative livelihoods perpetuates dependencies within the patron–client system of the artisanal fisheries and supports high exploitation and also destructive resource uses. Greater inclusion of local stakeholders in the governance may result in better conservation practices, sustainable resource use, and improved livelihoods for the people.*

**Abstrak**

*Selama proyek SPICE, aspek ekologis dan sosial di perairan Kepulauan Spermonde, Sulawesi Selatan, Indonesia, dipelajari secara intensif. Kepulauan dan perairan ini mengundang banyak perhatian untuk lebih memahami bagaimana tingkat pemanfaatan sumber daya laut yang intensif berakibat pada degradasi sistem terumbu karang. Kerangka kerja proyek penelitian SPICE, secara khusus, menargetkan kajian-kajian mengenai (a) proses ekologis dalam sistem terumbu karang, (b) struktur genetik populasi untuk menentukan konektivitasnya, dan (c) dinamika sosial-ekologi yang berkaitan dengan penggunaan sumber daya, jejaring sosial dan struktur tata kelola. Komponen pemodelan juga dimasukkan kedalam kajian mengenai (d) integrasi berbagai komponen ekologi, sosial dan lingkungan dalam karakterisasi sistem sosial-ekologis. Hasil-hasil penelitian menunjukkan bahwa sumber daya terumbu karang di Kepulauan Spermonde sangat tereksplorasi dan terancam juga oleh limbah polusi dari proses di daratan. Kurangnya mata pencaharian alternatif memperkuat ketergantungan para nelayan tradisional pada sistem patron-klien dan meningkatkan penggunaan sumber daya yang tidak berkelanjutan dan merusak. Keikutsertaan pemangku kepentingan lokal yang lebih erat dalam tata kelola sumber daya alam Kepulauan Spermonde sangat memungkinkan hasil praktik konservasi yang lebih baik, penggunaan sumber daya berkelanjutan, dan peningkatan mata pencaharian bagi masyarakat.*

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## 5.1 Introduction—coral reefs in Indonesia and the Spermonde Archipelago

With its roughly 17,500 islands, Indonesia is located in the Coral Triangle along with Malaysia, Papua New Guinea, the Philippines, the Solomon Islands, and East Timor. Indonesia is renowned for a very high biodiversity in coastal ecosystems, especially in coral reefs. Of 590 known coral species, it is believed that more than 75% have been identified in Indonesian waters (Burke et al., 2012; Veron et al., 2009). It is estimated that more than 50% of Indo-Pacific and more than 37% of world reef fish species are represented in Indonesian waters (Asian Development Bank, 2014a; UNEP-WCMC, 2014). This extremely high biodiversity is also found in other coastal habitats such as mangroves (41 of 54 true mangrove species (Asian Development Bank, 2014a; Hogarth, 1999)) and seagrass meadows (13 species of tropical seagrasses (Asian Development Bank, 2014a)).

Coral reefs cover around 39,500 km<sup>2</sup> of Indonesian coastal waters amounting to approximately 16% of global coral reefs (Burke et al., 2012) and providing many crucial

ecosystem functions and services. The length of Indonesia's coastline is around 81,000 km, with 270,000 km<sup>2</sup> of shelf areas (depth up to 200 m). More than 900 of the Indonesian islands are permanently inhabited with much of the population living within 10 km of the coast. Thus, these communities are highly dependent on goods and services from coral reefs for livelihoods and other resources for local (coastal) economies. In 2007, fisheries contributed 2.4% to the national GDP and 1.9% to the total export value of all products, with more than 2.1 million people being employed in this sector ([Asian Development Bank, 2014b](#)). From 2000 until 2010, Indonesia provided 70% of the corals for the global ornamental and aquaria trade ([Wood et al., 2012](#)), while the whole of Southeast Asia accounted for 85% ([Asian Development Bank, 2014b](#)). [Burke et al. \(2002\)](#) specify the annual economic net benefit of a healthy Southeast Asian coral reef in a range between \$23,100 to \$270,000 per km<sup>2</sup> when tourism and esthetic values are added to fisheries and coastal protection. Overall, the marine resources of the Coral Triangle support ~130 million people locally, with tens of millions more through exports ([Burke et al., 2011](#)).

Currently, local human activities connected to intensive resource use, e.g., “overfishing,” including destructive techniques, threaten nearly 85% of Indonesian coral reefs ([Burke et al., 2012](#)). According to [Burke et al. \(2011\)](#), Indonesia is one of the nine countries on earth, most vulnerable to the effects of coral reef degradation. Furthermore, the effects of coastal development and watershed pollution are major contributors to the decline of coral reefs in the region over the past three decades ([Allen, 2008](#)) and continue to constitute imminent threats. Since 1998, resource use has increased on more than 50% of the Indonesian reefs, mainly driven by unsustainable fishing practices and destructive resource extraction and partly due to growing coastal populations. As a result, 35% of the reefs are classified in a high or very high threat category ([Burke et al., 2012](#)), with only slight improvements since the situation in 2002 ([Burke et al., 2002](#)). Due to complex relationships in reef systems, even small changes in reef cover have the potential for trophic cascades and changing cycles of organic matter, which may subsequently affect ecosystem services and the people that rely on them ([Arias-Gonzalez et al., 2011](#)).

Besides local anthropogenic threats, regional natural disturbances, as well as global climate change play an important role. Large bleaching events have increased in frequency and are no longer limited to El Niño years. Reports from the Coral Bleaching Network's rapid survey indicate that bleaching affected 25%–75% of reefs in 21 of 22 Indonesian provinces in 2016. West Papua was the only province without a bleaching report for 2016 ([Agung et al., 2018](#)). Localized, human-derived pressure on coral reefs within Indonesia is considered to be of greater immediate concern than large-scale global pressures, and it cannot be ignored that local or regional disturbances severely aggravate the capacity for coral reefs to recover from global disturbances, such as bleaching events ([Carilli et al., 2009](#)).

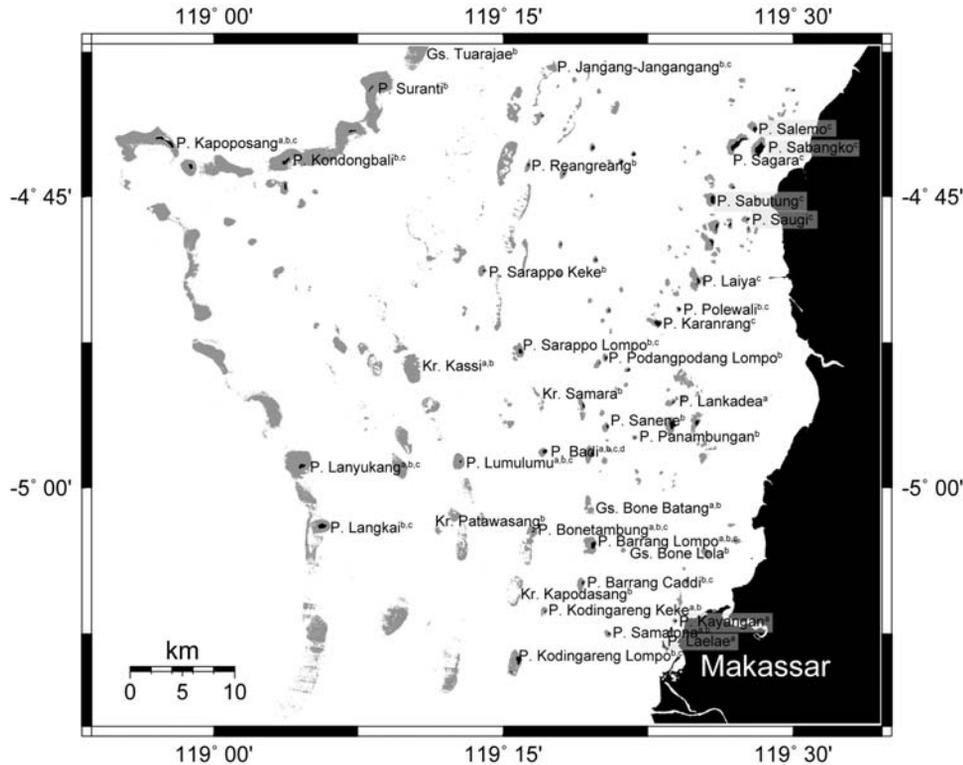
The Spermonde Archipelago is an area of particular interest because of its history of intensive coral reef resource exploitation and massive reef degradation. It was therefore

chosen as a research focus area of projects in all three Science for the Protection of Indonesian Coastal Ecosystems (SPICE) phases. The Spermonde Archipelago is located in the southwestern coastline of Sulawesi between the city of Makassar, the capital city of South Sulawesi, and the Makassar Strait. Makassar has a population of roughly 1.5 million people, and a further 1 million people inhabit the greater metropolitan area. This large population creates a high demand for the marine resources extracted from the archipelago (Schwerdtner-Máñez and Ferse, 2010; Ferse et al., 2014). Makassar is the largest city in eastern Indonesia, and its large maritime port (second largest in Indonesia) and airport serve as gateways to eastern Indonesia, thereby turning the city into a central export hub.

The Spermonde Archipelago consists of around 150 coral cays and reef islands of which approximately 50 are inhabited. The many submerged patch reefs, on a shallow limestone shelf, extend about 60 km offshore and 50 km along the coast and exhibit a clear nearshore–offshore gradient of biophysical conditions and anthropogenic impacts (Sawall et al., 2011; Seemann et al., 2013; Teichberg et al., 2018).

Depending on the availability of drinking water (Schwerdtner Máñez et al., 2012), the islands can be densely populated, with the population relying extensively on marine resources and offering residents very limited employment alternatives to fishing (Ferrol-Schulte et al., 2013). The local fishers employ various fishing methods, targeting a wide range of marine species and leading to a temporally and spatially variable exploitation pattern (Ferse et al., 2014). To a large extent, the Spermonde fishery functions in a tightly knit web of patron–client relationships. In these, patrons link artisanal fishers (clients) with national and international buyers via connections they have to traders in Makassar (Ferse et al., 2014; Miñarro et al., 2016), thereby transmitting changing demands and providing fishing techniques and equipment (see Section 5.4.2).

In recent decades, the coral reefs in the Spermonde Archipelago have undergone dramatic ecological changes, making the region an example for the contribution of very intensive fishing to the gradual destruction of a coastal ecosystem. The reefs are subject to a wide range of disturbances, derived both regionally from the main land and locally from the island's populations. The archipelago is home to the largest coral reef fishery in Indonesia (Pet-Soede and Erdmann, 1998), where fishers traditionally use long lines and fish traps. Over the past four decades, the use of more efficient and destructive fishing techniques (e.g., explosives, cyanide, compressors for diving) has increased the pressure on coastal ecosystems (Pet-Soede and Erdmann, 1998; Schwerdtner Máñez and Ferse, 2010). Glaser et al. (2015) report that blast fishing still continues, turning the reef into rubble unsuitable for coral recruitment. For the Pangkep Regency, the northern part of the Spermonde Archipelago, Yasir Haya and Fujii (2017) calculated that the proportion of live coral cover diminished from 7716 ha in 1994 to 4236 ha in 2014. For the island of Ballang Lompo, satellite images revealed an 80% loss of live coral cover between 1972 and 2016 and a more than 55% loss for seagrass habitat in the same timeframe (Nurdin et al., 2016).



**FIGURE 5.1** Map of the Spermonde Archipelago indicating the islands investigated during the SPICE program. Superscripts indicate in which project islands were explicitly investigated (a: ecology, b: genetics, c: social science, d: modeling).

In the following sections, we provide details of the work completed during the three phases of the SPICE program (2003–16) in the Spermonde Archipelago. This chapter covers the extensive ecological studies: from studies of the individual coral to studies of changes at the level of the reef community (Section 5.2), of the genetic population structure and population connectivity for a diversity of organisms (Section 5.3), and of social dependencies and governance (Section 5.4, see also Chapter 11), as well as analytical approaches, such as modeling (Section 5.5). The studies during the SPICE program covered many islands of the Spermonde Archipelago (Fig. 5.1).

## 5.2 Functioning of coral reefs

The coral reefs of the Spermonde Archipelago have been subject to a wide range of disturbances. Observed patterns within the coral reef communities of Spermonde are closely linked to anthropogenic disturbances originating from regional and/or local sources, which are superimposed on the effects of global climate change. Spatially and temporally varying disturbances from local sources determine persistent ecological

states of the coral reef systems, where differences in community composition and biodiversity are formed along a gradient of distance from shore. Indeed, studies have identified a positive relationship between species richness and distance from Makassar in coral (Edinger et al., 2000; Hoeksema, 2012), sponge (de Voogd et al., 2006), and foraminifera communities (Cleary and Renema, 2007). Beta diversity, or the difference in diversity between samples, of sea urchins, sponges, and corals displays a negative relationship with distance, suggesting communities closer to shore are more similar in their species composition (Becking et al., 2006) likely due in part to a loss of species diversity caused by disturbance. Among the many physical disturbances sustained by the reefs, some of the most impactful include destructive harvesting techniques of natural resources, such as blast fishing (Pet-Soede and Erdmann, 1998a,b; Pet-Soede et al., 1999; Pet-Soede et al., 2001), cyanide fishing (Erdman and Pet-Soede, 1997), and coral mining. Additionally, sewage and river discharge create a clear nearshore to offshore gradient of water quality (Nasir et al., 2016), thus contributing to coral degradation in nearshore reefs.

Through the three phases of the SPICE project, the coral reef ecosystems of the Spermonde Archipelago were intensely studied by joint teams from the Leibniz Centre for Tropical Marine Research, the University of Bremen, and the Hasanuddin University in Makassar (Research and Development Center for Marine, Coast, & Small Islands). Research comprised the organismal (Borell et al., 2008; Borell and Bischof, 2008; Sawall et al., 2011; Seemann et al., 2012; Sawall et al., 2014), population (Knittweis et al., 2009a,b; Knittweis and Wolff, 2010), community, and ecosystem levels (Sawall et al., 2012; Sawall et al., 2013; Plass-Johnson et al., 2015a,b; Plass-Johnson et al., 2016a,b; Plass-Johnson et al., 2018; Kegler et al., 2017a,b; Kegler et al., 2017; Kegler et al., 2018a; Teichberg et al., 2018). Importantly, the varying states of habitat degradation and the closely linked differences in coral reef ecosystem functioning are representative of many other coral reef ecosystems in the greater Southeast Asian region. Indicating a high dependency on natural resources derived from coral reefs and high levels of local and global disturbances, scientific output relating to the Spermonde Archipelago and the SPICE project provides critical ecological data to assist environmental management decisions at the local and regional levels. Given that these works have disentangled ecological, biological, and biophysical processes relating to disturbed coral reefs, the SPICE project has significantly enhanced fundamental understanding of coral reef system processes under high anthropogenic and natural stress—a situation likely to face reefs around the globe in the not-so-distant future (Hughes et al., 2017).

### 5.2.1 Water quality and biogeochemical processes

Nutrient input from various sources, including wastewater and fertilizer, is a major anthropogenic driver impacting coral reef functioning in the Spermonde Archipelago. Freshwater, riverine inputs from Tallo, Pangkep, and Maros estuaries have increased the supply of nutrients to the coastal waters of Spermonde Archipelago (Nasir et al., 2015),

resulting in a water quality gradient from near- to offshore reefs. Nutrient concentrations in the estuaries are higher in nitrogen (N), primarily ammonium and phosphorus (P), increasing in the rainy season. These nutrient inputs drive seasonal increases in phytoplankton concentrations within the estuaries and nearshore sites, ranging from 1 to 8 mg m<sup>-3</sup>. Riverine water is quickly mixed with marine waters, diluting nutrient concentrations at nearshore reef sites. However, long-term trends of poor water quality have been found, including high concentrations of chlorophyll *a* and suspended particulate matter (SPM), increased light attenuation, and occurrence of pathogenic bacteria (Kegler et al., 2017b; Sawall et al., 2011; Teichberg et al., 2018) during the many years of the SPICE program. These water quality indices generally improve at a short distance from shore (Sawall et al., 2011; Kegler et al., 2017b; Teichberg et al., 2018). Local inorganic and organic nutrient inputs from the islands, however, have been shown to influence primary production and bacterial concentrations on a smaller spatial scale, i.e., an individual coral reef system (Kegler et al., 2018a). Inorganic N, P, dissolved organic carbon (DOC), and transparent exopolymer particles (TEPs) were all elevated in back reef waters around an inhabited island, compared with an uninhabited island. This indicated that a lack of sewage treatment among inhabited islands can lead to detrimental water quality in reef systems (Kegler et al., 2018a). Mesozooplankton showed a remarkable difference in taxa composition between coast, shelf, and offshore areas in the Spermonde Archipelago, where the coastal zone was characterized by a high abundance of meroplankton and neritic copepod species, in contrast to an offshore community dominated by holoplanktonic organisms and oceanic copepod species (Cornils et al., 2010).

### 5.2.2 Benthic coral reef community dynamics of Spermonde Archipelago

The reefs of Spermonde are under intense pressure from more than 40,000 people inhabiting the Archipelago's islands, as well as from the coastal city of Makassar and agricultural activities on the coastal plains of South Sulawesi. Many of these activities cause indirect (yet strong) impacts on the reefs, e.g., via sedimentation and eutrophication related to terrestrial runoff and sewage seepage from the islands. In contrast, the harvesting of species with important ecological functions such as herbivory results in direct observable impacts on benthic communities. Blast fishing, which has persisted in the area for decades (Pet-Soede and Erdmann, 1998), has resulted in 20%–60% of the benthic live coral cover being reduced to rubble at 40%–60% of sites studied (Sawall et al., 2013; Teichberg et al., 2018). Prior to the 2018 ban on ornamental coral exports, some species, such as *Heliofungia actiniformis*, were harvested at sizes well below reproductive maturity, resulting in a change to their demographics at targeted reefs (Knittweis and Wolff, 2010). Partly, as a result of missing fisheries data, harvest quotas did not match population levels, and it was estimated that for some species, over 90% of the population was permitted to be removed within a year (Bruckner and Borneman, 2006).

The most notable observed change of the benthic community was a shift from live coral cover toward turf algae, macroalgae, and invertebrates (e.g., sponges and cnidarians).

However, this change was greater at nearshore than offshore reefs (Sawall et al., 2013; Teichberg et al., 2018; Plass-Johnson et al., 2018b). Furthermore, when there was more rubble, there were also more turf algae (Teichberg et al., 2018). When rubble is covered with turf algae rather than crustose coralline algae, reef recovery is impeded because coral recruits are attracted to the latter (Vermeij et al., 2011). Also, crustose coralline algae consolidate loose rubble, thereby increasing structural security of the rubble field (Smith et al., 2010). The increase in rubble may be caused by a number of factors including destructive fishing practices and coral predators, such as COTS, which consume live coral tissue, causing the carbonate skeleton to breakdown.

### 5.2.3 Bacterial communities and biofilms

Inorganic and organic nutrient inputs from different sources (i.e., terrestrial inputs from the mainland or sewage effluent from local populated islands) have an effect on bacterial abundance and community composition in the water, in sediments, on hard substrate and coral-associated agglomerations (Kegler et al., 2017b; Kegler et al., 2018a; Sawall et al., 2012). Bacterial communities were distinct across habitat types, including sediment, water-column (free-living and particle-attached), and coral mucus (Kegler et al., 2017b). Across the near- to offshore gradient, there were strong changes in bacterial community composition in the water column and sediment samples. Alarmingly, there was generally a high prevalence of potentially pathogenic bacteria in the water column across the entire gradient, e.g., high abundances of *Vibrio* spp. associated to diseases in nearshore sites (Kegler et al., 2017b). Additionally, although limited compared with large-scale impacts from the mainland, local island populations also influence water quality and bacterial community composition in the vicinity of populated islands (Kegler et al., 2018a). Several key water quality parameters, such as nitrate, phosphate, chlorophyll *a*, and TEP, were significantly higher at an inhabited than at an uninhabited island. Bacterial communities in sediments and particle-attached communities were significantly different between the two island types, with bacterial taxa commonly associated with nutrient and organic matter-rich conditions occurring in higher proportions at the inhabited island (Kegler et al., 2018a). Studies on biofilms on settlement tiles placed along the near- to offshore gradient showed a higher number of microbial operational taxonomic units (OTU) at nearshore sites, indicating a higher microbial diversity and a higher abundance of microbes, where the community was dominated by filamentous and turf algae (Sawall et al., 2012). It was also shown that nearshore pollution overrides the seasonal dynamics of microbial community structures, which may play a role in larvae settlement of sessile reef invertebrates near- versus offshore (Sawall et al., 2012). In another study by Kegler et al. (2017a), the most abundant bacteria on natural substrate and artificial tiles were Gammaproteobacteria, Alphaproteobacteria, and Cyanobacteria. Bacterial community composition (BCC) was strongly correlated with water quality, and significant differences in BCC between the inshore site and nearshore/midshelf were found. On artificial substrates, there was a significant difference in BCC in line with exposure time in the reef.

#### 5.2.4 Coral reef recruitment processes

Scleractinian coral recruitment is high in Spermonde with up to 700 recruits  $\text{m}^{-2} \text{yr}^{-1}$  occurring predominantly during the dry season (July–October). Some recruitment also occurred during the wet (November–February) and transitional season (March–June) in particular at midshelf and offshore reefs (Sawall et al., 2013). Despite a strong cross-shelf gradient in environmental conditions, coral recruitment displayed little variation among sites, suggesting adequate source populations. However, there was a reduction in diversity at the most nearshore sites (Lae Lae; Sawall et al., 2013). Lower diversity in recruitment at nearshore sites is most likely due to increased turf algae, which were found to be important space competitors of coral recruits (Plass-Johnson et al., 2016a). Thus, new recruits encounter an increased probability of interacting with turf algae with every site closer to shore. Recruitment may depend on species-specific interactions among corals and algae, but further testing is needed to determine whether some corals are able to outcompete turf algae.

#### 5.2.5 Coral physiology

An important factor that may impact coral development is the physiological adaptability to strong variation in abiotic conditions. Some coral species compete better under changing environmental conditions (Sawall et al., 2011, 2014). In studies on *Stylophora pistillata*, starvation led to reduced photosynthetic yield compared with fed corals when exposed to elevated water temperatures, indicating a link between heterotrophic feeding and photoinhibition under thermal stress (Borell and Bischof, 2008). For *S. pistillata* and *Galaxea fascicularis*, feeding with zooplankton resulted in sustained photosynthetic activity under elevated water temperatures, while starvation resulted in decreased zooxanthellae densities and photosynthesis. Both corals displayed reduced protein concentrations when starved, and lipid levels decreased in starved *S. pistillata* (Borell et al., 2008). The scleractinian coral *Stylophora subseriata* showed high physiological plasticity across the cross-shelf gradient: Colonies in more eutrophic nearshore waters showed higher photosynthesis and calcification, photosynthetic efficiency, zooxanthellae density, chlorophyll *a* concentrations as well as protein and lipid content (Sawall et al., 2011; Seemann et al., 2012). *Porites lutea* also showed higher photosynthetic rates and zooxanthellae densities in eutrophic nearshore reefs compared with oligotrophic midshore reefs but did not show enhanced rates of calcification as found in *S. subseriata*, indicating that additional energy is allocated toward stress mitigation (e.g., mucus production) rather than growth in nearshore reefs (Sawall et al., 2014). Despite overall decreases in live coral cover, the potential for acclimation of a few coral species to varying environmental conditions indicates some level of resilience to local disturbances.

#### 5.2.6 Relationships between benthic and fish communities

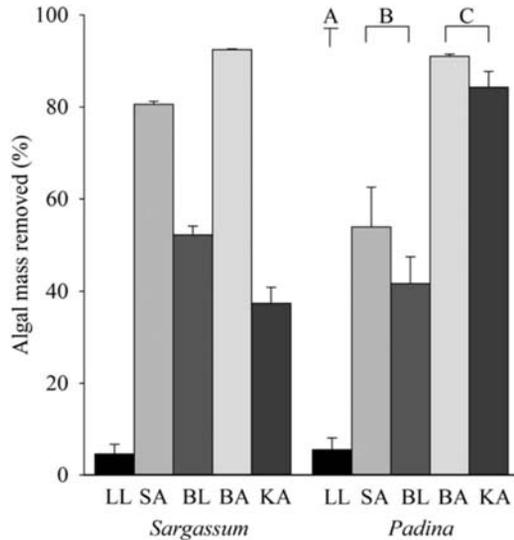
In agreement with indicators of coral reef habitat health (e.g., hard coral cover), indices of fish community health, such as species richness, abundances, and biomass, also

increased with distance from shore (Plass-Johnson et al., 2015a, 2016b, 2018b). In the Spermonde Archipelago, fish surveys revealed that communities at nearshore sites had greater variability in their trait-based functional composition than offshore sites (Plass-Johnson et al., 2016a,b). This is likely driven by the patchiness of hard coral habitat at disturbed sites in comparison with the offshore sites. Thus, nearshore sites were composed of some fish species that exploit hard coral resources and others that used rubble, turf algae, or sand. While variation in trait-based diversity across levels of habitat disturbance begins to reveal mechanisms underlying the relationship between habitat and fish, understanding the trophic plasticity of fish species may reveal strategies for dealing with changing environments. For instance, the parrotfish *Chlorurus bleekeri* and the farming damselfish *Dischistodus prosopotaenia* used differing feeding strategies, to either expand (parrotfish) or maintain (damselfish) (respectively) their nutritional resources in response to a changing habitat (Plass-Johnson et al., 2018a).

Further work conducted in the Spermonde Archipelago shows that the herbivorous fish functional group may display functional compensation based on the high species diversity within the region. Although there was high species turnover among all investigated sites, the important function of herbivory was continuously maintained at most sites by different species compositions (Plass-Johnson et al., 2015a,b), with often high grazing rates on macroalgae. The apparent high regional-level functional redundancy for macroalgal browsers contrasts with observations from less species-rich assemblages, notably reefs in the Caribbean (Micheli et al., 2014; Roff and Mumby, 2012). Coral reef herbivores play an important ecological role because they clear the substratum of biota that compete with scleractinian recruits, often repelling the larvae before settlement. While the results of this study display the potential for significant algal removal by herbivorous fish species, herbivory was not observed at the site nearest to shore, indicating that high levels of degradation also strongly affect ecologically important fish community functions and possibly resulting in the formation of negative feedback loops (Fig. 5.2).

### 5.2.7 Consequences of disturbances for coral reef functioning

Recent research has noted that the coral reefs of Southeast Asia are currently more threatened by localized human impacts, such as terrestrial effluents and resource use than by global stressors such as warming water temperatures and acidification (Burke et al., 2011). The various reef states found in the Spermonde Archipelago along a cross-shelf gradient suggest that phase shifts from coral-dominated states to algal-dominated states are driven by both bottom-up and top-down processes and might be influenced by negative social–ecological feedbacks reinforcing these negative states (Glaser et al., 2018). The long-term effects of water quality and overfishing on coral reef benthic composition can also be overshadowed by localized intense and acute disturbances (Baum et al., 2015). This is more evident further offshore, where water quality and herbivore abundances are relatively high, but other disturbances, including outbreaks of



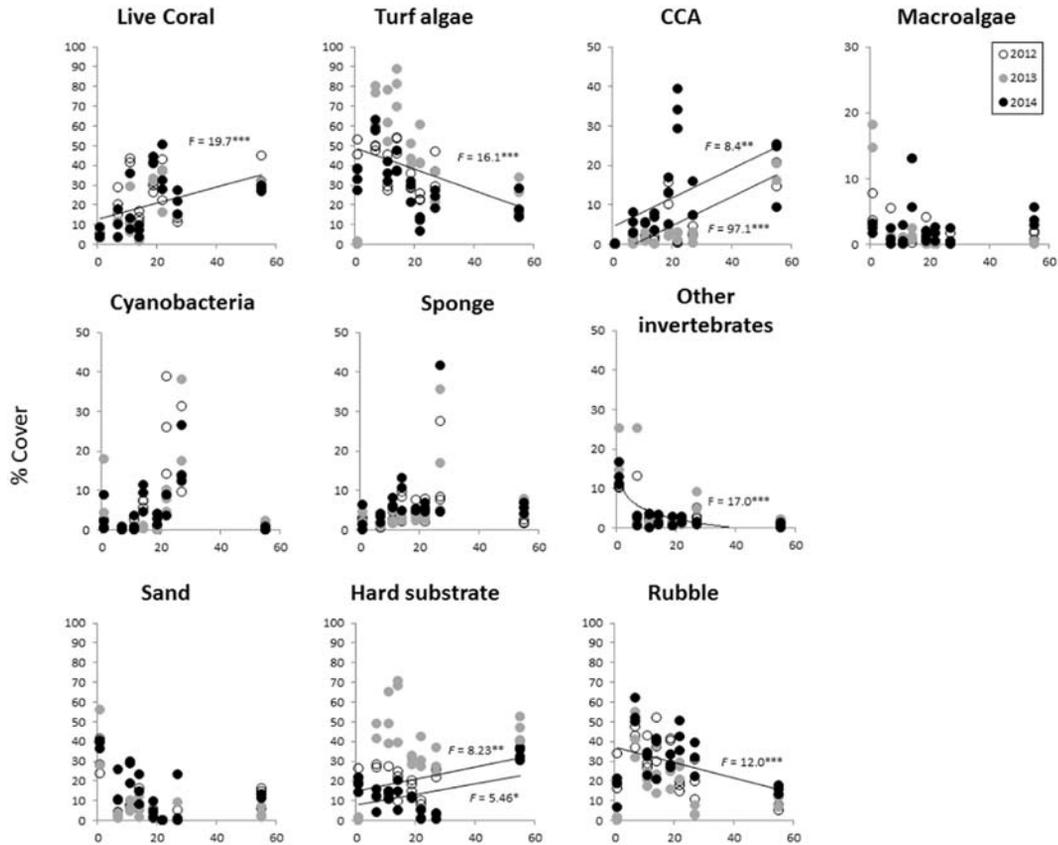
**FIGURE 5.2** Results from herbivory assays. Average ( $\pm$ SE) amount of *Sargassum* and *Padina* removed per 24-h period. Islands are arranged from closest to furthest from Makassar (BA, Badi; BL, Barrang Lompo; LL, Lae Lae; KA, Kapoposang; SA, Samalona; see Fig. 5.1). Data represent total mass loss after the correction for controls. Lettering above *Padina* indicates islands that were not significantly different in the PERMANOVA pairwise post hoc test. *Sargassum* treatments were all significantly different from each other. From Plass-Johnson et al. (2015a), Figure 2.

crown-of-thorn starfish and destructive fishing practices, such as blast fishing, lead to declines in reef health (Teichberg et al., 2018).

When integrating all water quality, benthic, and pelagic indices in the Spermonde Archipelago, it is possible to see differing levels of the state of health of the reefs with increasing distance from the mainland (Plass-Johnson et al., 2018b). Additionally, the benthic condition index, calculated as the percent live coral cover divided by the sum of the percent cover of other important benthic groups (macroalgae, turf algae, sponge, and cyanobacteria), showed a general decreasing trend closer to shore (Teichberg et al., 2018, Fig. 5.3). The evident trend is related to distance from the mainland; however, further midreef and outer-reef islands also showed evidence of how localized disturbances, such as outbreaks of crown-of-thorns starfish (Plass-Johnson et al., 2015b, Fig. 5.4), or overgrowth of cyanobacteria and sponges in areas with intensive bomb fishing (Teichberg et al., 2018), which can compete with large-scale gradients. This index also showed signs of quick recovery from acute local disturbances, indicating some resilience to disturbances with time.

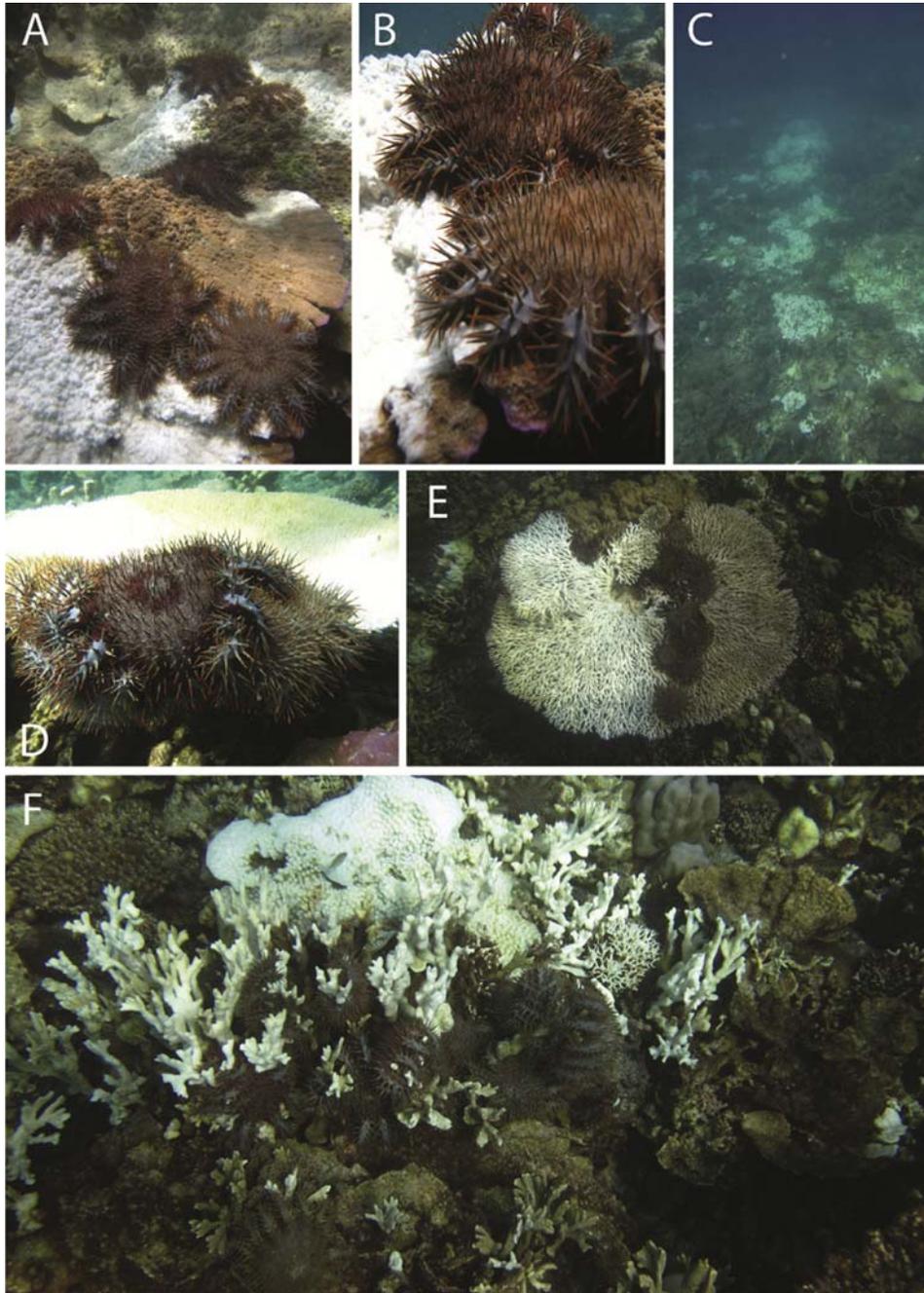
### 5.3 Genetic connectivity of reefs in the Coral Triangle region

Connectivity is the exchange of individuals among populations, which is the driving force for colonization of new areas, replenishment of depleted populations,



**FIGURE 5.3** Percentage of benthic cover of dominant groups of coral reef organisms and substrate type measured at different islands in 2012 (white), 2013 (gray), and 2014 (black). Sites are represented by distance from shore (km) on the x-axis. Regressions are indicated for variables that showed a significant increase or decrease with distance. Asterisks indicate level of significance (\*\*\*) indicates  $P < .001$ ; \*\* indicates  $P > .001$  and  $< 0.1$ , \* indicates  $P > .01$  and  $< 0.5$ ). From [Teichberg et al. \(2018\)](#), Figure 5.

recolonization, and maintenance of genetic diversity ([Cowen and Sponaugle, 2009](#)). Virtually all coral reef species disperse in their early life history stages as eggs and/or larvae, utilizing ocean currents as vectors. However, the extent and direction of dispersal, i.e., the actual distances and directions traveled with ocean currents, remain unclear ([Jones et al., 2009](#)). Do they return to their parental reef (self-recruitment), do they disperse only short distances to neighboring reefs, or do they undergo large distance dispersal of hundreds or even thousands of kilometers? Are these populations open or closed, i.e., show an influx of recruits from other populations and vice versa (open) or predominantly retain their own offspring to sustain their population (closed)? In which direction do eggs and larvae disperse? Genetic analysis can help unravel some of these questions by detecting the genetic “footprint” of dispersed larvae or migrating adults in the local population’s gene pool. In addition to using this method to track the exchange



**FIGURE 5.4** Crown-of-thorns starfish (*Acanthaster planci*, COTS) activity at Barrang Lompo (A, D and F), Bonetambung (B and E), and Lumulumu (C) recorded during September 2012. At Barrang Lompo, COTS were observed feeding on multiple genera of coral in very high densities. Eighteen COTS were observed feeding in roughly 2 m<sup>2</sup> at Barrang Lompo (F). (C) A track, approximately 20 m long, of fresh feeding scars left by COTS in September 2012. From [Plass-Johnson et al. \(2015b\)](#).

of individuals between populations, genetic diversity indices can also serve as a proxy for population size and thereby help to identify very reduced, isolated, or vulnerable populations.

Knowledge about dispersal distances and patterns is a very important baseline information for conservation efforts and the spatial design of marine-protected area (MPA) networks. As explained in the introduction, the Coral Triangle is the global center of marine coastal biodiversity. However, its coral reefs are threatened by anthropogenic impacts, such as overexploitation, pollution, and climate change, as has been shown in the previous sections of this chapter. To provide vital knowledge for conservation efforts, this subproject of SPICE aimed to investigate connectivity of coral reefs at different spatial scales, zooming in from the Coral Triangle to Spermonde and single reefs within this archipelago.

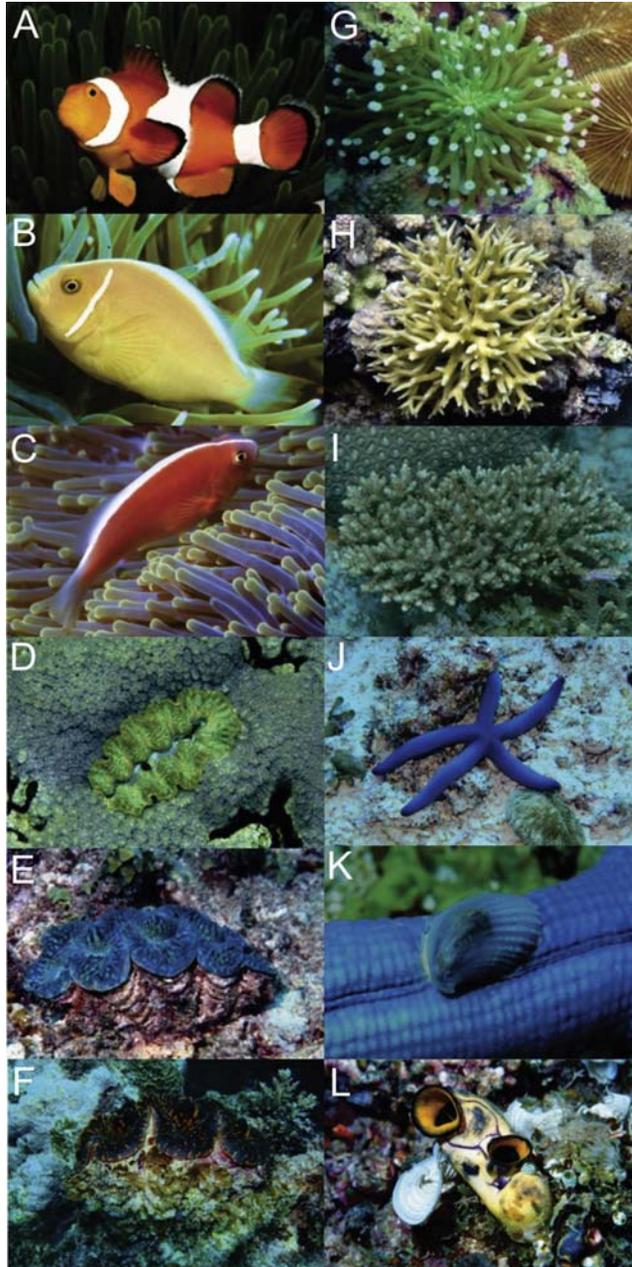
There are different approaches to investigate connectivity, ranging from in situ methods, such as chemically tagging larval fish otoliths or analyzing their natural isotopic composition, to in silico biophysical modeling, which integrates knowledge on the ecology of early life history stages with oceanography. However, by far, the most commonly applied approach investigates the genetic population structure to estimate gene flow, i.e., the exchange of genetic material among populations, as a proxy for connectivity. The advantage of genetic methods is their universal applicability to all kinds of organisms, while the aforementioned analysis of otoliths is restricted to fish and small spatial scales.

In the framework of the SPICE project, the genetic population structure of 12 species of coral reef organisms was investigated at different spatial scales. This included different life history traits and dispersal potentials, ranging from ecosystem engineers, such as stony corals and giant clams, to sea stars, ascidians, and anemonefish (Fig. 5.5; Table 5.1). The mode of spawning (i.e., pelagic or demersal eggs; brooders) as well as the pelagic larval duration (PLD) can have a pronounced effect on the dispersal potential. Species that spawn eggs into the water column and/or have a long PLD are expected to disperse over long distances and therefore frequently show a weak genetic differentiation among populations. On the contrary, species that release larvae into the water column and/or have a short PLD are expected to show limited connectivity and thus exhibit populations that are genetically strongly differentiated.

To investigate the genetic population structure of these species, different population genetic markers were applied, ranging from single-locus mitochondrial and nuclear DNA sequences to multilocus nuclear microsatellite analyses. The latter was also applied for parentage analysis to estimate self-recruitment. Thousands of tissue samples were collected in a minimal invasive way underwater while SCUBA-diving at 63 sites in the Coral Triangle region (Fig. 5.6).

### 5.3.1 Large-scale connectivity across the Coral Triangle region

A general population genetic structure that can be observed in many marine taxa on this large scale is the genetic differentiation between Indian and Pacific Ocean populations (Crandall et al., 2019). Sea level low stands of up to 120 m during the Pliocene and

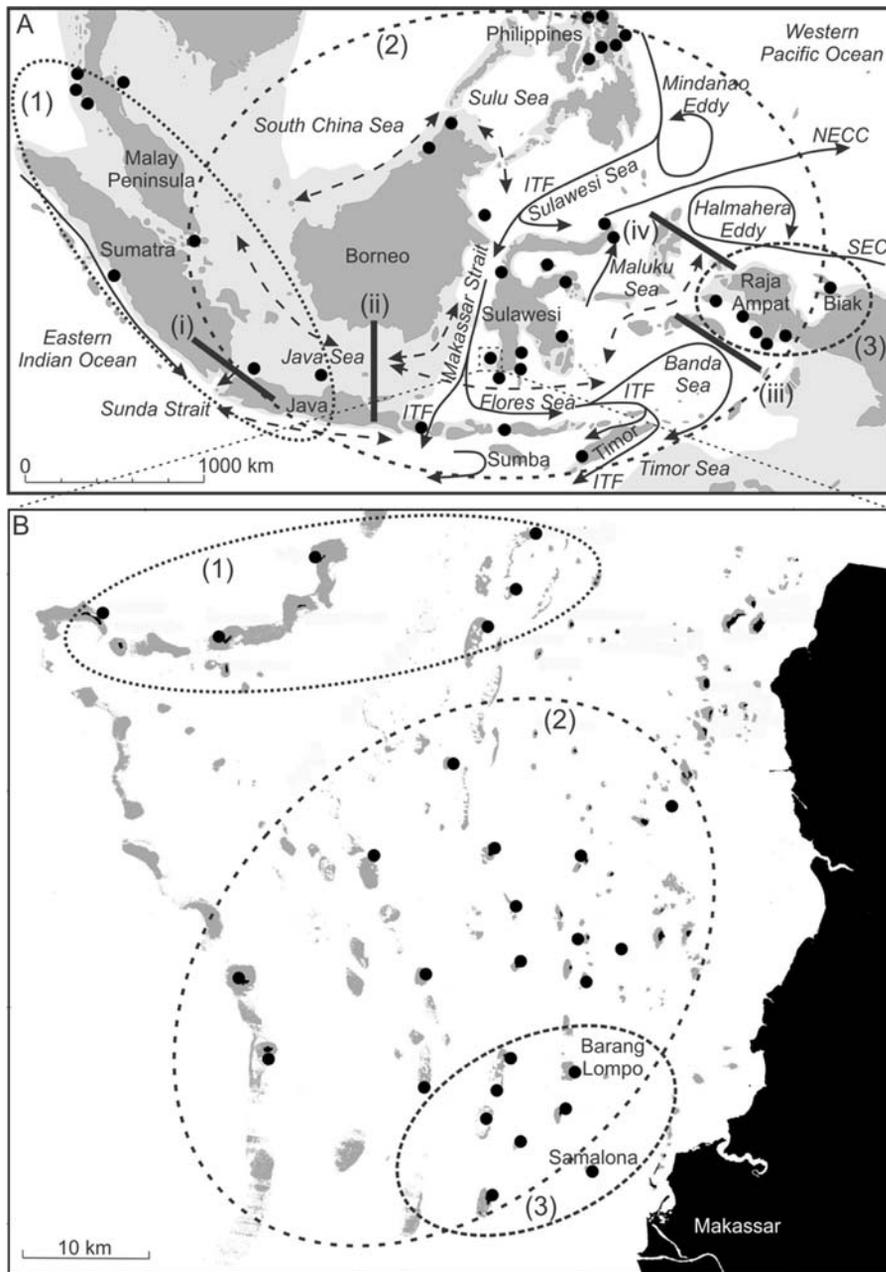


**FIGURE 5.5** Species investigated for the connectivity study: (A) clown anemonefish, *Amphiprion ocellaris*; (B) pink anemonefish, *Amphiprion perideraion*; (C) skunk clownfish, *Amphiprion akallopisos*; (D) boring giant clam, *Tridacna crocea*; (E) small giant clam, *Tridacna maxima*; (F) fluted giant clam, *Tridacna squamosa*; (G) mushroom coral, *Heliofungia actiniformis*; (H) bird's nest coral, *Seriatopora hystrix*; (I) branching coral, *Acropora millepora*; (J) blue sea star, *Linckia laevigata*; (K) ectoparasitic gastropod, *Thyca crystallina*; (L) sea squirt, *Polycarpa aurata*. All photographs by M. Kochzius, except (G) by L. Knittweis.

**Table 5.1** Early life history traits of the study species and their dispersal potential.

Species	Mode of spawning	PLD (days)	Dispersal potential	Genetic marker	Tested barriers	Detected barrier	Strength of the barrier	Population genetic study
<b>Stony coral</b>								
<i>Acropora millepora</i>	PE, PL	60	High	Microsats	ii	ii	Weak	van der Ven et al. (2021)
<i>Heliopungia actiniformis</i>	BL, PL	3	Low	ITS	ii, iii	ii, iii	Strong	Knittweis et al. (2009b)
<i>Seriatopora hystrix</i>	BL, PL	<0.5–7	Low	Microsats	ii	ii	Strong	van der Ven et al. (2021)
<b>Giant clam</b>								
<i>Tridacna crocea</i>	PE, PL	9–12	Medium	COI, Microsats	i, ii, iii, iv	i, ii, iv	Strong	Kochzius and Nuryanto (2008); Hui et al. (2012), Hui et al. (2016, 2017)
<i>Tridacna maxima</i>	PE, PL	9–12	Medium	COI	i, ii, iv	ii, iv	Strong	Nuryanto and Kochzius (2009); Hui et al. (2016)
<i>Tridacna squamosa</i>	PE, PL	9–12	Medium	COI	ii, iii, iv	iv	Strong	Hui et al. (2016)
<i>Tridacna noae</i>	PE, PL	9–12	Medium	COI	iii, iv	iv	Strong	Keyse et al. (2018)
<b>Sea star</b>								
<i>Linckia laevigata</i>	PE, PL	22	High	COI, microsats	i, ii, iii, iv	i, iv	Weak	Kochzius et al. (2009); Alcazar and Kochzius (2016); Ratzimbazafy (2019)
<b>Parasitic gastropod</b>								
<i>Thyca crystallina</i>	?	?	High	COI	ii, iii, iv	none	n/a	Kochzius et al. (2009)
<b>Sea squirt</b>								
<i>Polycarpa aurata</i>	PE, PL	0.5–7	Low	Microsats	n/a	n/a	n/a	Timm et al. (2017)
<b>Anemonefish</b>								
<i>Amphiprion ocellaris</i>	DE, PL	8–12	Low	CR, microsats	i, ii, iii	ii, iii	Strong, weak	Timm and Kochzius (2008); Timm et al. (2012)
<i>Amphiprion perideraion</i>	DE, PL	18	Medium	CR, microsats	ii, iii, iv	ii, iii or iv	Strong, weak	Dohna et al. (2015)
<i>Amphiprion akallopisos</i>	DE, PL	15	Medium	CR, microsats	i	none	n/a	Huyghe and Kochzius (2017, 2018)

Utilized genetic markers: mitochondrial COI (cytochrome oxidase I) and CR (control region); nuclear ITS (internal transcribed spacer) and microsats (microsatellites). Detected barriers for gene flow: for codes, see Fig. 5.5. BL, brooded larvae; DE, demersal eggs; PE, pelagic eggs; PL, pelagic larvae; PLD, pelagic larval duration.



**FIGURE 5.6** (A) Map of the Coral Triangle region with sample sites for the species listed in Table 5.1 (not all species were sampled at all sites), as well as oceanographic patterns with dominant (*solid lines*) and seasonally changing (*dashed lines*) currents (Gordon, 2005; Gordon and Fine, 1996; Wyrtki, 1961). ITF, Indonesian throughflow; NECC, Northern Equatorial Counter Current; SEC, Southern Equatorial Current. Pleistocene maximum sea level low stand of 120 m is indicated by the light gray area, land by the dark gray area (Voris, 2000). Groups of genetically similar populations: (1) Eastern Indian Ocean and Java Sea, (2) Philippines, South China Sea, Sulawesi Sea, Makassar Strait, Flores Sea, Maluku Sea, and Savu Sea (3) Radja Ampat and Western Pacific. (i–iv) Potential barriers for dispersal. (B) Map of Spermonde Archipelago with samples sites (not all species were sampled at all sites). Groups of genetically similar populations: (1) outer-shelf reefs, (2) midshelf reefs, and (3) inner-shelf reefs. The light gray area indicates coral reefs, and the black area indicates land.

Pleistocene glacials—exposed shelves in Southeast Asia and Australia formed the Indo-Pacific Barrier, which separated populations of the two ocean basins (Hoeksema, 2007, Fig. 5.6A). In these periods of separation, the fauna diverged by allopatric or parapatric speciation but subsequently came in contact again after sea level rise during interglacials (Bowen et al., 2013). This separation left a unique signature in the genomes of many species, which can be used to trace dispersal after the rise of the sea level at the end of the last glacial.

Population genetic analyses show genetic differentiation between populations originating from the Indian and the Pacific Ocean in all taxa studied on this large scale (Table 5.1), except the gastropod *Thyca crystallina*, which is an ectoparasite of the sea star *Linckia laevigata*. This parasite does not show any significant genetic differentiation, which indicates high connectivity at the studied scales. The larvae of *T. crystallina* need to disperse widely to encounter their high-dispersed host *L. laevigata*, which shows a shallow but significant genetic population structure. The absence of population genetic patterns in *T. crystallina*, driven by its exceptional ecological demands, is not considered representative for the majority of organisms that were studied and will therefore not be included in the further discussion.

Across the Coral Triangle, a general pattern of genetic differentiation among the western, central, and eastern parts emerges from the population structures of the most analyzed species: (1) Eastern Indian Ocean and Java Sea, (2) Philippines, South China Sea, Sulawesi Sea, Makassar Strait, Flores Sea, Maluku Sea, and Savu Sea, and (3) Raja Ampat and Western Pacific. Additionally, two gene flow barriers (i, ii) were identified in the western part of the Coral Triangle in the Sunda Strait and the Java Sea, while two others appeared around Raja Ampat (iii, iv) in the eastern part of the Coral Triangle (Fig. 5.6A, Table 5.1).

A clear separation of the Eastern Indian Ocean populations can be observed in all taxa, which includes the Java Sea in some species, such as in the giant clam *Tridacna maxima* (Nuryanto and Kochzius, 2009; Hui et al., 2017) and the anemonefish *Amphiprion ocellaris* (Timm and Kochzius 2008; Timm et al., 2012). This separation of the Eastern Indian Ocean is also observed in connectivity studies based on biophysical modeling (Kool et al., 2011; Trembl et al., 2015). Other species also show a clear genetic differentiation of the Java Sea populations from the central part of the Coral Triangle, including the stony corals *H. actiniformis* (Knittweis et al., 2009b) and *Seriatopora hystrix* (van der Ven et al., 2021), as well as the anemonefish *Amphiprion perideraion* (Dohna et al., 2015). However, in some species, this differentiation is very weak, for instance, in the broadcast spawning stony coral *A. millepora* (van der Ven et al., 2021). Conversely, in the giant clams *Tridacna crocea* (Kochzius and Nuryanto, 2008; Hui et al., 2016, 2017) and *Tridacna squamosa* (Hui et al., 2016), as well as in the star fish *L. laevigata* (Alcazar and Kochzius, 2016; Kochzius et al., 2009), populations from the Java Sea belong genetically to the central part of the Coral Triangle region.

Populations of all studied species in the central part of the Coral Triangle region seem to be well connected along the Indonesian Throughflow (ITF), all the way from the

Philippines through the Strait of Makassar down to the Flores Sea. This pattern of connectivity is also supported by biophysical modeling (Trembl et al., 2015). Populations in the South China Sea along the coast of northern Borneo also belong to this genetic cluster, indicating high exchange. This pattern of high connectivity was also revealed by biophysical modeling, showing larval dispersal from the South China Sea off northern Borneo across the Sulu Sea into the Sulawesi Sea, following the ITF to the south (Kool et al., 2011).

Different genetic marker systems provide slightly different results in the anemonefish *A. ocellaris* (Timm et al., 2012). Based on nuclear microsatellites, the population close to the southern tip of the Malay Peninsula also belongs to the genetic cluster of the central Coral Triangle region, which is also the case for the giant clam *T. squamosa* (Hui et al., 2016). However, the mitochondrial control region in the anemonefish *A. ocellaris* shows a unique genetic signature, separating this population from all other sites, which is supported by biophysical modeling (Kool et al., 2011).

Raja Ampat and Biak in the East also show a strong genetic differentiation in all species, indicating limited connectivity of the eastern Coral Triangle region to the central part. Limited gene flow from the Western Pacific (Biak) is probably caused by the Halmahera Eddy, which redirects the westward flow of the South Equatorial Current (SEC) into the eastward Northern Equatorial Counter Current (NECC). Biophysical modeling also shows that this causes a barrier for dispersal (Trembl et al., 2015). However, again the mitochondrial and nuclear markers show a different picture in the anemonefish *A. ocellaris* (Timm et al., 2012) and also in the giant clam *Tridacna crocea* (Hui et al., 2017), with the nuclear microsatellites indicating strong connectivity of Raja Ampat with the central Coral Triangle region.

### 5.3.2 Small-scale connectivity in the Spermonde Archipelago

The Spermonde Archipelago (Fig. 5.6B) shows an ecological zonation of the zoobenthos along a continuous inshore-to-offshore and shallow-to-deep environmental gradient, which makes it possible to divide reefs into inner-shelf, midshelf, and outer-shelf zones (Cleary et al., 2005, Section 5.2). The aim of this study was to test if this environmental gradient is reflected in the connectivity among the different reefs by analyzing the genetic population structure of several taxa, such as the stony corals *H. actiniformis* (Knittweis et al., 2009b), *S. hystrix*, and *A. millepora* (van der Ven et al., 2021), as well as the sea squirt *Polycarpa aurata* and the anemonefish *A. ocellaris* (Timm et al., 2017). An overall pattern of north–south differentiation into three genetic groups can be seen that roughly follows the zonation of inner-shelf, midshelf, and outer-shelf reefs (Fig. 5.6). Populations of the northern outer-shelf show more exchange among each other than inner-shelf populations do, where connectivity seems to be much more restricted (Timm et al., 2017). While the populations of the northern outer-shelf reefs are clearly genetically separated from mid- and inner-shelf reefs in all species, the geographic location of the barrier differs among species. The genetic differentiation within Spermonde might be due to different oceanographic conditions. Especially the northern

outer-shelf reefs are strongly under the influence of the ITF, which probably imports larvae from upstream and facilitates dispersal among reefs. This input of new genetic material leads to a higher genetic diversity in the anemonefish *A. ocellaris*, which was significant in the mitochondrial marker. However, this pattern was not observed in the nuclear microsatellite analysis (Timm et al., 2017). Further inshore, the currents might gradually become weaker, and therefore, connectivity among populations is reduced, leading to a strong genetic differentiation, especially in the anemonefish *A. ocellaris* and the sea squirt *P. aurata* (Timm et al., 2017).

### 5.3.3 Self-recruitment at the islands of Barrang Lompo and Samalona

The antagonist of dispersal is self-recruitment, which determines to which extent a population is self-containing or depends on the influx of recruits from other populations by dispersal. It is another important aspect in the context of connectivity for the spatial design of MPAs. To study self-recruitment, the anemonefishes *A. ocellaris* and *A. perideraion* were chosen as model species and were investigated at the islands of Barrang Lompo and Samalona in the Spermonde Archipelago (Madduppa et al., 2014a). Fin clips of almost the whole adult population and juvenile individuals were collected in the reefs around these two islands. Nuclear microsatellite markers were used in a parentage analysis approach to match offspring with their parents. This was done for *A. ocellaris* at Barrang Lompo in 2008 and 2009, as well as at Samalona in 2009. *A. perideraion* was sampled in 2009 at Barrang Lompo.

The analysis shows interspecific, spatial, and temporal variability of self-recruitment in the two anemonefish species (Table 5.2). *A. ocellaris* shows a very high self-recruitment of 65.2% in Samalona, while both species had a lower but very similar

**Table 5.2** Comparison of percent self-recruitment (% SR) in different anemonefishes (*Amphiprion* spp.).

Species	PLD	Location	Country	Reef type	% SR	References
<i>A. ocellaris</i>	8–12	Barrang Lompo (2008)	Indonesia	IR	44	Madduppa et al. (2014a)
<i>A. ocellaris</i>	8–12	Barrang Lompo (2009)	Indonesia	IR	52	Madduppa et al. (2014a)
<i>A. ocellaris</i>	8–12	Samalona	Indonesia	IR	65.2	Madduppa et al. (2014a)
<i>A. perideraion</i>	18	Barrang Lompo	Indonesia	IR	46.9	Madduppa et al. (2014a)
<i>A. percula</i>	10–13	Kimbe Island (2007)	Papua New Guinea	IR	64	Berumen et al. (2012)
<i>A. percula</i>	10–13	Kimbe Island (2004)	Papua New Guinea	IR	42	Planes et al. (2009)
<i>A. percula</i>	10–13	Kimbe Bay (2009)	Papua New Guinea	IR, CR	12.9	Almany et al. (2017)
<i>A. percula</i>	10–13	Kimbe Bay (2011)	Papua New Guinea	IR, CR	20.2	Almany et al. (2017)
<i>A. polymnus</i>	9–12	Schumann Island	Papua New Guinea	CR	31.5	Jones et al. (2005)
<i>A. polymnus</i>	9–12	Bootless Bay (2005)	Papua New Guinea	CR	25	Saenz-Agudelo et al. (2009)
<i>A. polymnus</i>	9–12	Bootless Bay (2008)	Papua New Guinea	CR	7.1	Saenz-Agudelo et al. (2011)
<i>A. akallopisos</i>		Zanzibar	Tanzania	IR	21.3	Huyghe (2018)
<i>A. bicinctus</i>	11	Qita al Girsh	Saudi Arabia (Red Sea)	IR	0.6	Nanninga et al. (2015)

CR, coastal reef; IR, isolated reef; PLD, pelagic larval duration.

self-recruitment of 47.4% (*A. ocellaris*) and 46.9% (*A. perideraion*) in Barrang Lompo. An interannual variation in self-recruitment is observed in *A. ocellaris* from the coral reef in Barrang Lompo, with 44% in 2008 and 52% in 2009. A temporal variation in self-recruitment was also observed in the anemonefishes *Amphiprion percula* and *Amphiprion polymnus* (Table 5.2). Site fidelity, i.e., returning to the same part of the reef where the larva had hatched, ranged from 0% to 44% in *A. ocellaris* and from 0% to 19% in *A. perideraion* at Barrang Lompo. At Samalona, site fidelity ranged from 8% to 11% in *A. ocellaris*. Exchange among the populations of *A. ocellaris* between the two islands was also investigated, showing that individuals of the larger adult population from Samalona are identified as parents of 21% of the juveniles from Barrang Lompo, while adults from the latter are parents of only 4% of the juveniles from Samalona. Percentage of self-recruitment observed in *A. ocellaris* and *A. perideraion* is higher than in all other investigated anemonefish species so far but are similar to Kimbe Island in Papua New Guinea (Table 5.2). This high amount of self-recruitment at Samalona and Barrang Lompo is concordant with the strong genetic differentiation of the *A. ocellaris* populations at these islands, which is further supported by the limited connectivity in the sea squirt *P. aurata* (Timm et al., 2017).

#### 5.3.4 Application of connectivity data in marine-protected area network design

The majority of the studied species, such as stony corals, giant clams, blue starfish, and anemonefish, are important in the marine ornamental trade, in which Indonesia is one of the main exporters (UNEP-WCMC, 2014; Wabnitz et al., 2003). In the Spermonde Archipelago, marine ornamental fishery started in the late 1980s, and by the late 1990s, a wholesaler company from Makassar received a permit for the collection of marine ornamentals in Spermonde, which are shipped from Makassar to Jakarta or Bali by airplane. Even though marine ornamental fishery is not the main source of income in Spermonde, it covers 13%–43% of the expenses of island households and is thus economically important. Indeed, on one studied island, marine ornamental fishery even covered 84% of the household expenses (Madduppa et al., 2014b).

By far, the most collected marine ornamental species is the anemonefish *A. ocellaris*, which is very popular due to the animation film “Finding Nemo.” Its host anemones are also collected for the international aquarium trade. It is estimated that each year, about 140,000 specimens of the anemonefish *A. ocellaris* and 31,000 host anemones (*Heteractis magnifica*, *Stichodactyla gigantea*, and *Stichodactyla mertensii*) are collected in Spermonde. The resulting high fishing pressure has a very strong impact on these target species, and underwater surveys show significantly lower densities on reefs with high exploitation (HE) in comparison with reefs with low exploitation (LE) rates. Also, body length and group size of the anemonefish *A. ocellaris* were significantly smaller at HE sites than at LE sites (Madduppa et al., 2014b). High fishing pressure also has negative implications for the genetic diversity of the anemonefish *A. ocellaris*. In Barrang Lompo

(HE), where the population density was threefold smaller than in Samalona (LE), genetic diversity (the number of alleles, private alleles, and allelic richness in nuclear microsatellites) was also significantly reduced (Madduppa et al., 2018).

Based on the results of the aforementioned studies on connectivity in the Coral Triangle region, the following management recommendations can be made. On a large scale, at least five regions should be considered as separate management units in the Coral Triangle region, taking into account the four detected barriers to gene flow (Fig. 5.6A): (1) Eastern Indian Ocean, (2) Java Sea, (3) South China Sea, Sulu Sea, Philippines, Sulawesi Sea, Makassar Strait, Flores Sea, and Banda Sea, (4) Raja Ampat, and (5) Western Pacific off Papua New Guinea. In the third large-scale management unit along the ITF, especially upstream populations (South China, Sulu Sea, Philippines, and Sulawesi Sea) need special conservation attention, because they are source populations for all other populations downstream along the ITF (Makassar Strait, Flores Sea, and the Banda Sea).

In the Spermonde Archipelago from the population genetic view, at least three different management units should be considered: (1) northern outer-shelf reefs, (2) central outer- and midshelf reefs, and (3) southern inner-shelf reefs (Fig. 5.6B). Since reefs of the northern outer-shelf are well connected with each other, MPAs do not need to be closely spaced. However, in the southern mid- and inner-shelf reefs, the situation is different, because populations show restricted connectivity even among closely located islands, with high self-recruitment shown in the anemonefish *A. ocellaris*. Therefore, a network of MPAs on each reef should be considered as the best management option.

## 5.4 Social systems associated with the use of coral-based resources and reef-specific challenges

The social–ecological system (SES) conceptualizations (Glaser et al., 2012) that relate to Spermonde Archipelago differ in accordance with the issue or problem in focus. The social actors and systems associated with Spermonde’s ornamental and live reef fish fisheries are mainly international (foreign traders and consumers), while those associated with blast fishing and pollution are predominantly local and regional; therefore, there are also at least two reef-related, issue-specific SES definitions.

### 5.4.1 Participatory assessment of Spermonde’s coral reef fisheries

During the second and third phases of SPICE, social scientists visited and worked on more than a third of the roughly 50 inhabited islands of the Spermonde Archipelago (Fig. 5.1). Drawing on natural science work from the first project phase, in particular on research on the ornamental coral trade, an extensive participatory social science research agenda was developed. For this, social scientists from the Leibniz Centre for Tropical Marine Research and the University of Bremen worked together with their counterparts at the Coral Reef Research Centre (now Research and Development Center

for Marine, Coast & Small Islands [sic]) and the Anthropology Department of Hasanuddin University in Makassar. The overarching interest was to assess the livelihoods of fisherfolk using the coral reefs of Spermonde and the governance institutions covering those waters. Key themes were fishery and trade in ornamental coral, life reef fish and other reef products, reef governance and management, including the emergence of associated rules and institutions (see [Chapter 11](#)), and fishing techniques.

A number of preparatory visits to several of the islands between 2004 and 2007 were followed by the funded social science research on the reef-based SES of the Spermonde Archipelago. This began in 2007, in the second phase of the SPICE project, with a joint workshop in Makassar. A focus of the research was to be on several key coral reef fisheries (ornamental fish and corals, live reef fish, sea cucumbers) and on destructive fishing methods. Islands identified as locations of particular relevance or hubs of activity for these fisheries were therefore selected as focal locations for the social science research ([Ferse et al., 2014](#); [Glaser et al., 2015](#)). The backbone of the approach were five ship-based excursions conducted in 2009, 2010, 2012, and 2013, each of which brought bilateral teams of a total of about 20 social scientists and students per excursion to multiple islands. The first excursion combined icebreaking activities (film screenings, town hall meetings, and photo sessions) to familiarize project teams and village communities with each other and with main shared themes, with focus group discussions, individual key-informant interviews, and an interview-based survey. This was followed by theme-focused interviews, with extensive daily team discussions and complementary data collection during the second excursion. During a third ship-based excursion, results were presented back to and discussed with communities, making use of a short documentary film produced on the research work during the first excursion (<https://vimeo.com/5246067>; [Glaser et al., 2010c](#)).

Two additional excursions, including similar multinational research teams conducting focus group discussions, surveys, and interviews, were conducted in the final phase of SPICE. These ship-based excursions were complemented by a range of additional research activities conducted mostly by students and doctoral candidates from several Indonesian and German partner institutions. A main underlying objective was to obtain local perspectives on contested issues, such as the involvement in and organization of destructive fishing practices. A participatory and transdisciplinary research approach was used, which allowed for the articulation of different local perceptions, opinions, and aspirations. The importance of the social science team's inclusive and enabling approach to generating new and relevant knowledge together with local stakeholders was acknowledged by several of the local respondents. These had previously voiced disappointment with government representatives visiting islands in the frame of a government-initiated program for the 'participatory' development of community-based MPAs. Actual participation in the official program planning process was found to be low (as was the resulting awareness of and compliance with the thus generated protected areas, see [Glaser et al., 2010a](#)). As one reason, a local respondent stated about the government representatives: "They always tell us what we cannot do, but never what we can do".

### 5.4.2 Investigating marine social–ecological feedbacks and dynamics

Similar to coral reef fisheries elsewhere in the Coral Triangle and beyond, the reefs of Spermonde are used in many different ways and covered by a range of multiple, sometimes overlapping, governance institutions. These include rules-in-use surrounding particular fishing gears, informal regulations pertaining to the reefs surrounding individual islands, village-level MPAs, and district-level regulations (Glaser et al., 2010a; Deswandi, 2012, p. 207; Gorris, 2016; see Chapter 11 for a more detailed description of the governance aspects). At least 24 distinct fishing methods (see Table A5.1, Fig. A5.1) are used in the reefs and surrounding waters, comprising a variety of net, hook-and-line and trap fishing techniques, gleaning, and spear fishing, as well as highly destructive methods (e.g., blast and cyanide fishing) that additionally pose significant health risks to the fishers (Ferse et al., 2014).

The different islands of the Spermonde Archipelago form a kaleidoscope of multiple fishing methods and cultures, with individual islands often concentrating on particular fishing methods. For example, there are islands with a particularly large number of bamboo trap fishers (Bonetambung), while others are hubs in the live reef fish fishery (e.g., Barrang Caddi) or the ornamental coral fishery (e.g., Barrang Lompo) with specific techniques and gears. In assessing the fishery, a SES analysis approach was taken to understand in particular the links between multiple ecological and social components of the focal system. In defining the SES(s) of interest, a problem-focused definition was used, comprising three elements: (1) a biogeophysical system (i.e., the Spermonde Archipelago), (2) its associated social agents with their institutions, which are not necessarily situated within the biogeophysical system, and (3) a specific problem context, such as the overuse of a particular resource (e.g., sea cucumbers) (Glaser et al., 2010b). Several of the reef resources in Spermonde are harvested for international, rather than local or national, markets. Thus, developments on international markets, such as changes in aquarium technology, demand for particular species or changes in the regulation of other important sources for target species and drive the dynamics of these fisheries (Ferse et al., 2014). Furthermore, many of the fisheries, in particular those that employ destructive and illegal gears and target overseas markets, are informally organized in a patron–client system, locally known as *punggawa/sawi* (Radjawali, 2011; Ferse et al., 2012). In this system, fishers form dyadic relationships with patrons that comprise financial loans and gear provided to fishers on credit by patrons. In return, fishers are expected to sell their catch to their particular patron at submarket prices in return for their loans. Patrons furthermore provide links to traders on other islands or in Makassar via their personal connections and, in the case of illegal fishing gear, provide a form of security from prosecution by relying on personal contacts to law enforcement agencies in Makassar (Radjawali, 2011). As fishers usually lack the connection to traders in Makassar and beyond, the link to a patron is a key mechanism for them to access markets beyond the local island, and in some cases to pursue illegal but lucrative fisheries. The patron–client institution shapes those fisheries, influencing target species and gears and modifying fishers' freedom of choice and room for maneuver (Ferse et al., 2014).

### 5.4.3 Reef-related livelihoods and implications for the present and future health of fishers and reefs

In contrast to the mostly specialized fisheries in temperate regions, fishers exploiting the coral reefs of Spermonde are often utilizing a range of fishing techniques, which they switch and combine based on, for example, demand, seasons, or weather patterns. While the vast majority of households on the islands depend in some way on marine resources, fishing is not necessarily the main, and certainly not the only, livelihood of most islanders (Ferse et al., 2014). For example, although the Archipelago is a main source region for ornamental corals, none of the ornamental coral collectors interviewed depended exclusively on the collection of corals, and most collected corals opportunistically, along with other species they deemed valuable (Ferse et al., 2012). Yet, marine resources constitute the mainstay of the majority of islanders' livelihoods, either directly via fishery, or indirectly via processing and trade. As many of the target species with the highest market value (e.g., sea cucumbers, ornamental corals, and groupers) are reef associated, the livelihoods of islanders depend directly on the future health and productivity of coral-dominated reef ecosystems. The poor soil and scarcity in available land on most of the inhabited islands leave little scope for alternative, non-reef-dependent livelihoods such as farming, with the exception of small garden plots on some of the islands. Freshwater resources are also increasingly scarce on many islands. This may be related to larger climate change-related drivers such as sea level rise but is also connected to increasing demand from rising numbers of inhabitants so that many Spermonde islands are approaching the limits of their carrying capacity (Schwerdtner Mánuez et al., 2012). A further impairment to expanding livelihood options beyond marine resource use is the fact that many boys on the islands join their fathers or elder brothers in fishing at an early age, quitting school and thus foregoing options for formal employment, for example, in the nearby provincial capital Makassar (Glaser et al., 2015).

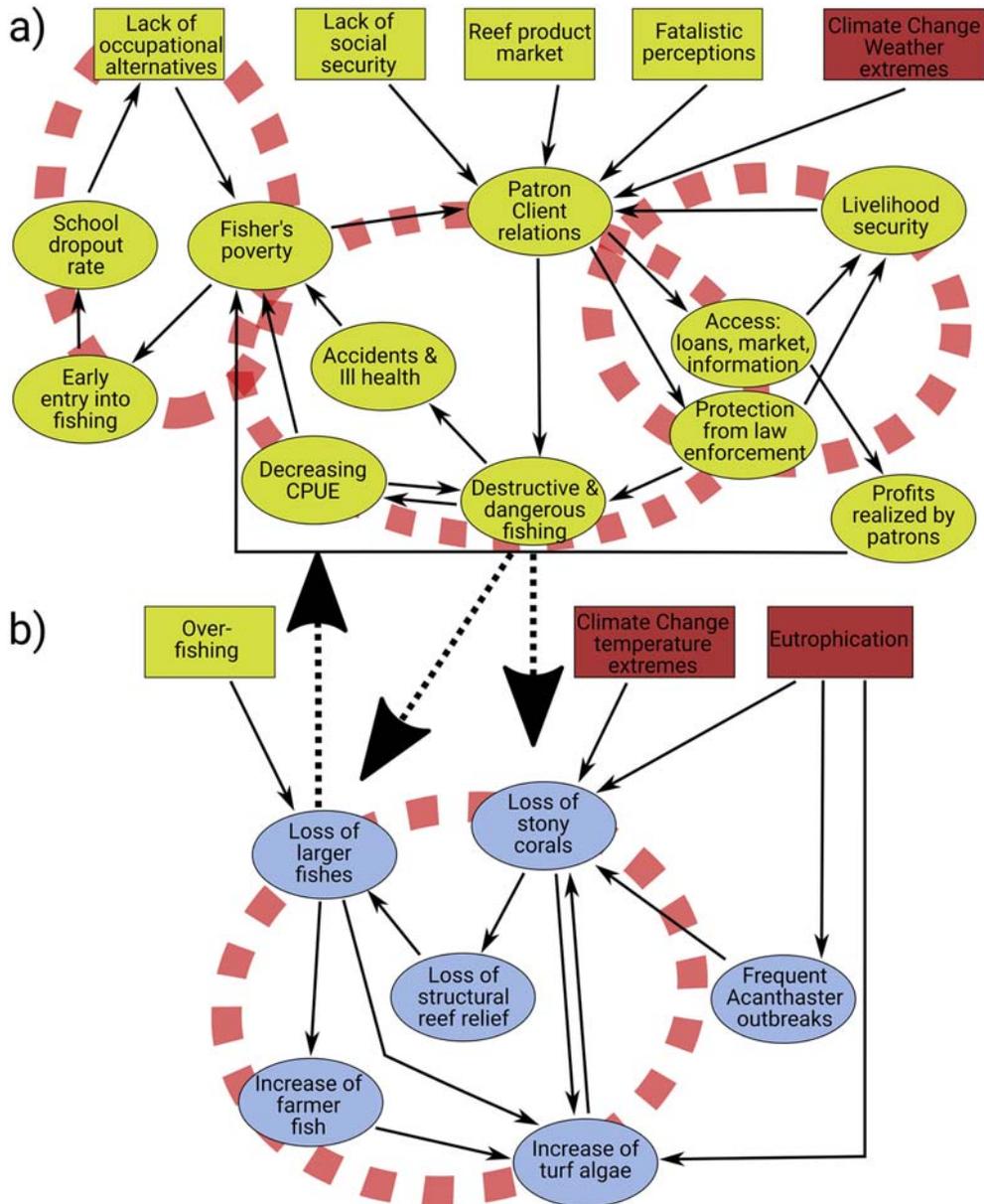
Prior to a blanket ban on all exports of ornamental corals in May 2018, over 70% of all corals in the marine aquarium trade originated from Indonesia. The Spermonde Archipelago was one of the four main collection areas for marine ornamentals in Indonesia (Ferse et al., 2012). According to a statement by the global trade group Ornamental Fish International, this ban has resulted in the loss of 10,000 jobs in the Indonesian aquarium coral fishery and trade within a year of being issued. In 2015, the use of compressors and scuba gear for diving was prohibited throughout the Archipelago (Hafez Muhammad and Sainab Husain Paragay, pers. comm. 2015). These bans underline the precariousness of reef resource-related livelihoods in Spermonde. While the versatility in gear use and access to credit and gear via patrons is likely to increase the adaptive capacity of fishers faced with such challenges, there is also the possibility of unintended consequences, such as increased indebtedness or the shift to high-yield destructive techniques. For example, Jaiteh et al. (2017) found that a ban on shark finning in Indonesia has resulted in an increase in high-risk activities such as blast fishing, illegal transboundary fishing, and people smuggling.

#### 5.4.4 Changing target species, perceptions of reef resources, and implications for food security

The reef fisheries of Spermonde are highly dynamic, and opportunity and innovation appear to have been an important feature of these fisheries since the first fishers began settling the sandy islands of the Archipelago, which in some islands was over 200 years ago (Schwerdtner Máñez et al., 2012). Some species, such as sea cucumbers, have been targeted and exported for centuries, before recent changes in fishing technology (in this case, the introduction of compressor diving) allowed for the exploitation of previously untapped deeper parts of the reefs and for longer collection periods underwater. This resulted in a rapid increase in harvested amounts and an eventual overexploitation and decrease of the fishery as a whole (Schwerdtner Máñez and Ferse, 2010). The introduction of compressor diving and the overseas trade links established in export-oriented fisheries of earlier periods enabled the successive introduction of other fisheries using similar gears and trade routes, such as live reef fish and ornamental corals (Ferse et al., 2014). In general, the reef fisheries are highly versatile, and new techniques and target species are readily taken up by fishers. A key role in this is played by the fishing patrons, who enable connections to traders on other islands and to exporters in Makassar, introduce knowledge of new target species, and facilitate the uptake of new fishing methods. This is achieved by, for example, providing credit, gear, or information on the use of gears, gained by tapping into their extensive social networks including connections to traders in Makassar.

As a result of the versatility of the fishery and the rapid response to new market opportunities, a number of distinct peaks in fishing activity and production could be observed over time for a range of target species, such as sea cucumbers, live reef fish, ornamental corals, and moray eels (Schwerdtner Máñez and Husain Paragay, 2013; Ferse et al., 2014). Patrons are also key knowledge brokers in the reef fishery, acting as nodes in the flow of resources and information between international markets and exporters on one end of the trade chain, and individual fishers at the other. As a result, there is a disconnect in terms of information on the state of the reef ecosystem, which means that little information on ecological dynamics and feedbacks is available to actors further down the trade chain, such as traders and other patrons who are influential opinion leaders and decision-makers. Surveyors and employees of line agencies responsible for the management of fisheries and marine environments often lack resources for fishery monitoring in the field and instead rely on visits to fish markets or information from points of export, thus receiving distorted or incomplete information. The impairment or even lack of essential information flow on ecosystem changes from those who directly work with the ecosystem to main decision-makers is further aggravated by patrons who actively promote questionable views such as “it is impossible to overfish the sea” or “there will always be fish in the sea as long as there are leaves on trees,” often invoking religious texts in doing so. The diversity of patrons trading different kinds of marine resources additionally instills a sense in fishers that there is a patron to sell each and

every (marine) resource that might be fished or extracted to. This further exacerbates the overharvesting of reef resources (Ferse et al., 2014). The increased commodification of reef resources also has direct consequences for islanders' food security (Fig. 5.7): fish with a high nutritional value and high market value are frequently sold to Makassar rather than consumed locally, and financial returns are then used to buy processed food with lower nutritional value.



**FIGURE 5.7** In the Spermonde Archipelago, an interconnected set of predominantly social vicious cycles is locking the social–ecological system in an undesirable and increasingly resilient state. From Glaser et al. (2018), Fig. 1.

### 5.4.5 Conclusions for the management of coral reef resources in the Spermonde Archipelago

The social–ecological research conducted by the interdisciplinary team within the SPICE project generated three main conclusions. These all concern inclusiveness and are that (1) knowledge of the coral reef ecosystems of the Archipelago, (2) transparency of conservation-related benefits and their distribution, and (3) integration of coastal management planning and implementation need to be improved among and for all stakeholders (Glaser et al., 2015, see also Chapter 11 in this volume). A more socially and ecologically sustainable development and adaptive coastal governance is possible when these critical issues are addressed over time horizons that span beyond terms of political office. Local hierarchies and elites that form and maintain their own networks remain challenging on the road toward developing sustainable development options. In particular, the key roles played by fishing patrons need to be recognized and taken into account in the development of governance frameworks and management interventions as well as in the design of environmental and social policies. Patrons are the core knowledge brokers, enablers of unsustainable fishing, and importantly, the main providers of social security and adaptive capacity for vulnerable fishers. While many discussions have taken place on how to achieve meaningful participation in decision-making processes, a substantial and effective support in law enforcement (e.g., to reduce illegal, unreported, and unregulated fishing) seems to be the preferred and also more effective solution, not only for Spermonde but also for other regions in Indonesia. Finally, any governance and management interventions need to ensure a strengthening of local adaptive capacity and distribution of conservation benefits, which is regarded as legitimate and equitable by concerned stakeholders, if the danger of undermining the sustainability of the coral reef social–ecological system is to be avoided.

## 5.5 Modeling to support the management of reef systems

The SPICE project in the Spermonde Archipelago developed applications to improve the management of marine resources use in an integrative interdisciplinary modeling approach of reef processes and associated social drivers. The rationale for emphasizing model development lies in the importance of scientifically informed decisions, and the approach employed involves the extrapolation of dynamics and an application of possible scenarios, for instance, for environmental change or pollution trajectories. Together with the involvement of human actors and the consideration of institutional rule settings, the resulting simulations may provide valid projections to guide decisions in resource management. For the Spermonde Archipelago, these modeling efforts focused on managing the resilience of reef systems to human impact in the context of analyzing the effects of global climate change on reef dynamics by identifying preconditions for phase shifts in the context of local environmental conditions. Through the identification of driving factors, it is possible to distinguish between global and local

factors, which can then be addressed through management (e.g., [Kubicek et al., 2012](#)). Thereby, the integration of information from different available sources proves immensely important not only for representing spatial heterogeneity but also for considering ecological processes on specific integration levels to facilitate the analysis of cross-level processes ([Reuter et al., 2010](#)). Ultimately, this should help to estimate the impact of human resource use under different management schemes and evaluate options for future pathways of change (mitigation, adaptation and transformation) under a set of potential environmental trajectories.

### 5.5.1 Simulating the impact of fisheries on coral reef dynamics

The spatially explicit simulation model **SEAMANCORE** (Spatially Explicit simulation model for Assisting the local MANagement of COral REefs, [Miñarro et al., 2018](#)) was developed to serve as a decision support tool for local resource management of Indo-Pacific coral reefs. A number of models address the effects of human impacts on ecological dynamics to inform management approaches. However, these models frequently ignore benthic or fish dynamics reaction to external anthropogenic stressors, and virtually none offers a user-friendly platform for nonscientist managers to access easily ([Miñarro et al., 2018](#)).

The model developed in this SPICE project may be used to explore the likely outcomes of different combinations of resource management and environmental scenarios by simulating the population dynamics of a coral reef community in reaction to environmental factors and different fishing approaches. It represents the spatial dynamics of a coral reef under the influence of local and global stressors, focusing on selected fish and benthic functional groups, the ecological relationships among them, and how they are affected by external stressors. The model integrates the available knowledge (for instance, social drivers and management strategies) derived in the SPICE projects in Spermonde and in past studies on Indonesian reef systems.

Modeling studies on reef benthos dynamics have targeted different stressors on reef dynamics (e.g., [Mumby et al., 2007](#); [Sandin and McNamara, 2012](#)), its resilience ([Bozec and Mumby, 2015](#)), and dynamics of coral diseases ([Brandt and McManus, 2009](#)) but often exclude the feedback processes with upper trophic levels, e.g., fish functional groups. Models linking fish and benthic dynamics (e.g., [Ainsworth and Mumby, 2015](#); [Rogers et al., 2014](#)) are frequently not spatially explicit, thus missing specific impacts on fishing grounds. The small-scale approach of SEAMANCORE is aimed at local management. Many models used for managing marine resources are more spatially aggregated to cover entire jurisdictional areas (e.g., [Buddemeier et al., 2008](#); [Weijerman et al., 2015](#)). However, in the case of tropical islands, community-based management is important, and in Spermonde as elsewhere, it is often determined locally ([McClanahan et al., 2006](#); [Mumby and Steneck 2008](#); [Glaser et al., 2010a](#)).

For Pacific coral reef models, parameterization is challenging due to lack of data until the 1980s and regionally varying historical baseline data ([Bruno and Selig, 2007](#)).

Exceptions for model studies for the region include an ECOSIM model by [Ainsworth et al. \(2008\)](#) targeting management research priorities for Raja Ampat and a spatially explicit mean-field model ([Gurney et al., 2013](#)) assessing bleaching scenarios relating to the effect of fisheries on coral reef dynamics. Building upon earlier models developed to aid local coral reef management (e.g., [Buddemeier et al., 2008](#); [Holmes and Johnstone, 2010](#); [Weijerman et al., 2015](#)), we propose a spatially explicit simulation model as a new user-friendly ecological tool to assess the effects of simultaneous global and local stressors on coral reef communities. As an extension to the small-scale processes of coral–algae interaction developed in [Kubicek et al. \(2012\)](#), [Kubicek et al. \(2019\)](#), components, such as selected fish and benthic functional groups, are added as well as how they are affected by external stressors. The model may be used to explore likely outcomes of different resource management and environmental scenarios by simulating the population dynamics of a coral reef and the effects of different fishing methods. Results thus include assessing the trade-offs involved in the different options for the reef fishery regulations.

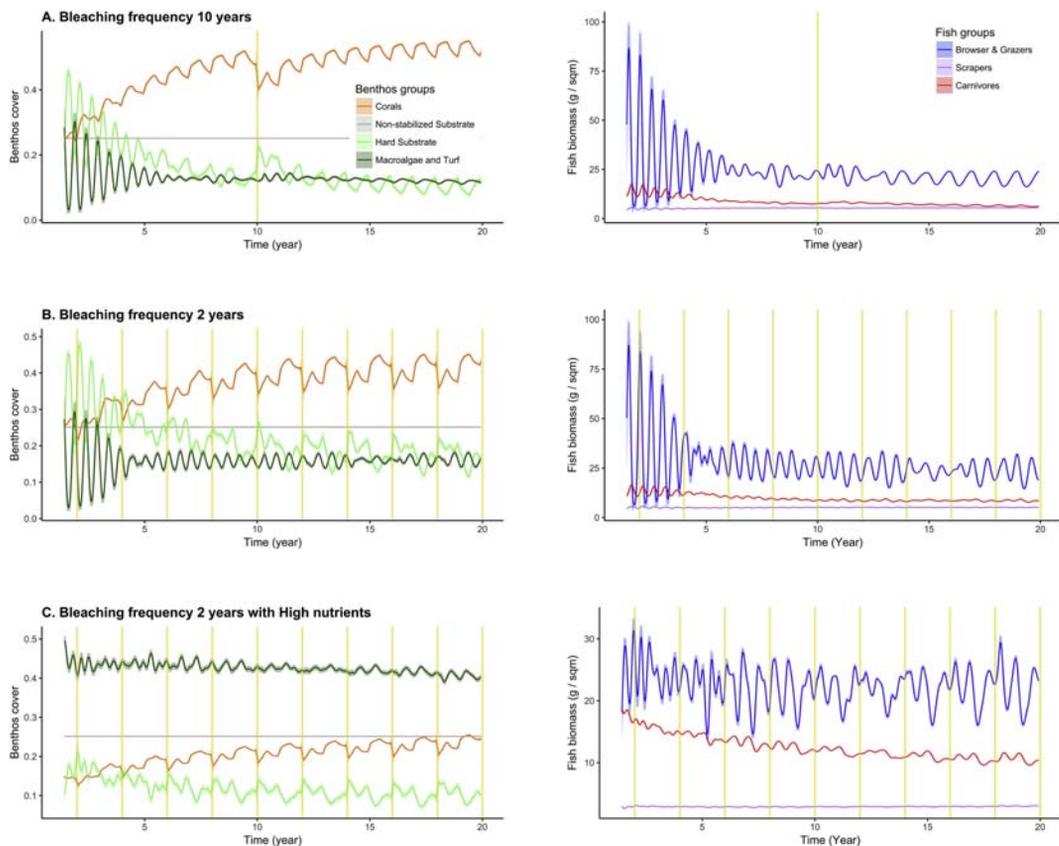
SEAMANCORE was designed to assess the influence of local processes at the coral reef scale, such as spatial competition outcomes or fishery exploitation, coupled with the effects of management strategies. It is implemented as a two-dimensional continuous grid representing the benthos (coral and algae interaction) and three interacting functional fish groups (Browsers & Grazers, Scrapers, and Carnivores). Currently, the maximum grid size is  $1000 \times 1000$  m ( $1 \text{ km}^2$ ). The model represents interactions within the benthos (e.g., corals, algae) as well as trophic interactions within the fish groups and with the benthos. Different environmental scenarios and scenarios of fisheries (i.e., fishing methods and intensities) may be specified to represent different gear choices, including both legal and illegal fishing methods. Fishing is explicitly modeled with parameters for intensity, zonation, and selectivity, while the other stressors, bleaching and eutrophication, are more broadly specified through scenario settings. A gray-scale bathymetric map of the field site may be set up to define depth categories influencing the probability of occurrence of organisms and ecological processes and to determine whether the grid cells will be affected by stressors.

The model is parameterized to represent coral reefs of the Indo-Pacific, and input parameters and initial conditions can be changed according to the case-specific abundance of functional groups, fishing pressure, and biophysical conditions, such as the depth profile, bleaching frequency, and nutrient input. The flexibility in its input parameters facilitates scenario testing by local stakeholders. The current exemplary study is parameterized using field data collected from islands of the Spermonde Archipelago exposed to different stressor combinations and intensities ([Miñarro et al., 2018](#)). The model is designed with a user-friendly menu-based interface that does not require programming experience for simulating numerous scenarios that can be customized with depth profile maps and initial coral reef conditions of fish and benthos functional group abundance. All detailed settings of the model are accessible in the advanced mode. The model can be used to explore the likely trajectories of a specific

coral reef ecosystem under different scenarios of depth profile, nutrient regimes, bleaching frequency, and fishery management strategies.

In a first application, the model was used to explore various scenarios of stressors, fishing, and bleaching regimes in a virtual coral reef, using approaches defined by [Kubicek et al. \(2015\)](#) to validate the model. Being spatially explicit, reef zonation patterns emerged as a result of model rules. The model was tested using an extensive sensitivity analysis for evaluating the influence of uncertainty due to parameter variability to ensure its usage under different scenario conditions ([Fig. 5.8](#)). Outputs include the relative abundances of key functional groups over time, which are commonly accepted indicators of ecosystem health and comparable against target conservation values or acceptable published levels for such abundances.

Specifically, the simulations show the expected complex behavior of the reef and some of its associated fish species with a number of positive and negative feedback



**FIGURE 5.8** Results from SEAMANCORE model runs for different bleaching frequencies and nutrient levels. Three scenarios of bleaching frequency: every 10 (A), 2 (B), and 2 years with high nutrients (C). The time series considered 20 years, benthos cover is given as a proportion, fish biomass in  $\text{g m}^{-2}$ . All data are averaged across the three depth categories of the depth map. From [Miñarro et al. \(2018\)](#), Fig. 5.

relationships that shape the trajectories of benthos dynamics and fish functional group in difficult to foresee ways. In particular, the feedback processes between coral cover and fish biomass (Graham et al., 2006; Sandin et al., 2008) are shaping the dynamics, but also the interactions involving the benthos. Simulations show the reef capacity to sustain moderate levels of disturbance below the threshold of natural variation, but a severely reduced capacity to cope if scenarios combine high nutrient levels with high bleaching frequencies (Miñarro et al., 2018). For future applications, we expect that linking fish demographics with changing habitat quality derived from simulating feedback processes on and within benthos will prove insightful for fisheries management.

### 5.5.2 A model on gear choices of fishermen

For the Spermonde Archipelago, the immense importance of the patron–client system for organizing fisheries with respect to gear choice and target organisms is well documented (e.g., Ferse et al., 2012; Ferrol-Schulte et al., 2014; Miñarro et al., 2016, see also Chapters 5.4 and 11). Artisanal fishermen (clients) are obliged to sell their catch to fish traders (patrons) who act as middlemen for the regional market. Clients are often highly indebted to the patrons and trade social security in times of low catches for targeting specific fish groups demanded by patrons, often with concessions to patrons in terms of product price received. This system is thought to potentially put high pressure on stocks, thereby risking unsustainable exploitation strategies (Nurdin and Grydehøj, 2014).

The modeling study by Leins (2017) supplements the simulation model by Miñarro et al. (2018) with a detailed social–ecological component and investigates the implications of the patron–client system on the sustainability of fishing in Spermonde. The model represents the social system of fisheries in the Spermonde Archipelago with respect to patron–client dependencies as well as independent fishers and depicts different fishing methods, their economic implications for the fishers, and their effects on spatially distributed resources.

Fishers are represented as autonomously acting agents with a distinct behavioral repertoire (activity rules), which depends on their social status, available assets and equipment, as well as acquired knowledge and external conditions. The actions of a fisher may again change the model's status and environmental settings. The knowledge of a fisher agent is distinguished into three categories: (1) *general knowledge* that has fixed values and equally applies for all fishers; (2) *individual knowledge* that changes depending on the individual fisher's actions and experience, e.g., catch history, own economic situation, and (3) *perception* of global and local conditions from the (partial) point of view of an individual fisher. Two types of fish resources (high and low value) are spatially distributed on the map, thus characterizing the fishing grounds. Dynamics of a stock depend on its specific growth function as well as on exploitation intensity and choice of gear, thus determining whether a stock thrives or decreases with time.

In the model, each fisher decides every day upon their activities depending on their knowledge. This involves, for instance, the decision to go fishing, which fishing ground

to target, how long to stay there, and when to leave. The experiences from these activities will then complement the fisher's knowledge and directly impact his household's economic situation, for instance, depending on catch values and costs of the fishing trip. Ultimately, fishers may also change their social status (dependent or independent fisher), depending on their economic trajectory. Model rules and parameterization were very much based on the knowledge derived in the SPICE project by many project partners (e.g., [Deswandi, 2012](#), p. p207; [Ferse et al., 2012](#); [Miñarro, 2017](#); [Miñarro et al., 2016](#); [Navarrete-Forero et al., 2017](#); [Radjawali, 2012](#)).

We applied the model for a set of different scenarios relating to potential management strategies, such as increasing awareness to reduce illegal fishing activities, economic setting affecting fish prices, or strict law enforcement (e.g., intensive control of illegal activities and different values for fines). Results indicated that for none of the scenarios featuring a majority of dependent fishers, it was possible to concurrently achieve recovering reef quality and healthy fish stocks. Interestingly, with the implemented algorithms, an increase in law enforcement also increased the economic stress of fishers, leading to intensified exploitation ([Leins, 2017](#)). Here, and also for details of the financial agreements/transaction between patrons and clients, limited knowledge restricts model implementation. Further studies should also include alternative livelihood options and the behavior of the patrons who have strong personal interest to keep the system intact. Thus, an extended model could facilitate more detailed simulations with a wider set of potential management strategies toward a sustainable and economically and socially beneficial artisanal coral reef fishery in the Spermonde Archipelago.

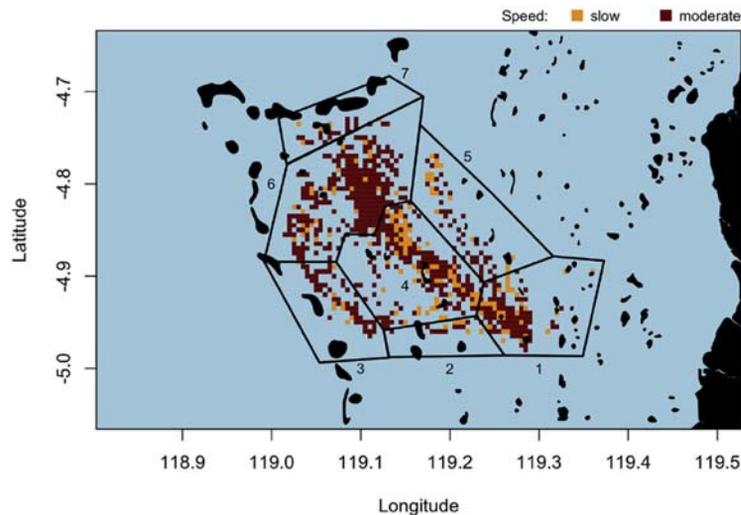
### 5.5.3 Spatial patterns of fishing ground distribution

Artisanal fisheries in the Spermonde Archipelago nearly exclusively target reef species and exhibit a highly diverse approach with localized impacts on reefs (see Chapter 5.4). A fundamental issue for impact assessment is the explicit extent and location of fishing activities, which can then be related to the status of specific coral reefs and allow for the establishment of a direct relation between ecosystem state and the spatial extent and effect of specific fishing methods. This information is needed to understand diverging spatial dynamics in reefs and derive targeted management recommendations such as spatial regulations, for instance, for MPAs. Such studies demand regular fisheries monitoring and the identification of the missing spatial information on resource use impact to relate information on habitat quality to specific anthropogenic activities.

In comparison with industrial fishing enterprises, artisanal fishers and fisheries managers only rarely use technical approaches to determine fishing locations. Their methods often include anecdotal information derived from other fishers (e.g., [Gorris, 2016](#)) or conducting a census using patrols or research vessels ([Pet-Soede et al., 2001](#); [Turner et al., 2015](#)). These approaches either lack precision or are very cost and time intensive. Small and easy-to-use GPS trackers, however, provide a precise tool to quantify and locate fishing at a relatively low cost involving participatory sampling ([Metcalfe et al., 2016](#)).

In the SPICE project, we used a combination of measuring catch landings (biomass and species composition), interviews of hook and line fishermen about the use of the different fishing grounds, and the distribution of GPS data loggers among fishers to identify fishing grounds by gear-dependent patterns of boat movement (Navarrete Forero et al., 2017). The study was conducted during the wet season 2014/15 on Badi Island of the Spermonde Archipelago. The tracks of fishermen were used to generate a map of fishing grounds, thereby also indicating how frequently and for what time period each of these fishing grounds was visited. As typical boat speeds can be related to specific fishing gears, the movement information of the GPS tracks allowed the derivation of a spatial pattern of gear used and target species. This was then evaluated using catch composition assessment of landings by participating fishermen.

The results of this study show that patterns of fishing grounds' distribution can be related to target species and catch composition, and results may be interpreted in the context of patron–client relationships that structure the artisanal fisheries in Spermonde (Miñarro et al., 2016). Fishers traveled up to 100 km per day in small engine-powered canoes. Most of the fishing activities by fishers of the Island of Badi involved two gears (octopus bait and trolling line for live groupers) and three major fishing grounds (Fig. 5.9). These areas were located northwest of Badi, the home port, and on the way to Kondongbali Island. Typically, octopus dominated the catch landings in terms of biomass (CPUE = 10.1 kg boat day<sup>-1</sup>), whereas groupers (Serranidae, CPUE = 1.7 kg boat



**FIGURE 5.9** Map of fishing activity of hook and line fishermen from Badi Island, Spermonde Archipelago. Cell color represents the prevalent fishing speed (slow: 0–3 km h<sup>-1</sup>, moderate 4–8 km h<sup>-1</sup>) associated with different gears. Polygon numbers represent names of fishing grounds: (1) Badi, (2) Lumu-lumu, (3) Lanyukan, (4) Tintingan, (5) Sarappo, (6) Malla'bang, (7) Kondongbali. From Navarrete-Forero et al. (2017), Fig. 3.

day<sup>-1</sup>), targeted for their high market value (around 42 \$ per kg vs. 2.3 \$ per kg for Octopus), gave the highest revenues. The Serranidae fish family also constituted the most diverse group in the landed catch with the leopard coral grouper (*Plectropomus leopardus*) being the species with the highest catch statistics (52.5%).

The study by [Navarrete Forero et al. \(2017\)](#) shows that boat tracking with cheap and easy-to-use GPS tracker is a powerful tool that provides information on spatial resource use when combined with interviews and catch surveys. In this case, the study was benefited from a high level of participation by fishermen.

## 5.6 Summary and outlook

Located at the heart of the Coral Triangle, the Spermonde Archipelago was a treasure trove of marine biodiversity. But anthropogenic impacts from a growing coastal population, along with global warming, have led to a widespread demise of coral reefs and the related ecosystem services. The complex geography, great variety of stakeholders, and a number of threats including the unsustainable and destructive exploitation of resources and pollution pose serious challenges to the management of the archipelago. Results from the research of the SPICE project show the following: (1) The ecology of the archipelago is characterized by widespread habitat degradation and several documented environmental gradients that drive differences in species distribution. (2) Missing livelihood alternatives and a system of middlemen (patrons) and dependent clients stabilize unsustainable approaches to resource use by the islanders of the archipelago. (3) The analysis of genetic population structure and connectivity among populations in the Spermonde Archipelago provides evidence for different connectivity patterns in the outer-, middle-, and inner-shelf systems and separation of the southern inner-shelf reefs. Beyond the Spermonde Archipelago, especially the outer-shelf reefs are well connected to reefs upstream the ITF. (4) Mechanistic models allow for the integration of specific characteristics of the system, the most relevant components to sustainable reef management, their specific dynamics or life histories, and interactions to test the ecosystem-wide effects of management schemes under different biophysical scenarios.

While the implementation of effective management strategies may provide improvements at the local scale, small-scale efforts are potentially undermined by the impact of regional and global stressors, such as pollution inflows from the hinterland, outbreaks of crown-of-thorns starfish, and heat waves so that a return from algae-dominated (or other benthos groups) to coral-dominated reefs will be increasingly difficult in the future. However, research in the SPICE program has also shown that some resilient corals are able to survive in marginal environments and polluted coastal waters. This resilience might provide some frontloading to other stressors such as warming and acidification, so that despite the observed loss in coral cover and diversity, it could be possible that the species-rich coral community may be replaced by an impoverished, but resilient coral community in the near future.

Despite the improved understanding of the social–ecological system of Spermonde Archipelago generated by the SPICE program and many other actors, more

investigations are needed to monitor the state of the reefs, changes in the coral community, and the processes of acclimation and adaptation to a changing environment. A better understanding of social networks and the governance system is also required, and resilient but undesirable social–ecological dynamics need to be addressed.

Our research also highlights that more information, in particular on spatial differences in resource use intensity and feedback processes with benthos, is needed to increase the scope of the developed model. Last but not least, stakeholder involvement and participation of local actors in decisions should be more extensively employed to both increase knowledge exchange between science, practitioners, and decision-makers and support capacity development on many different levels. This would facilitate the co-development of context-appropriate rules for reef use and fishing behavior and of innovative alternative livelihoods to provide better conditions for sustainable resource use.

#### Knowledge gaps and directions of future research

The SPICE project in the Spermonde Archipelago pursued a holistic interdisciplinary investigation of coral reef dynamics under a range of environmental constraints and scenarios of anthropogenic exploitation and pollution. All the actors in the SPICE program and many more generated an improved understanding of the social–ecological system of the Spermonde Archipelago through their research.

However, more and detailed investigations are needed to

- monitor the state of the reefs, changes in the coral community and the processes of acclimation and adaptation to a changing environment;
- specifically generate an improved understanding of social networks and the governance system to facilitate a better knowledge exchange between science, practitioners, and decision-makers for developing codevelopment of context-appropriate rules for reef use and fishing behavior and of innovative alternative livelihoods; and
- increase the projection accuracy of the developed models by including more detailed information and processes, in particular on spatial differences in resource use intensity and the feedback processes with benthos communities.

We are certain that all these further research activities together would provide valuable support for a sustainable resource use in the Spermonde Archipelago.

#### Implications/recommendations for policy and society

Investigations during SPICE showed that the Spermonde Archipelago is characterized by a severe degradation of its marine habitats. Additionally, we identified environmental gradients from the coast to the outer-shelf islands which shape benthic as well as fish communities. Missing livelihood alternatives and depleting marine resources result in island populations increasing efforts to sustain livelihood and the necessity of utilizing new resources.

*Continued*

## Implications/recommendations for policy and society—cont'd

Key management recommendations include the following critical issues:

- Recognition of the multifaceted key role played by fishing patrons. This needs to be taken in account in developing concepts for environmental and social policies and in the development of governance frameworks and management interventions.
- Extended knowledge of effects of intensive exploitation on ecology of reef systems is required. However, small-scale efforts for sustainable management are potentially undermined by regional and global stressors. These will have to be addressed on the according spatial scales and political levels.
- Any development of a management framework should ensure a strengthening of local adaptive capacity and distribution of conservation benefits. The considered time horizons should span beyond terms of political office to ensure a more socially and ecologically sustainable development and adaptive coastal governance.

As one of the most important points, stakeholder involvement and participation of local actors in decisions should be more extensively employed. The increased knowledge exchange between science, practitioners, and decision-makers should aim at facilitating the co-development of context-appropriate rules for sustainable resource use in the Archipelago.

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## References

- Agung, M.H., Prabuning, D., Yudianto, P., Dewanto, H.Y., Sari, S.K., Kimura, T., Tun, K., Chou, L.M. (Eds.), 2018. Status of Coral Reefs in East Asian Seas Region. Ministry of the Environment of Japan and Japan Wildlife Research Center, Tokyo, Japan, p. 58 (Chapter 2.2).
- Ainsworth, C.H., Mumby, P., 2015. Coral-algal phase shifts alter fish communities and reduce fisheries production. *Global Change Biology* 21 (1), 165–172.
- Ainsworth, C.H., Varkey, D.A., Pitcher, T.J., 2008. Ecosystem simulations supporting ecosystem-based fisheries management in the Coral triangle, Indonesia. *Ecological Modelling* 214 (2–4), 361–374.

- Alcazar, D.S.R., Kochzius, M., 2016. Genetic population structure of the blue sea star *Linckia laevigata* in the Visayas (Philippines). *Journal of the Marine Biological Association of the United Kingdom* 96, 707–713.
- Allen, G.R., 2008. Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 541–556.
- Almany, G.R., Planes, S., Thorrold, S.R., Berumen, M.L., Bode, M., Saenz-Agudelo, P., et al., 2017. Larval fish dispersal in a coral-reef seascape. *Nature Ecology and Evolution* 1, 0148.
- Arias-Gonzalez, J.E., Johnson, C., Seymour, R.M., Perez, P., Alino, P., 2011. Scaling up models of the dynamics of coral reef ecosystems: an approach for science-based management of global change. In: Dubinsky, Z., Stambler, N. (Eds.), *Coral Reefs: An Ecosystem in Transition*. Springer, pp. 373–390.
- Asian Development Bank, 2014a. *Regional State of the Coral Triangle—Coral TRIANGLE Marine Resources: Their Status, Economies, and Management*. Mandaluyong City, Philippines.
- Asian Development Bank, 2014b. *State of the Coral Triangle: Indonesia*. Mandaluyong City, Philippines.
- Baum, G., Januar, H.I., Ferse, S.C.A., Kunzmann, A., 2015. Local and regional impacts of pollution on coral reefs along the thousand islands north of the Megacity Jakarta, Indonesia. *PLoS One* 10, e0138271.
- Becking, L., Cleary, D., de Voogd, N., Renema, W., de Beer, M., van Soest, R.W.M., Hoeksema, B.W., 2006. Beta diversity of tropical marine benthic assemblages in the Spermonde Archipelago, Indonesia. *Marine Ecology* 27, 67–88. <https://doi.org/10.1111/j.1439-0485.2005.00051.x>.
- Berumen, M.L., Almany, G.R., Planes, S., Jones, G.P., Saenz-Agudelo, P., Thorrold, S.R., 2012. Persistence of self-recruitment and patterns of larval connectivity in a marine protected area network. *Ecology and Evolution* 2, 444–452.
- Borell, E., Bischof, K., 2008. Feeding sustains photosynthetic quantum yield of a scleractinian coral during thermal stress. *Oecologia* 157 (4), 593–601.
- Borell, E.M., Yuliantri, A.R., Bischof, K., Richter, C., 2008. The effect of heterotrophy on photosynthesis and tissue composition of two scleractinian corals under elevated temperature. *Journal of Experimental Marine Biology and Ecology* 364 (2), 116–123.
- Bowen, B.W., Rocha, L.A., Toonen, R.J., Karl, S.A., 2013. The origins of tropical marine biodiversity. *Trends in Ecology and Evolution* 28, 359–366.
- Bozec, Y.M., Mumby, P.J., 2015. Synergistic impacts of global warming on the resilience of coral reefs. *Philosophical Transactions of the Royal Society B: Biological Science* 370 (1659), 20130267.
- Brandt, M.E., McManus, J.W., 2009. Dynamics and impact of the coral disease white plague: insights from a simulation model. *Diseases of Aquatic Organisms* 87 (1–2), 117–133.
- Bruckner, A.W., Borneman, E.H., 2006. Developing a sustainable harvest regime for Indonesia's stony coral fishery with application to other coral exporting countries. In: *Proceedings of the 10th International Coral Reef Symposium*, pp. 1692–1697.
- Bruno, J.F., Selig, E.R., 2007. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2 (8), e711.
- Buddemeier, R.W., Jokiel, P.L., Zimmerman, K.M., Lane, D.R., Carey, J.M., Bohling, G.C., et al., 2008. A modeling tool to evaluate regional coral reef responses to changes in climate and ocean chemistry. *Limnology and Oceanography: Methods* 6 (9), 395–411.
- Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. *Reefs at Risk Revisited*. World Resource Institute, Washington, DC.
- Burke, L., Reytar, K., Spalding, M., Perry, A., 2012. *Reefs at Risk Revisited in the Coral Triangle*. World Resource Institute, Washington, DC.

- Burke, L., Selig, E., Spalding, M., 2002. Reefs at Risk in South-East Asia. World Resource Institute, Washington, DC.
- Carilli, J.E., Norris, R.D., Black, B.A., Walsh, S.M., McField, M., 2009. Local stressors reduce coral resilience to bleaching. *PLoS One* 4 (7), e6324.
- Cleary, D.F.R., Becking, L.E., de Voogd, N.J., Renema, W., de Beer, M., van Soest, R.W.M., et al., 2005. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure to the Spermonde Archipelago, Indonesia. *Estuarine, Coastal and Shelf Science* 65, 557–570.
- Cleary, D.F.R., Renema, W., 2007. Relating species traits of foraminifera to environmental variables in the Spermonde Archipelago, Indonesia. *Marine Ecology Progress Series* 334, 73–82. <https://doi.org/10.3354/meps334073>.
- Cornils, A., Schulz, J., Schmitt, P., Lanuru, M., Richter, C., Schnack-Schiel, S.B., 2010. Mesozooplankton distribution in the Spermonde archipelago (Indonesia, Sulawesi) with special reference to the Calanoida (Copepoda). *Deep Sea Research Part II: Topical Studies in Oceanography* 57, 2076–2088.
- Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1, 443–466.
- Crandall, E.D., Riginos, C., Bird, C., Liggins, L., Trembl, E., Beger, M., et al., 2019. The molecular biogeography of the Indo-Pacific: testing hypotheses with multispecies genetic patterns. *Global Ecology and Biogeography* 28, 943–960.
- de Voogd, N., Cleary, D., Hoeksema, B., Noor, A., van Soes, R., 2006. Sponge beta diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia. *Marine Ecology Progress Series* 309, 131–142. <https://doi.org/10.3354/meps309131>.
- Deswandi, R., 2012. Understanding Institutional Dynamics: The Emergence, Persistence, and Change of Institutions in Capture Fisheries in Makassar, Spermonde Archipelago, South Sulawesi, Indonesia (Ph.D. thesis). University of Bremen, p. p207.
- Dohna, T.A., Timm, J., Hamid, L., Kochzius, M., 2015. Limited connectivity and a phylogeographic break characterize populations of the pink anemonefish, *Amphiprion perideraion*, in the Indo-Malay archipelago: inferences from a mitochondrial and microsatellite loci. *Ecology and Evolution* 5, 1717–1733.
- Edinger, E.N., Kolasa, J., Risk, M.J., 2000. Biogeographic variation in coral species diversity on coral reefs in three regions of Indonesia. *Divers Distribution* 6, 113–127. <https://doi.org/10.1046/j.1472-4642.2000.00076.x>.
- Erdman, L., Pet-Soede, M., 1997. How fresh is too fresh? The live reef food fish trade in eastern Indonesia. *Live Reef Fish Information Bulletin* 3, 41–45.
- Ferrol-Schulte, D., Ferse, S.C.A., Glaser, M., 2014. Patron-client relationships, livelihoods and natural resource management in tropical coastal communities. *Ocean and Coastal Management* 100, 63–73.
- Ferrol-Schulte, D., Wolff, M., Ferse, S., Glaser, M., 2013. Sustainable livelihoods approach in tropical coastal and marine social–ecological systems: a review. *Marine Policy* 42, 253–258. <https://doi.org/10.1016/j.marpol.2013.03.007>.
- Ferse, S.C.A., Glaser, M., Neil, M., Schwerdtner Máñez, K., 2014. To cope or to sustain? Eroding long-term sustainability in an Indonesian coral reef fishery. *Regional Environmental Change* 14, 2053–2065.
- Ferse, S.C.A., Knittweis, L., Krause, G., Maddusila, A., Glaser, M., 2012. Livelihoods of ornamental coral fishermen in South Sulawesi/Indonesia: implications for management. *Coastal Management* 40, 525–555.
- Glaser, M., Baitoningsih, W., Ferse, S.C.A., Neil, M., Deswandi, R., 2010a. Whose sustainability? Top-down participation and emergent rules in marine protected area management in Indonesia. *Marine Policy* 34, 1215–1225.

- Glaser, M., Breckwoldt, A., Deswandi, R., Radjawali, I., Baitoningsih, W., Ferse, S.C.A., 2015. Of exploited reefs and Fishers – a holistic view on participatory coastal and marine management in an Indonesian archipelago. *Ocean and Coastal Management* 116, 193–213.
- Glaser, M., Ferse, S., Neil, M., Plass-Johnson, J., Satari, D.Y., Teichberg, M., Reuter, H., 2018. Breaking resilience for a sustainable future: Thoughts for the Anthropocene. *Frontiers in Marine Science* 5, 34.
- Glaser, M., Krause, G., Halliday, A., Glaeser, B., 2012. Towards global sustainability analysis in the Anthropocene. In: Glaser, M., Krause, G., Ratter, B.M.W., Welp, M. (Eds.), *Human-nature Interaction in the Anthropocene: Potentials of Social-Ecological Systems Analysis*. Routledge, pp. 193–222 (Chapter 10).
- Glaser, M., Krause, G., Oliveira, R.S., Fontalvo-Herazo, M., 2010b. Mangroves and people: a social-ecological system. In: Saint-Paul, U., Schneider, H. (Eds.), *Mangrove Dynamics and Management in north Brazil*. Springer, Heidelberg, Germany, pp. 307–351.
- Glaser, M., Radjawali, I., Ferse, S.C.A., Glaeser, B., 2010c. Nested' participation in hierarchical societies? Lessons for social-ecological research and management. *International Journal of Society Systems Science* 2, 390–414.
- Gordon, A.L., 2005. Oceanography of the Indonesian seas and their throughflow. *Oceanography* 18, 14–27.
- Gordon, A.L., Fine, R.A., 1996. Pathways of water between the Pacific and Indian oceans in the Indonesian seas. *Nature* 379, 146–149.
- Gorris, P., 2016. Deconstructing the reality of community-based management of marine resources in a small island context in Indonesia. *Frontiers in Marine Science* 3. <https://doi.org/10.3389/fmars.2016.00120>.
- Graham, N.A., Wilson, S.K., Jennings, S., Polunin, N.V., Bijoux, J.P., Robinson, J., 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 103 (22), 8425–8429.
- Gurney, G.G., Melbourne-Thomas, J., Geronimo, R.C., Aliño, P.M., Johnson, C.R., 2013. Modelling coral reef futures to inform management: can reducing local-scale stressors conserve reefs under climate change? *PLoS One* 8 (11), e80137.
- Hoeksema, B., 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: the coral triangle. In: Renema, W. (Ed.), *Biogeography Time, and Place: Distributions, Barriers, and Islands*, pp. 117–178.
- Hoeksema, B., 2012. Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde shelf, South Sulawesi. *The Raffles Bulletin of Zoology* 60, 183–212.
- Hogarth, P.J., 1999. *The Biology of Mangroves*. Oxford University Press, Oxford, England.
- Holmes, G., Johnstone, R.W., 2010. Modelling coral reef ecosystems with limited observational data. *Ecological Modelling* 221 (8), 1173–1183.
- Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., et al., 2017. Coral reefs in the anthropocene. *Nature* 546, 82–90.
- Hui, M., Kochzius, M., Leese, F., 2012. Isolation and characterisation of nine microsatellite markers in the boring giant clam (*Tridacna crocea*) and cross-amplification in five other tridacnid species. *Marine Biodiversity* 42, 285–287.
- Hui, M., Kraemer, W.E., Seidel, C., Nuryanto, A., Joshi, A., Kochzius, M., 2016. Comparative genetic population structure of three endangered giant clams (Tridacnidae) throughout the Indo-west Pacific: implications for divergence, connectivity, and conservation. *Journal of Molluscan Studies* 82, 403–414.

- Hui, M., Nuryanto, A., Kochzius, M., 2017. Concordance of microsatellite and mitochondrial DNA markers in detecting genetic population structure in the boring giant clam, *Tridacna crocea*, across the Indo-Malay Archipelago. *Marine Ecology - An Evolutionary Perspective* 38, e12389.
- Huyghe, F., 2018. Evolutionary and Ecological Connectivity of the Skunk Clown Fish in the Indian Ocean and Their Importance for the Design of marine Protected Areas (Ph.D. Thesis). Vrije Universiteit Brussel (VUB), Belgium.
- Huyghe, F., Kochzius, M., 2017. Highly restricted gene flow between disjunct populations of the skunk clownfish (*Amphiprion akallopisos*) in the Indian Ocean. *Marine Ecology - An Evolutionary Perspective* 38, e12357.
- Huyghe, F., Kochzius, M., 2018. Sea surface currents and geographic isolation shape the genetic population structure of a coral reef fish in the Indian Ocean. *PLoS One* 13 (3), e0193825.
- Jaiteh, V.F., Loneragan, N.R., Warren, C., 2017. The end of shark finning? Impacts of declining catches and fin demand on coastal community livelihoods. *Marine Policy* 82, 224–233.
- Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., Steneck, R.S., van Oppen, M.J.H., et al., 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* 28, 307–325.
- Jones, G.P., Planes, S., Thorrold, S.R., 2005. Coral reef fish larvae settle close to home. *Current Biology* 15, 1314–1318.
- Kegler, P., Kegler, H.F., Gärdes, A., Ferse, S.C.A., Lukman, M., Alfiansah, Y.R., et al., 2017a. Bacterial biofilm communities and coral larvae settlement at different levels of anthropogenic impact in the Spermonde Archipelago, Indonesia. *Frontiers in Marine Science* 4, 270. <https://doi.org/10.3389/fmars.2017.00270>.
- Kegler, H.F., Kegler, P., Luckmann, A., Jennerjahn, T.C., Gärdes, A., 2018a. Small scale shifts in microbial communities due to local island populations in the Spermonde Archipelago, Indonesia. *PeerJ* 6, e4555.
- Kegler, H.F., Lukman, M., Teichberg, M., Plass-Johnson, J., Hassenrück, C., Wild, C., et al., 2017b. Bacterial community composition and potential driving factors in different reef habitats of the Spermonde archipelago, Indonesia. *Frontiers in Microbiology* 8 (662). <https://doi.org/10.3389/fmicb.2017.00662>.
- Keuse, J., Treml, E.A., Huelsken, T., Barber, P.H., DeBoer, T., Kochzius, M., Riginio, C., 2018b. Historical divergences associated with intermittent land bridges overshadow isolation by larval dispersal in co-distributed species of *Tridacna* giant clams. *Journal of Biogeography* 45, 848–858. <https://doi.org/10.1111/jbi.13163>.
- Knittweis, L., Jompa, J., Richter, C., Wolff, M., 2009a. Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde archipelago, South Sulawesi, Indonesia. *Coral Reefs* 28 (3), 793–804.
- Knittweis, L., Kraemer, W., Timm, J., Kochzius, M., 2009b. Genetic structure of *Heliofungia actiniformis* (Scleractinia: Fungiidae) populations in the Indo-Malay Archipelago: implications for live coral trade management efforts. *Conservation Genetics* 10, 241–249. <https://doi.org/10.1007/s10592-008-9566-5>.
- Knittweis, L., Wolff, M., 2010. Live coral trade impacts on the mushroom coral *Heliofungia actiniformis* in Indonesia: potential future management approaches. *Biological Conservation* 143 (11), 2722–2729.
- Kochzius, M., Nuryanto, A., 2008. Strong genetic population structure in the boring giant clam *Tridacna crocea* across the Indo-Malay archipelago: implications related to evolutionary processes and connectivity. *Molecular Ecology* 17, 3775–3787.
- Kochzius, M., Seidel, C., Hauschild, J., Kirchhoff, S., Mester, P., Meyer-Wachsmuth, I., et al., 2009. Genetic population structures of the blue starfish *Linckia laevigata* and its gastropod ectoparasite *Thyca crystallina*. *Marine Ecology Progress Series* 396, 211–219.

- Kool, J.T., Paris, C.B., Barber, P.H., Cowen, R.K., 2011. Connectivity and the development of population genetic structure in Indo-West Pacific coral reef communities. *Global Ecology and Biogeography* 20, 695–706.
- Kubicek, A., Breckling, B., Hoegh-Guldberg, O., Reuter, H., 2019. Climate change drives trait-shifts in coral reef communities. *Scientific Reports* 9. Article number: 3721.
- Kubicek, A., Jopp, F., Breckling, B., Lange, C., Reuter, H., 2015. Context-oriented model validation of individual-based models in ecology: a hierarchically structured approach to validate qualitative, compositional and quantitative characteristics. *Ecological Complexity* 22, 178–191.
- Kubicek, A., Muhando, C., Reuter, H., 2012. Simulations of long-term community dynamics in coral reefs - how perturbations shape trajectories. *PLoS Computational Biology* 8 (11), e1002791. <https://doi.org/10.1371/journal.pcbi.1002791>.
- Leins, J., 2017. Social Dependencies in Artisanal Reef Fisheries: Drawbacks and Improvement Strategies –Application of an Agent-Based Model (M.Sc. thesis). University of Oldenburg.
- Madduppa, H.H., Timm, J., Kochzius, M., 2014a. Interspecific, spatial and temporal variability of self-recruitment in anemonefishes. *PLoS One* 9 (2), e90648.
- Madduppa, H.H., Timm, J., Kochzius, M., 2018. Reduced genetic diversity in clown anemonefish (*Amphiprion ocellaris*) in exploited reefs of the Spermonde Archipelago, Indonesia. *Frontiers in Marine Science* 5, 80.
- Madduppa, H.H., von Juterzenka, K., Syakir, M., Kochzius, M., 2014b. Socio-economy of marine ornamental fishery and its impact on the population structure of the clown anemonefish *Amphiprion ocellaris* and its host anemones in Spermonde Archipelago, Indonesia. *Ocean and Coastal Management* 100, 41–50.
- McClanahan, T.R., Marnane, M.J., Cinner, J.E., Kiene, W.E., 2006. A comparison of marine protected areas and alternative approaches to coral-reef management. *Current Biology* 16 (14), 1408–1413.
- Metcalfe, K., Collins, T., Abernethy, K.E., Boumba, R., Dengui, J.C., Miyalou, R., et al., 2016. Addressing uncertainty in marine resource management; combining community engagement and tracking technology to characterize human behavior. *Conservation Letters* 10, 460–469.
- Micheli, F., Mumby, P.J., Brumbaugh, D.R., Broad, K., Dahlgren, C.P., Harborne, A.R., et al., 2014. High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biological Conservation* 171, 186–194.
- Miñarro, S., Leins, J., Acevedo-Trejos, E., Fulton, E.A., Reuter, H., 2018. SEAMANCORE: a spatially explicit simulation model for assisting the local MANAGEMENT of CORal REefs. *Ecological Modelling* 384, 296–307.
- Miñarro, S., Navarrete Forero, G., Reuter, H., van Putten, I.E., 2016. The role of patron-client relations on the fishing behaviour of artisanal fishermen in the Spermonde Archipelago (Indonesia). *Marine Policy* 69, 73–83.
- Miñarro, S., 2017. Modelling Coral Reefs to Support Their Local Management: A Case Study in the Spermonde Archipelago, Indonesia (Dissertation). Universität Bremen, Bremen.
- Mumby, P.J., Hastings, A., Edwards, H.J., 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450 (7166), 98.
- Mumby, P.J., Steneck, R.S., 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology and Evolution* 23 (10), 555–563.
- Nanninga, G.B., Saenz-Agudelo, P., Zhan, P., Hoteit, I., Berumen, M.L., 2015. Not finding Nemo: limited reef-scale retention in a coral reef fish. *Coral Reefs* 34, 383–392.
- Nasir, A., Lukman, M., Tuwo, A., Hatta, M., Tambaru, R., Nurfadilah, 2016. The use of C/N ratio in assessing the influence of land-based material in coastal water of South Sulawesi and Spermonde Archipelago, Indonesia. *Frontiers in Marine Science* 3, 266. <https://doi.org/10.3389/fmars.2016.00266>.

- Nasir, A., Tuwo, A., Lukman, M., Usman, H., 2015. Impact of increased nutrient on the variability of chlorophyll-a in the west coast of South Sulawesi, Indonesia. *International Journal of Scientific Engineering and Research* 6, 821–826.
- Navarrete-Forero, G., Miñarro, S., Mildenerberger, T.K., Breckwoldt, A., Sudirman, S., Reuter, H., 2017. Participatory boat tracking reveals spatial fishing patterns in an Indonesian artisanal fishery. *Frontiers in Marine Science* 4 (409), 1–12. <https://doi.org/10.3389/fmars.2017.00409>.
- Nurdin, N., Grydehøj, A., 2014. Informal governance through patron–client relationships and destructive fishing in Spermonde Archipelago, Indonesia. *J. Mar. Isl. Cult.* 3, 54–59.
- Nurdin, N., Komatsu, T., Rani, C., Fakhriyyah, S., 2016. Coral reef destruction of Small island in 44 years and destructive fishing in Spermonde Archipelago, Indonesia. *IOP Conference Series: Earth and Environmental Science* 47, 012011.
- Nuryanto, A., Kochzius, M., 2009. Highly restricted gene flow and deep evolutionary lineages in the giant clam *Tridacna maxima*. *Coral Reefs* 28, 607–619.
- Pet-Soede, L., Cesar, H.S.J., Pet, J.S., 1999. An economic analysis of blast fishing on Indonesian coral reefs. *Environmental Conservation* 26, 83–93.
- Pet-Soede, L., Erdmann, M.V., 1998a. Blast fishing in southwest Sulawesi, Indonesia. *Naga, the ICLARM Quarterly* 21 (2), 4–9.
- Pet-Soede, C., Van Densen, W.L.T., Hiddink, J.G., Kuyl, S., Machiels, M.A.M., 2001. Can fishermen allocate their fishing effort in space and time on the basis of their catch rates? An example from Spermonde archipelago, SW Sulawesi, Indonesia. *Fisheries Management and Ecology* 8, 15–36.
- Pet-Soede, L., Erdmann, M., 1998b. An overview and com-parison of destructive fishing practices in Indonesia. *SPC Live Reef Fish Information Bulletin* 4, 28–36.
- Planes, S., Jones, G.P., Thorrold, S.R., 2009. Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences of the United States of America* 106, 5693–5697.
- Plass-Johnson, J.G., Bednarz, V.N., Hill, J.M., Jompa, J., Ferse, S.C.A., Teichberg, M., 2018a. Contrasting responses in the niches of two coral reef herbivores along a gradient of habitat disturbance in the Spermonde Archipelago, Indonesia. *Frontiers in Marine Science* 5, 32. <https://doi.org/10.3389/fmars.2018.00032>.
- Plass-Johnson, J.G., Ferse, S.C.A., Jompa, J., Wild, C., Teichberg, M., 2015a. Fish herbivory as key ecological function in a heavily degraded coral reef system. *Limnology and Oceanography* 60, 1382–1391.
- Plass-Johnson, J.G., Heiden, J., Abu, N., Lukman, M., Teichberg, M., 2016a. Experimental analysis of the effects of consumer exclusion on recruitment and succession of a coral reef system along a water quality gradient in the Spermonde Archipelago, Indonesia. *Coral Reefs* 35, 229–243.
- Plass-Johnson, J.G., Schwieder, H., Heiden, J., Weiland, L., Wild, C., Jompa, J., et al., 2015b. *Acanthaster planci* outbreak in the Spermonde Archipelago, Indonesia. *Regional Environmental Change* 15, 1157–1162.
- Plass-Johnson, J.G., Taylor, M.H., Husain, A.A.A., Teichberg, M., Ferse, S.C.A., 2016b. Non-random variability in functional composition of coral reef fish communities along an environmental gradient. *PLoS One* 11, e0154014.
- Plass-Johnson, J.G., Teichberg, M., Bednarz, V.N., Gärdes, A., Heiden, J., Lukman, M., et al., 2018b. Spatio-temporal patterns in coral reef communities of the Spermonde Archipelago, 2012–2014, II: fish assemblages display structured variation related to benthic condition. *Frontiers in Marine Science* 5, 36. <https://doi.org/10.3389/fmars.2018.00036>.
- Radjawali, I., 2011. Social networks and the live reef food fish trade: examining sustainability. *Journal of Indonesian Social Sciences and Humanities* 4, 65–100.

- Radjawali, I., 2012. Examining local conservation and development: live reef foodfishing in the Spermonde Archipelago, Indonesia. *Journal of Integrated Coastal Zone Management* 12.
- Ratsimbazafy, H.A., 2019. A Spatial Arrangement and Governance System for the Future Malagasy Network of marine Protected Areas (Ph.D. Thesis). Belgium. Vrije Universiteit Brussel (VUB).
- Reuter, H., Jopp, F., Blanco-Moreno, J.-M., Damgaard, C., Matsinos, Y., DeAngelis, D., 2010. Ecological hierarchies and self-organisation— pattern analysis, modelling and process integration across scales. *Basic and Applied Ecology* 11, 572–581. <https://doi.org/10.1016/j.baae.2010.08.002>.
- Roff, G., Mumby, P.J., 2012. Global disparity in the resilience of coral reefs. *Trends in Ecology and Evolution* 27, 404–413.
- Rogers, A., Blanchard, J.L., Mumby, P.J., 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* 24 (9), 1000–1005.
- Saenz-Agudelo, P., Jones, G.P., Thorrold, S.R., Planes, S., 2009. Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis under different gene flow scenarios. *Molecular Ecology* 18, 1765–1776.
- Saenz-Agudelo, P., Jones, G.P., Thorrold, S.R., Planes, S., 2011. Connectivity dominates larval replenishment in a coastal reef fish metapopulation. *Proceedings of the Royal Society B: Biological Sciences* 278, 2954–2961.
- Sandin, S.A., McNamara, D.E., 2012. Spatial dynamics of benthic competition on coral reefs. *Oecologia* 168, 1079–1090.
- Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander, A.M., et al., 2008. Baselines and degradation of coral reefs in the northern line islands. *PLoS One* 3 (2), e1548.
- Sawall, Y., Jompa, J., Litaay, M., Maddusila, A., Richter, C., 2013. Coral recruitment and potential recovery of eutrophied and blast fishing impacted reefs in Spermonde Archipelago, Indonesia. *Marine Pollution Bulletin* 74 (1), 374–382.
- Sawall, Y., Richter, C., Ramette, A., 2012. Effects of eutrophication, seasonality and macrofouling on the diversity of bacterial biofilms associated with coral reefs of the Spermonde Archipelago, Indonesia. *PLoS One* 7 (7), e39951.
- Sawall, Y., Teichberg, M., Seemann, J., Litaay, M., Jompa, J., Richter, C., 2011. Nutritional status and metabolism of the coral *Stylophora subseriata* along a eutrophication gradient in Spermonde Archipelago (Indonesia). *Coral Reefs* 30, 841–853.
- Sawall, Y., Ttiwong, S.K., Jompa, J., Richter, C., 2014. Calcification, photosynthesis and nutritional status of the hermatypic coral *Porites lutea*: contrasting case studies from Indonesia and Thailand. *Galaxea, Journal of Coral Reef Studies* 16, 1–10.
- Schwerdtner Máñez, K., Ferse, S.C.A., 2010. The history of Makassan Trepang fishing and trade. *PLoS One* 5, e11346.
- Schwerdtner Máñez, K., Husain, P.S., 2013. First evidence of targeted moray eel fishing in the Spermonde Archipelago, South Sulawesi, Indonesia. *Traffic Bulletin* 25, 4–7.
- Schwerdtner Máñez, K., Husain, S., Ferse, S.C.A., Máñez Costa, M., 2012. Water scarcity in the Spermonde Archipelago, Sulawesi, Indonesia: past, present and future. *Environmental Science and Policy* 23, 74–84.
- Seeman, J., Sawall, Y., Auel, H., Richter, C., 2013. The use of lipids and fatty acids to measure the trophic plasticity of the coral *Stylophora subseriata*. *Lipids* 48 (3), 275–286.
- Seemann, J., Carballo-Bolanos, R., Berry, K.L., González, C.T., Richter, C., Leinfelder, R.R., 2012. Importance of heterotrophic adaptations of corals to maintain energy reserves. In: *Proceedings of the 12th International CoralReef Symposium*, Cairns, Australi, p. 19A.

- Smith, J.E., Hunter, C.L., Smith, C.M., 2010. The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia* 163, 497–507. <https://doi.org/10.1007/s00442-009-1546-z>.
- Teichberg, M., Wild, C., Bednarz, V.N., Kegler, H., Lukman, M., Gärdes, A., et al., 2018. Spatio-temporal patterns in coral reef communities of the Spermonde Archipelago, 2012-2014, I: Comprehensive reef monitoring of water and benthic indicators reflect changes in reef health. *Frontiers in Marine Science* 5, 33. <https://doi.org/10.3389/fmars.2018.00033>.
- Timm, J., Kochzius, M., 2008. Geological history and oceanography of the Indo-Malay Archipelago shape the genetic population structure in the False Clown Anemonefish (*Amphiprion ocellaris*). *Molecular Ecology* 17, 3999–4014.
- Timm, J., Kochzius, M., Madduppa, H.H., Neuhaus, A.I., Dohna, T., 2017. Small-scale genetic population structure of coral reef organisms in Spermonde Archipelago, Indonesia. *Frontiers in Marine Science* 4, 294.
- Timm, J., Planes, S., Kochzius, M., 2012. High similarity of genetic population structure in the False Clown Anemonefish (*Amphiprion ocellaris*) found in microsatellite and mitochondrial control region analysis. *Conservation Genetics* 13, 693–706.
- Tremblay, E.A., Roberts, J., Halpin, P.N., Possingham, H., Riginos, C., 2015. The emergent geography of biophysical dispersal barriers across the Indo-West Pacific. *Diversity and Distributions* 21, 465–476.
- Turner, R.A., Polunin, N.V.C., Stead, S.M., 2015. Mapping inshore fisheries: comparing observed and perceived distributions of pot fishing activity in Northumberland. *Marine Policy* 51, 173–181.
- UNEP-WCMC, 2014. Review of Corals from Indonesia (Coral Species Subject to EU Decisions where Identification to Genus Level Is Acceptable for Trade Purposes). UNEP-WCMC, Cambridge.
- van der Ven, M.R., Heynderickx, H., Kochzius, M., 2021. Differences in genetic diversity and divergence between brooding and broadcast spawning corals across two spatial scales in the Coral Triangle region. *Marine Biology* 168. <https://doi.org/10.1007/s00227-020-03813-8>.
- Vermeij, D., Dailor, Smith, 2011. Crustose coralline algae can suppress macroalgal growth and recruitment on Hawaiian coral reefs. *Marine Ecology Progress Series* 422, 1–7.
- Veron, J.E.N., Devantier, L.M., Turak, E., Green, A.L., Kininmonth, S., Stafford-Smith, M., et al., 2009. Delineating the coral triangle. *Galaxea. Journal of Coral Reef Studies* 11, 91–100.
- Voris, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time duration. *Journal of Biogeography* 27, 1153–1167.
- Wabnitz, C., Taylor, M., Green, E., Razak, T., 2003. From Ocean to Aquarium: The Global Trade in marine Ornamental Species. UNEP-WCMC, Cambridge, UK.
- Weijerman, M., Fulton, E.A., Kaplan, I.C., Gorton, R., Leemans, R., Mooij, W.M., et al., 2015. An integrated coral reef ecosystem model to support resource management under a changing climate. *PLoS One* 10 (12), e0144165.
- Wood, E., Malsch, K., Miller, J., 2012. International trade in hard corals: review of management, sustainability and trends. In: Proceedings of the 12th International Coral Reef Symposium. Cairns, Australia, pp. 9–13, 9–13 July 2012.
- Wyrtki, K., 1961. Physical Oceanography of the Southeast Asian Waters. University of California, La Jolla, CA.
- Yasir Haya, L.O.M., Fujii, M., 2017. Mapping the change of coral reefs using remote sensing and in situ measurements: a case study in Pangkajene and Kepulauan regency, Spermonde Archipelago, Indonesia. *Journal of Oceanography* 73, 623–645.

## Appendix A5

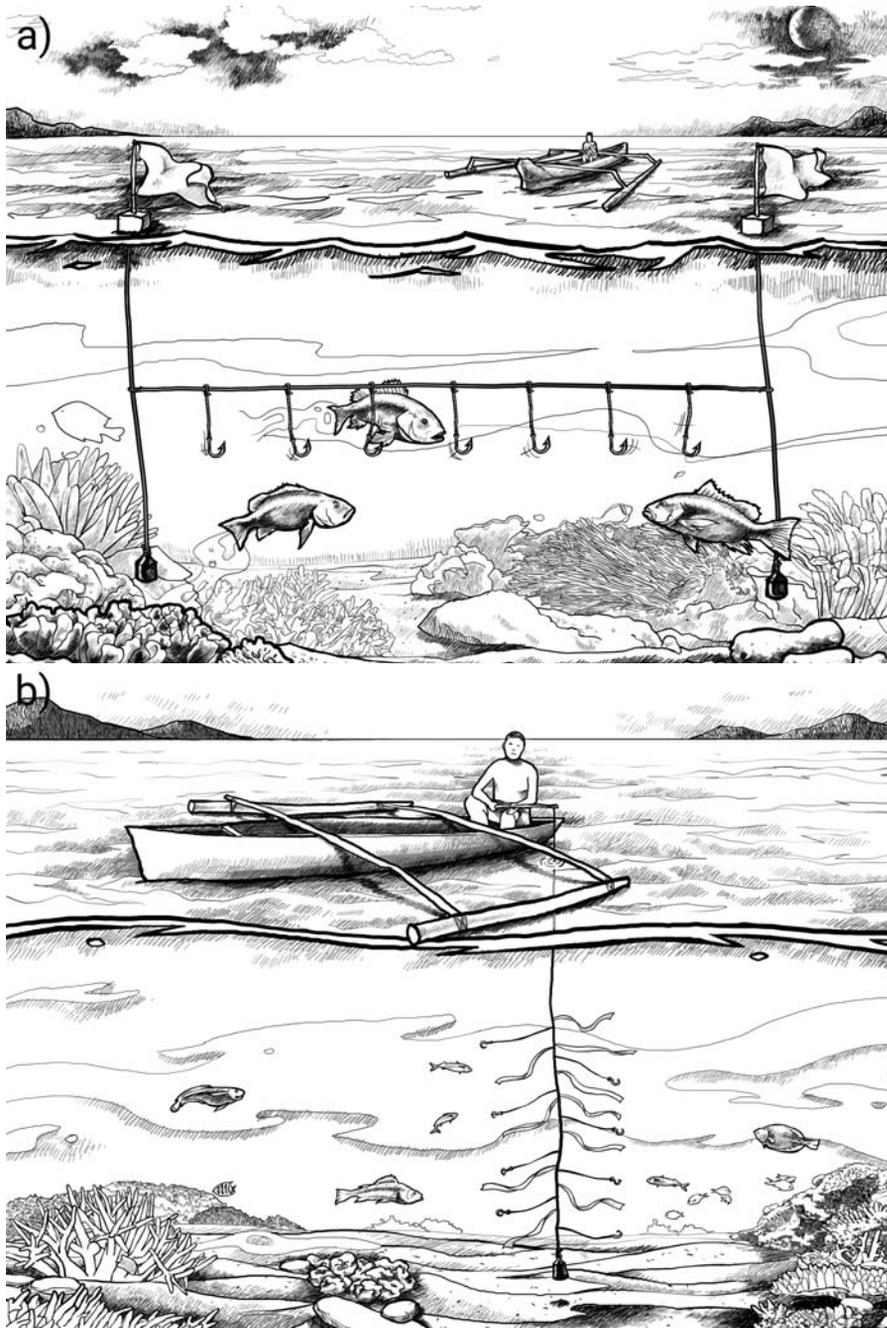
**Table A5.1** List of different gear types used in the Spermonde Archipelago and the targeted species.

Category	Gear type	Local name	Target species	Main market	Legal status
Hook and line	Horizontal long line	Rawe <sup>a</sup>	Lutjanidae, Carangidae, Serranidae, Nemipteridae	Local	Legal
	Vertical long line	Rinta	Clupeidae, pelagic bait fish	Local	Legal
	Trolling for piscivores	Kedo-kedo	Serranidae, Scombridae	Local/ export	Legal
	Trolling for squid	Doang-doang	Teuthida	Local	Legal
	Octopus bait	Pocong-pocong	Octopoda	Local/ export	Legal
	Shark bait	Tomba	Carcharhiniformes, Batoidea	Local/ export	Legal
Net	Gill net	Lanra	Clupeidae, Carangidae	Local	Legal
	Crab and shrimp gill net	Lanra	Crustacea	Local	Legal
	Scoop net	Sero	Pomacentridae, other small ornamentals	Export	Legal
	Purse seine	Gae/Rengge	Clupeidae, Engraulidae, Carangidae	Local	Legal
	Danish seine	Gae/Rengge	Leiognatidae, Synodontidae	Local	Legal
	Mobile lift net	Bagang Lopi	Carangidae, Clupeidae, Engraulidae, Teuthida	Local	Legal
	Stationary lift net	Bagang Tancap	Clupeidae, Leiognatidae, Teuthida	Local	Legal
	Beach seine	Jaring (mairo)	Miscellaneous	Local	Legal
	Mini trawl	Rere/ Renreng	Miscellaneous	Local/ export	Illegal
Traps	Fish trap	Bubu	Lethrinidae, Lutjanidae, Serranidae	Local/ export	Legal
	Crab trap	Rakkang	Crustacea	Local/ export	Legal
	Flying fish trap	Buaro/Bale-bale	Exocoetidae	Export	Legal
Others	Compressor diving	Penyalam/ Hookah	Holothuridae, Gastropoda, Nephropidae, Anthozoa	Export	Legal
	Spear gun	Patte'	Lutjanidae, Scombridae, Serranidae, Scaridae, Siganidae, Acanthuridae	Local	Legal
	Reef gleaning	?	Gastropoda, Bivalvia	Local	Legal
	Fish-attracting device	Rumpon	Various pelagic fishes	Local/ export	Legal
	Blast fishing	Pembom/ Panges	Various fishes	Local	Illegal
	Cyanide fishing	Pembius/ Paselang	Live ornamental and food reef fishes, Nephropidae	Export	Illegal

See Fig. A5.1 for illustrations. Gear types in blue are not illustrated.

<sup>a</sup>Rawe Makassar denotes a particular kind of horizontal long line, which is combined with a gill net.

From Ferse et al. (2014).



**FIGURE A5.1** Illustrations of different fishing methods. The drawings are by Saranat Tiemkeo. (A) Horizontal long line, (B) vertical long line, (C) trolling for piscivores, (D) trolling for squid, (E) octopus bait, (F) shark bait, (G) gill net, (H) purse seine, (I) mobile lift net, (J) stationary lift net, (K) mini trawl, (L) fish trap, (M) crab trap, (N) compressor diving, (O) fish-attracting device, (P) blast fishing, (Q) cyanide fishing.

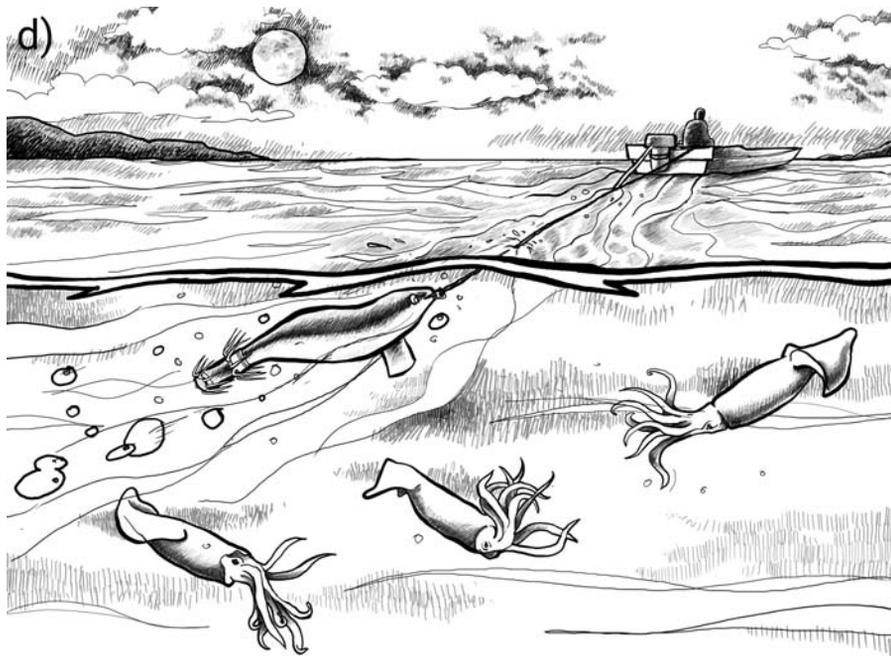
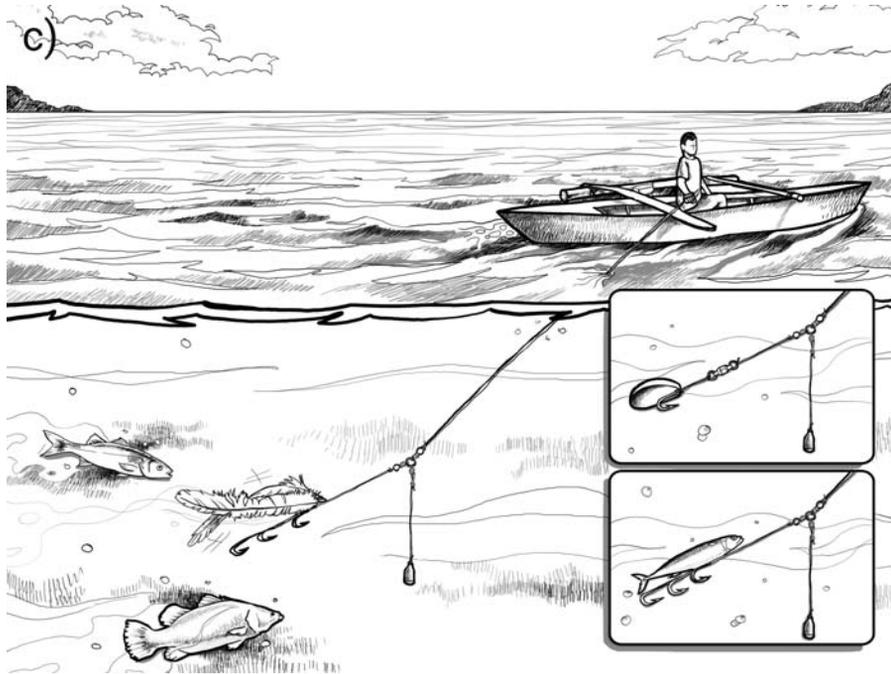


FIGURE A5.1 Cont'd

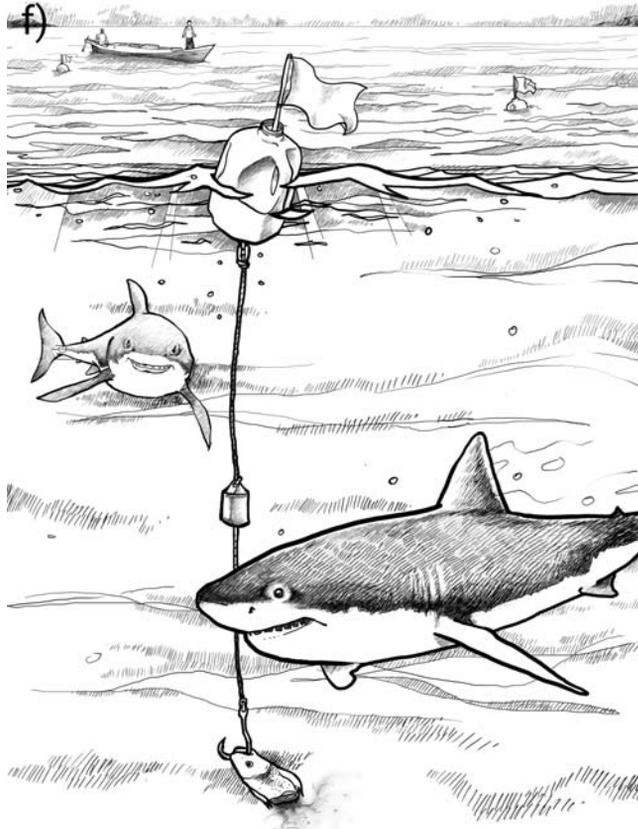
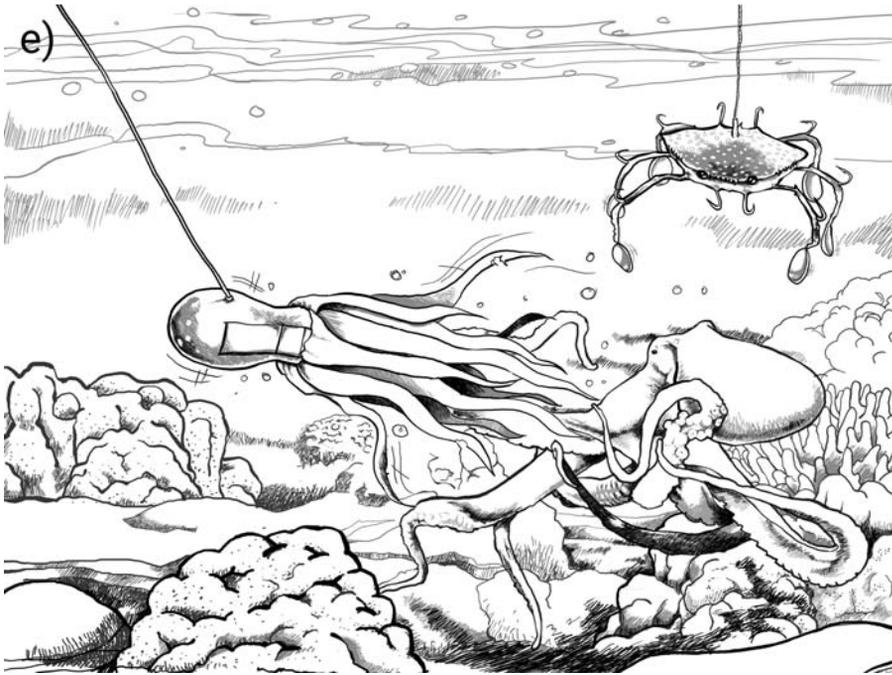


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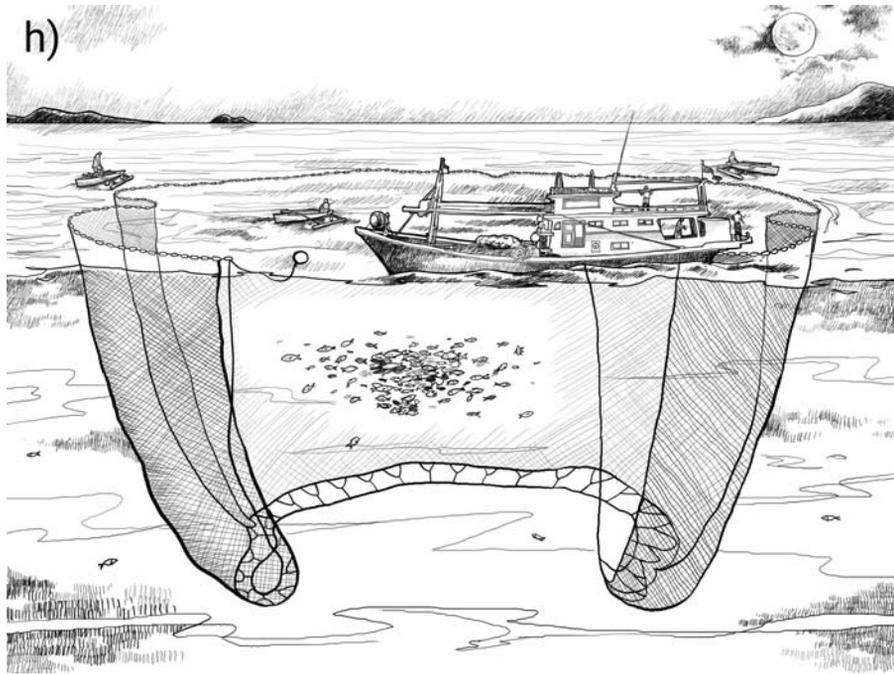
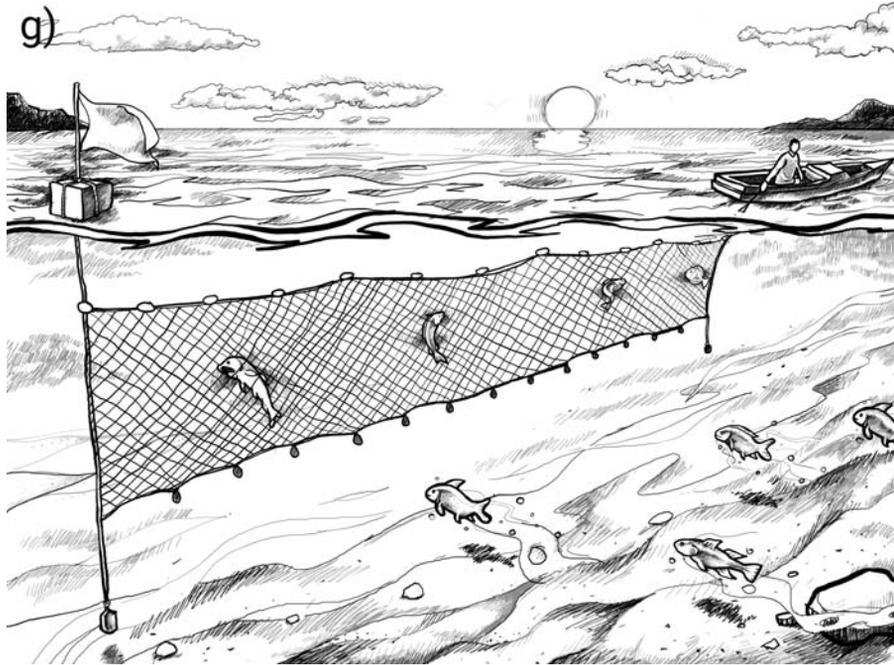


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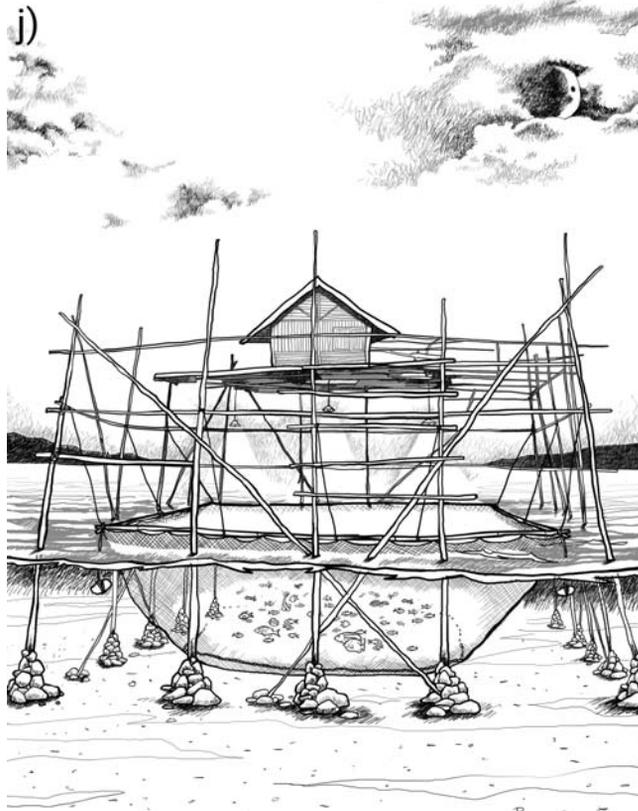
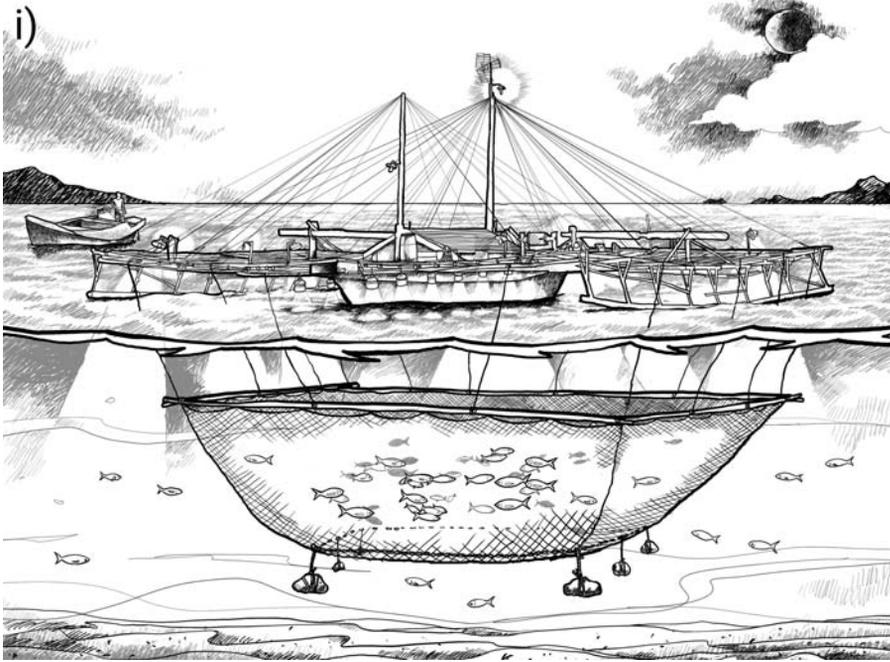


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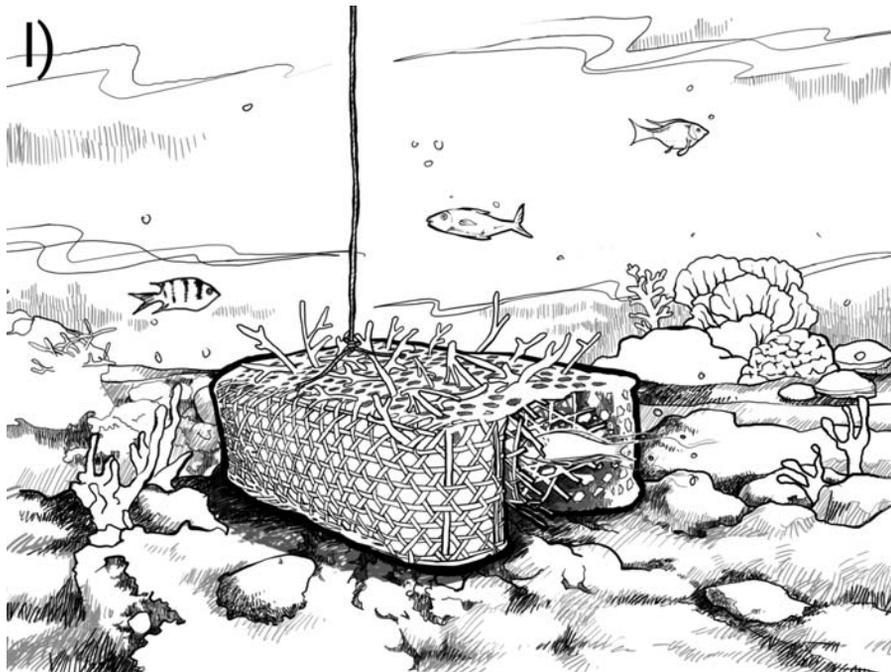
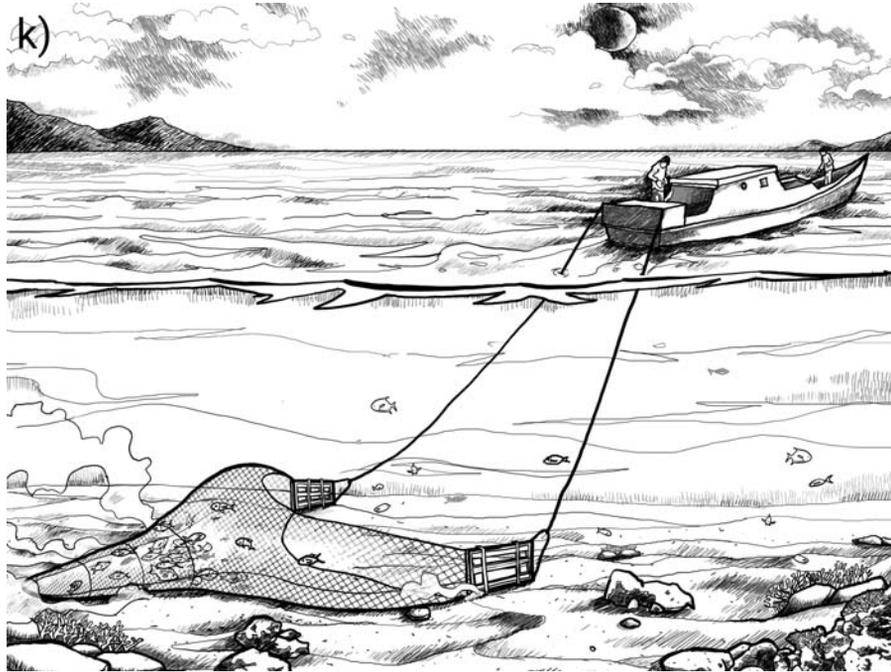


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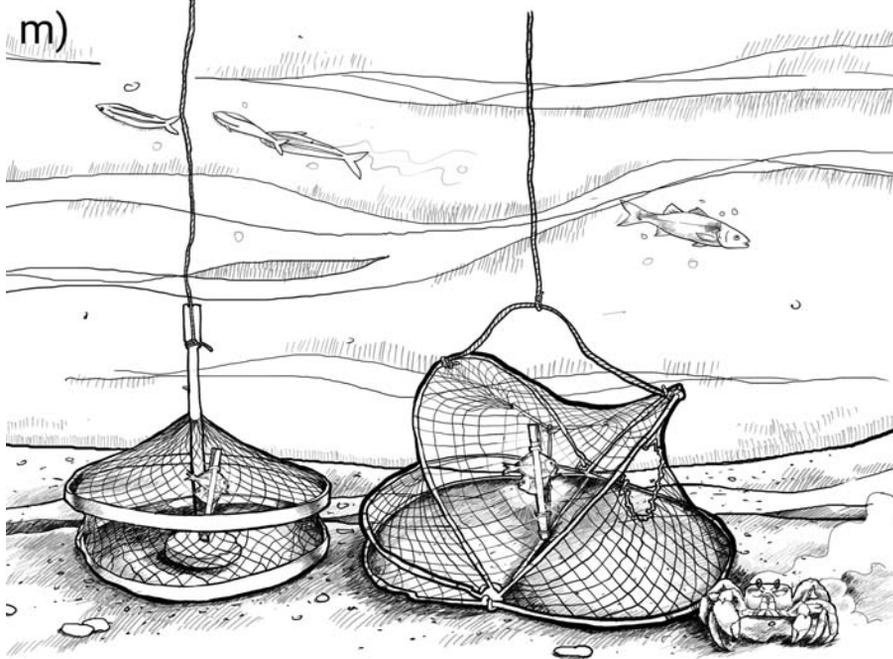


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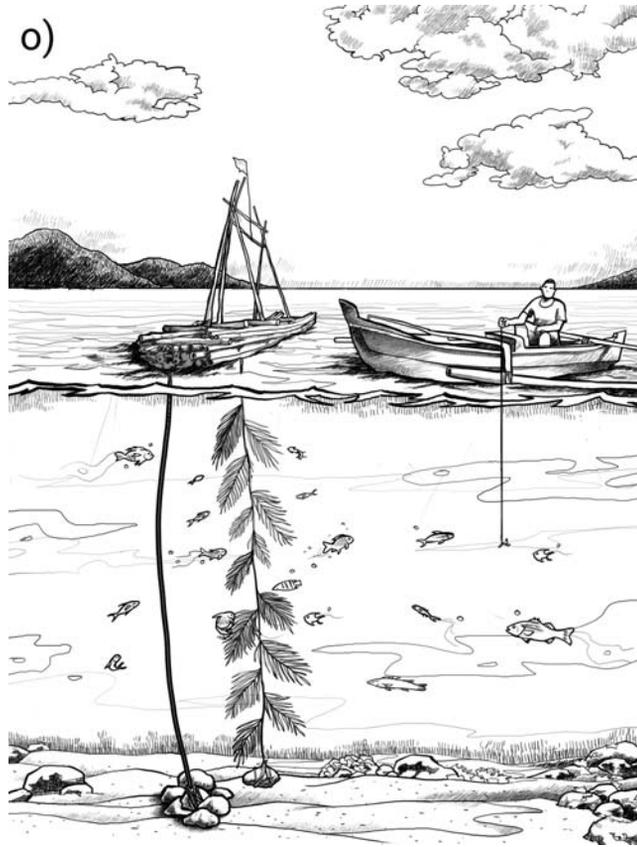


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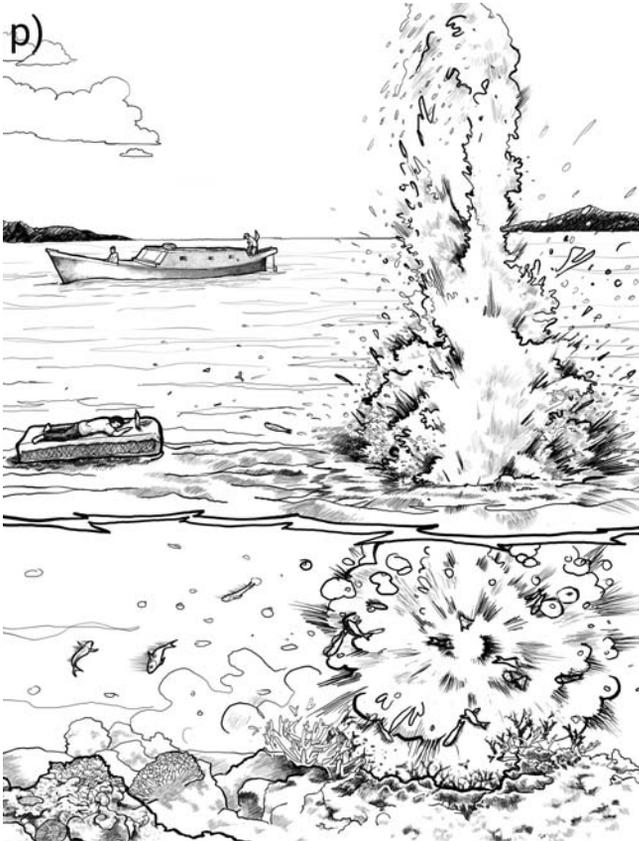


FIGURE A5.1 Cont'd



FIGURE A5.1 Cont'd