
17 3D Analysis of Coral Reef Informs Anemonefish Habitat

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17.1 INTRODUCTION

Coral reef fishes are among the richest animal communities in the world. Complex seascape structures, which are closely related to coral reef morphology, enhance species diversity (Pittman and Olds 2015). High species diversity and complex habitat structures complicate our understanding of ecological phenomena in situ, including habitat selection, interspecific competition, and multispecies coexistence (Chapter 16 and Chapter 18). Can we simplify this to some degree?

Anemonefishes comprise 28 species and symbiotically associate with at least ten host anemone species in coral reef regions (Dunn 1981; Fautin and Allen 1997; Ollerton et al. 2007). Among ten host species, six (*Entacmaea quadricolor*, *Heteractis crispa*, *H. magnifica*, *Stichodactyla gigantea*, *S. mertensii*, and *Cryptodendrum adhaesivum*) inhabit hard substrates, while the others (*Macroactyla doreensis*, *H. malu*, *H. aurora*, *S. haddoni*) inhabit sandy bottoms. Since anemonefish spawn demersal eggs, adults inhabit anemones attached to hard substrates, except for some: *Amphiprion polymnus* inhabiting *S. haddoni* in sandy bottoms bring empty shells of bivalves as spawning sites nearby their anemones (Moyer and Steen 1979); *C. adhaesivum* inhabiting reefs are used by only juvenile *Amphiprion clarkii* because the former have very short tentacles and no space under the edge of their oral discs, which provide insufficient refuge for most all anemonefishes (Fautin and Allen 1997). Thus, *E. quadricolor*, *H. crispa*, *H. magnifica*, *S. gigantea*, and *S. mertensii* are major targets of interspecific competition by anemonefishes. In addition, anemonefishes include generalists that use six or more host species (e.g., *Amphiprion clarkii*, *A. akindynos*, and *A. chrysopterus*), specialists that use several (e.g., *A. ocellaris*, *A. perideraion*, and *A. polymnus*), and extreme specialists

that use only one host (e.g., *A. frenatus*, *A. mccullochi*, and *A. biaculeatus*, see Fautin and Allen 1997; Litsios et al. 2012; Nguyen et al. 2020).

While interspecific competition effects on host selection and cohabitation by anemonefishes are often unclear (see Chapter 16 and Chapter 18), distribution patterns of anemonefishes and host anemones in relation to geomorphic zones (see below) can clarify habitat use strategies. This chapter describes distribution patterns of several species of host anemone and anemonefishes in 3D structure coral reefs, especially two fringing reefs: namely the small reef (Sesoko Reef) of Sesoko Island, among the Okinawa Islands, and the large reef (Shiraho Reef) of Ishigaki Island, among the Sakishima Islands. Both are located in Okinawa, southern Japan. Habitat use strategies of anemonefishes are discussed in relation to geomorphic zones.

17.2 GEOMORPHIC ZONE AND MAPPING ANEMONE ON AERIAL IMAGE

Reef-building corals gradually grow vertically and horizontally to form a 3D reef facilitated by endosymbiotic Symbiodiniaceae zooxanthellae. Accordingly, fringing reefs develop along coastlines, where seawater is generally clear and warm (20 to 30°C), with geomorphic zonation including an outer reef slope (facing deep open water), reef crest (transitional area between the upper reef slope and reef flat), reef flat (wave-sweeping and shallow), backreef (calm and shallow with a sandy bottom), and subtidal near-shore zones (shallow sandy bottoms, Figure 17.1). In small fringing reefs, outer sandy sea bottoms may predominate. Although the terminology is not standardized (Blanchon 2011; Bellwood et al. 2018), aerial images show geomorphic zones (Figures 17.2a–b and 17.3a–b) with unique characteristics regarding water depth (deep/shallow), wave exposure

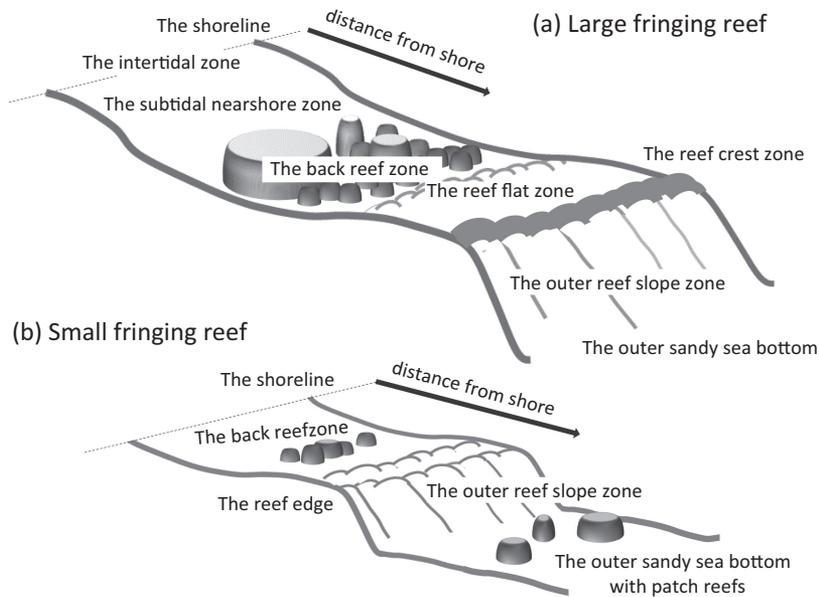


FIGURE 17.1 3D structure of fringing reefs and geomorphic zonation. a) A large fringing reef. b) A small fringing reef. See also Figure 16.4.

(high/low), water condition (fast/calm, open/sheltered), water temperature (stable/unstable), substrate (rock/sand), and crevices and holes (few/many). In fringing reefs, depth information in *centimetre* scales is critical because all but the outer reef zones are usually shallow (< 3 m deep).

Aerial images of coral reefs show seascape structures including sandy bottoms, rocky reefs, seagrass beds, and relative water depth (Figures 17.2 and 17.3). Furthermore, aerial images provide concise maps to record location information with complex coral reef structures (Hattori and Kobayashi 2009). By locating individual anemones in situ on concise maps, we can record their growth and survival, as they rarely relocate more than 0.5 m (Hattori personal observations). Maps can be subsequently updated to improve quality and to reflect changes in seascapes. Google Earth may provide high-resolution satellite images (Figure 17.2b), and more high-resolution aerial images can be obtained by low-flying drones (Figure 17.2c).

Since anemones used by anemonefish largely depend on photosynthate products produced by endosymbionts, as do reef-building corals, a larger tentacle-crown surface area facilitates capture of sunlight and prey, but the energy cost of maintaining a large body size increases in proportion to its volume (Dunn 1981; Sebens, 1982). Accordingly, anemone sizes depend on their habitat, and thus, large individuals are basically found in habitats suitable for large animals (Sebens 1982; Steen 1988). Thus, large anemones (the largest size of tentacle-crown surface area of an individual is regarded as the anemone size after two or more measurements, see Hattori 1991) are suitable hosts for anemonefishes (Fautin and Allen 1997). Information on geomorphic zones and anemone size should be incorporated when habitat use strategies of each anemonefish are discussed.

17.3 DISTRIBUTION OF ANEMONE AND ANEMONEFISHES ON A 3D REEF STRUCTURE

17.3.1 DISTRIBUTION OF *HETERACTIS CRISPA* ON A SMALL FRINGING REEF

Heteractis crispa are widely distributed (Ollerton et al. 2007), and are usually abundant in the backreef, outer reef slope, and outer sandy bottom (with patch reefs) up to 12 m deep (Dunn 1981; Hayashi et al. 2021). On the small fringing reef, Sesoko Reef, Hattori (1995) plotted all anemones observed in 1988 and 1989 onto a map and measured their respective water depth while snorkelling. Their locations were replotted in 1999, 2000, and 2009 onto a high-resolution aerial image (see Figure 17.2). Of the 76 observed in 1988 (71 had been recorded in 1983 by Hirose 1985), all had perished by 2009. Nine anemones (including two of those recorded in 1983) had been observed in 2000 (Hattori 2002) of which all inhabited the outer reef slope.

In Sesoko Reef, large anemones (> 1,000 cm²) tended to reside in the outer reef slope and in patchy reefs in the outer sandy sea bottom (beyond the reef edge zone, from 80 cm to 4 m deep at the lowest tide), while small anemones (< 500 cm²) mainly inhabited shallow reefs (< 80 cm deep) in the reef edge, reef flat, or backreef zones. As a small fringing reef, the reef crest and subtidal nearshore zones are unclear in Sesoko Reef (Figure 17.2). Their size was positively correlated with water depth and negatively correlated with growth from 1988 to 1989 (Hattori 2006), suggesting their suitable habitats were deeper sites (> 80 cm deep). Although the area of the reef edge zone is less than those of the reef flat and backreef zones (Figure 17.2), newly appeared anemones were abundant in this reef edge zone.

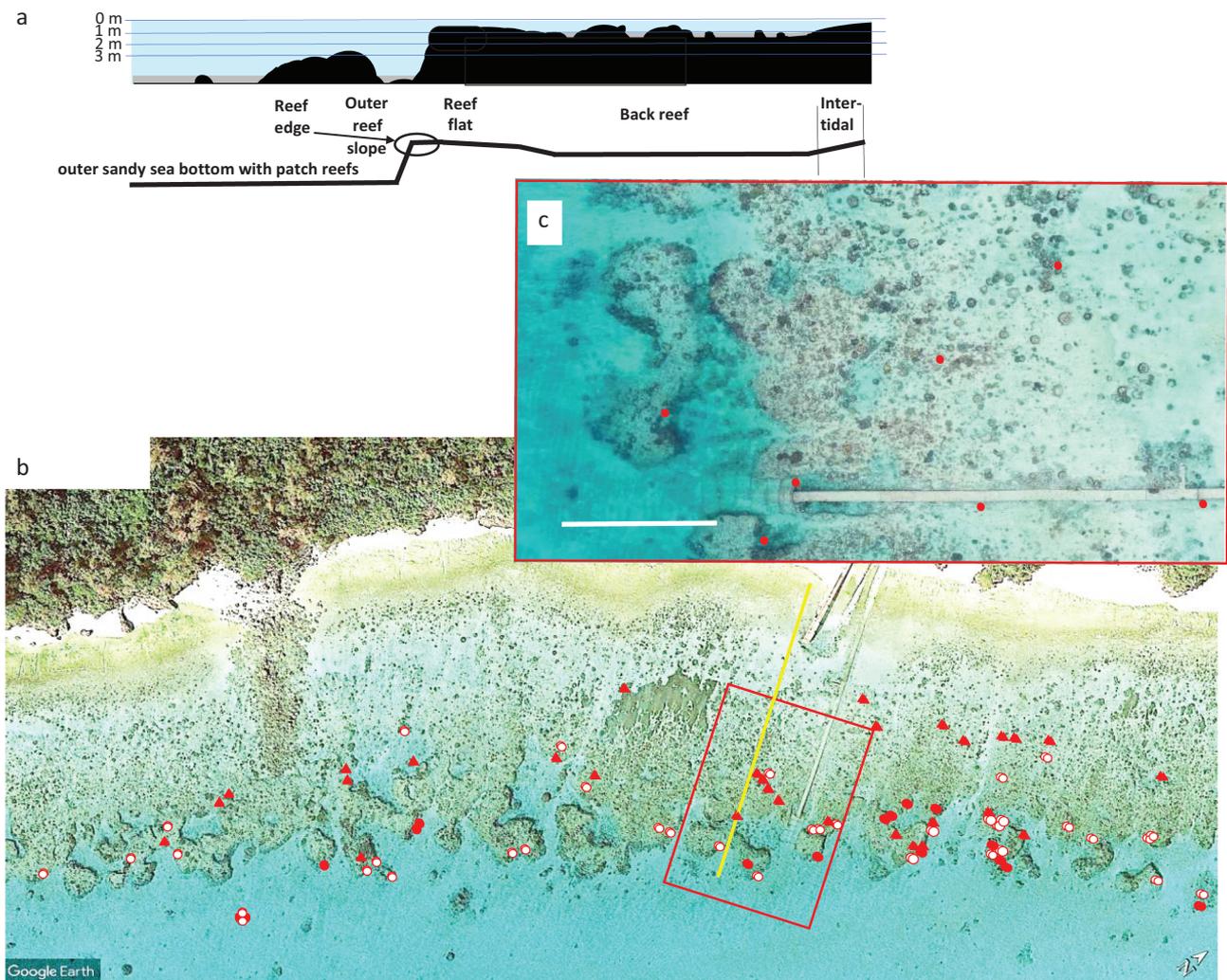


FIGURE 17.2 Geomorphic zonation of a small fringing reef (Sesoko Reef, Sesoko Island, Okinawa, Japan: 26°38'07.47" N, 127°51'56.82" E) and distributions of host anemones. a) Schematic view of the cross-section. b) Distributions of *Heteractis crispa* in 1988 shown in an aerial image from Google Earth (www.google.co.jp/intl/ja/earth/). Solid circles, open circles, and triangles indicate hosts with only *Amphiprion perideraion*, with *A. perideraion* and *A. clarkii*, and with only *A. clarkii*, respectively. Yellow line (120 m) indicates the cross-section in Figure 17.2a. Red square in Figure 17.2b indicates the range of Figure 17.2c. c) Distributions of *H. crispa* inhabited by *A. clarkii* in 2009 shown in an aerial image taken in 2017 by a low-flying drone (DJI Phantom 4 pro plus). Red circles indicate *H. crispa*. Many massive *Porites* corals are recognizable. White bar indicates 20 m.

Their high density was thought to be attributable to the high settlement rate of larval *H. crispa* because there were almost no large anemones in the reef edge zone (Hattori 2006). Drifting larvae of anemones do not have high mobility (like zooplankton) but juvenile anemones after settlement can move to some degree (presumably in cm scales) to select better microhabitats (Scott and Harrison 2008). Abundant hard and soft corals among a topography of exposed shallow reef edges slow local currents and allow drifting larvae to settle (Loya et al. 2001). Accordingly, they might have been near the surface (Figure 17.4) and settled in the reef edge zone. *Heteractis crispa* that settled in the outer reef zones would experience high survival and growth if inhabited by anemonefish. In contrast, anemones settled in the shallow habitats with refuges are not guaranteed survival

because of strong disturbances at the reef edge (waves induced by typhoons) and/or high-water temperatures in the shallow and calm backreef (causing loss of endosymbiotic zooxanthellae from anemones = bleaching, Saenz-Agudelo et al. 2011).

In the Ryukyu Islands, Okinawa, Japan, generalist *Amphiprion clarkii* and specialist *A. perideraion* use *H. crispa* (Hattori 1995, 2002; Hayashi et al. 2021). Since *A. clarkii* has high mobility, adult pairs often use two or more hosts in close proximity, whereas small juveniles use only one host until they move as adults to take breeding posts in large hosts (Hattori 1994; see Chapter 16). However, plots of *H. crispa* with inhabiting anemonefish clearly show that *A. perideraion* in the backreef zone are all located not near the shore but near the reef edge (Figure 17.2b). As generalists

are better migrants (Hattori 2002), they can temporarily use unsuitable habitats, because they can change hosts during growing up (Hattori 1994).

17.3.2 DISTRIBUTION OF *STICHODACTYLA GIGANTEA* ON A LARGE FRINGING REEF

Stichodactyla gigantea are often found on the outer reef slope to around 5 m deep (Dunn 1981), although they are

usually abundant in the subtidal nearshore zone (Mitchell 2005; Hattori and Kobayashi 2009). In the subtidal nearshore zone of Shiraho Reef (a large fringing reef), in 2003, Hattori and Kobayashi (2009) plotted *S. gigantea* onto an aerial image (Figure 17.3c–d). They measured the tentacle-crown surface area, water depth, and distance from dense seagrass beds, and examined their disappearance over three years. In this zone, *S. gigantea* was abundant at the sandy bottom, residing at 20 to 60 cm depths (at the lowest

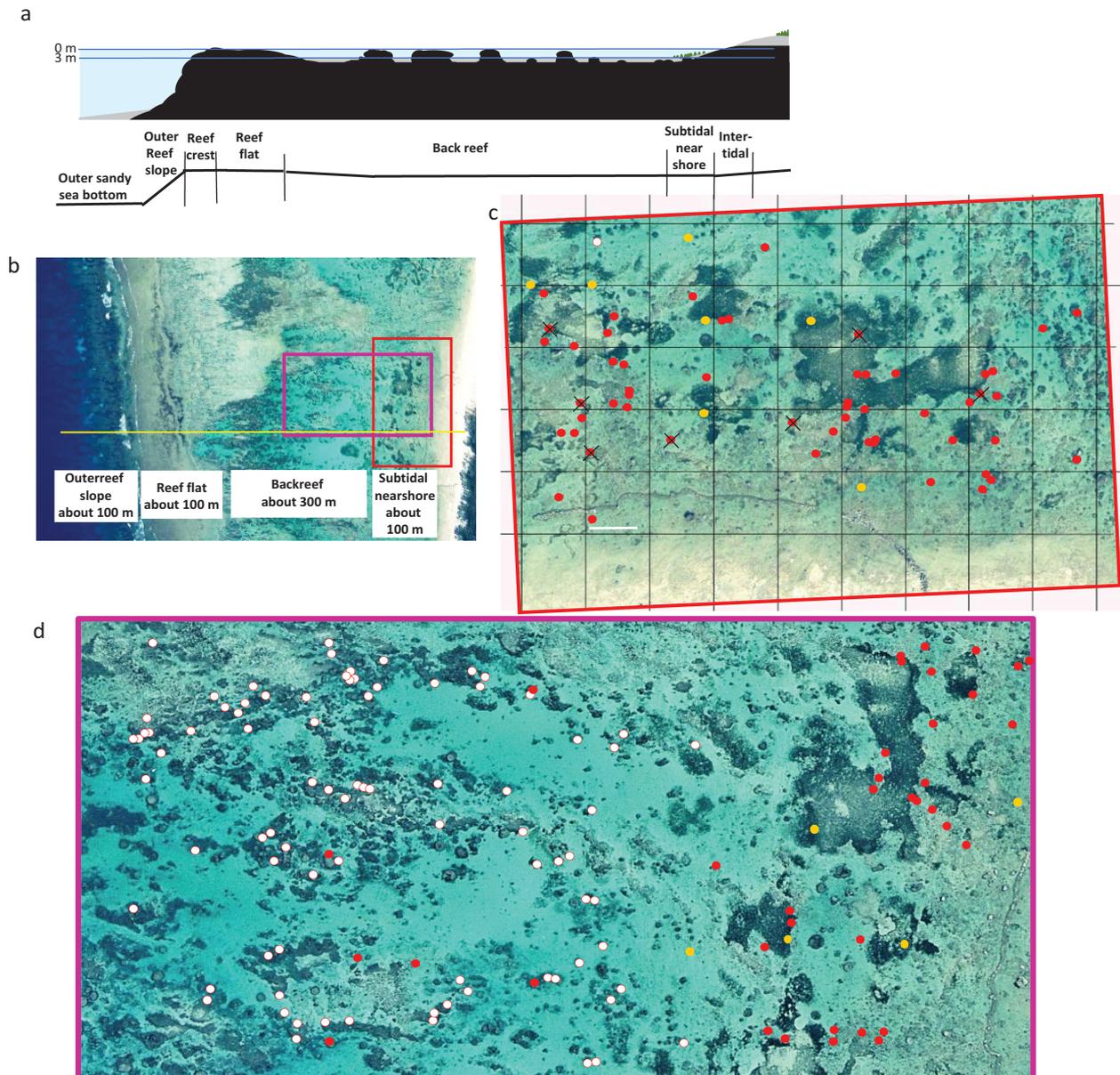


FIGURE 17.3 Geomorphic zonation of a large fringing reef (Shiraho Reef, Ishigaki Island, Okinawa, Japan: 24°22'19.22" N, 124°15'13.40" E) and distributions of host sea anemones. a) Schematic view of the cross-section and geomorphic zones. b) High-resolution aerial image of the reef taken on 20 September 2006 by PASCO Co. Japan (Ishigaki C-19-1608, Geospatial Information Authority of Japan, 2006, 2,540 dpi, altitude 1,500 m). Yellow line (890 m) indicates the cross-section in Figure 17.3a. Red square and pink square in Figure 17.3b indicate the range of Figure 17.3c and Figure 17.3d, respectively. c) Distributions of *Stichodactyla gigantea* and *S. haddoni* in 2003 shown in the aerial image. X indicates that anemone disappeared by 2006. Red circles and orange circles indicate *S. gigantea* with *A. ocellaris* and *S. haddoni* with *A. clarkii*, respectively. White bar indicates 20 m. White circle indicates *Entacmaea quadricolor*. d) Distributions of *E. quadricolor* (clonal assemblage), *S. gigantea*, and *S. haddoni* in 2002 shown in a high-resolution aerial image taken in 2007.

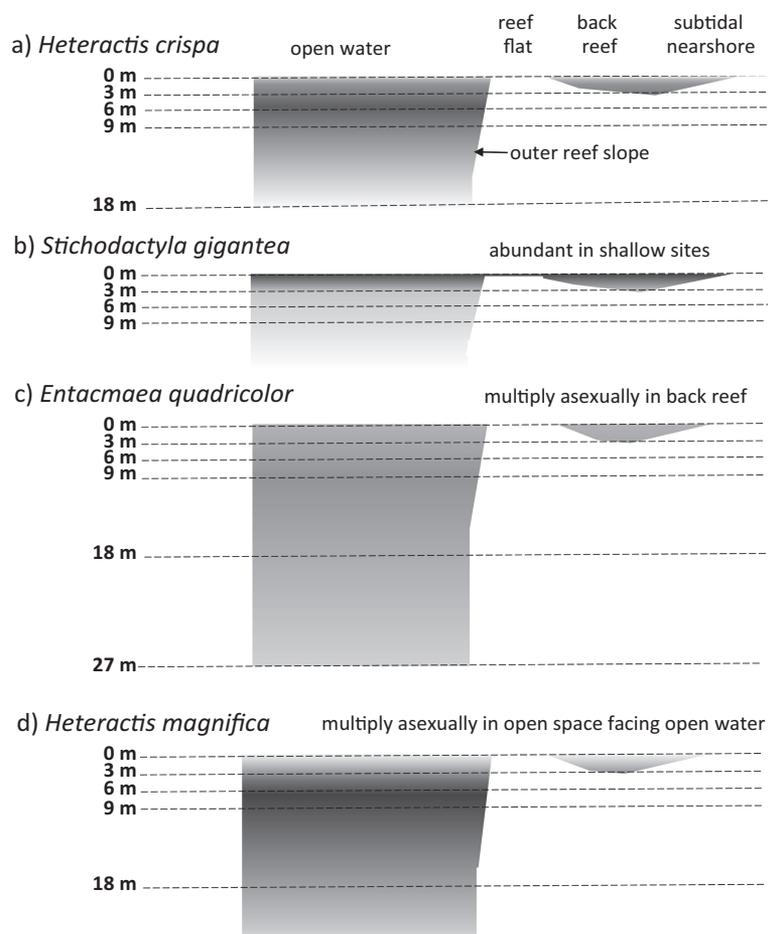


FIGURE 17.4 Hypothetical distributions of drifting larvae of four host anemone species outside and inside of a large fringing reef. Gradation indicates the relative density of larvae in the water column. Higher settlements of anemones are assumed to be closely related to higher density of larvae.

tide), about 0 to 6 m from dense seagrass beds, but were less abundant in small reefs (i.e., emergent rocks on sandy bottoms). Furthermore, there were almost no individuals on sandy bottoms deeper than 60 cm or within dense seagrass beds (< 20 cm deep). Although individuals inhabiting small reefs were few, they were larger, and their disappearance rate over three years was lower than those inhabiting sandy habitats (Hattori and Kobayashi 2009). Thus, small reefs are more suitable for *S. gigantea*. This distribution pattern of *S. gigantea* can be explained by two things: (1) higher settlement rates in the edge zone (20 to 60 cm deep) from dense seagrass beds (total area of this zone is larger than that of small reefs), and (2) low disappearance rate in small reefs (sandy bottoms are unstable). Drifting larvae of this anemone probably settle on hard substrates when the tidal current slows or stops at the lowest tide. The drifting larvae near the water surface likely explain the distribution pattern of *S. gigantea*, which are found in shallow sites in the nearshore, backreef, and outer reef slope zones (Figure 17.4).

This anemone is mainly used by *Amphiprion ocellaris* (Hayashi et al. 2021). However, this specialist mainly uses *H. magnifica* in relatively deep places (i.e., in the outer

reef slope and outer sandy sea bottoms with patch reefs) without competitors (Ricciardi et al. 2010). Reproductive ecology of *A. ocellaris* has been studied among *S. gigantea* in the subtidal nearshore zone, where sandy bottoms and seagrass beds predominate (Mitchell 2005; Hattori 2012). *Stichodactyla gigantea* require rocky substrates beneath sandy bottoms for adhesion, and *A. ocellaris* rely on emergent hard substrates as spawning sites, which are scarce in this zone (Hattori and Kobayashi 2009).

In the subtidal nearshore zone of Shiraho Reef, a data logger (Onset Hobo StowAway Tidbit Temperature Data Logger) recorded temperatures of approximately 13°C on 18 and 22 December and 38°C on 4 July and 1 August (Figure 17.5a; Hattori 2011), and indicated a fluctuation of water temperature within 24 h approximately from 0°C on 10, 16, 17 July, and 5 August to 11°C on 4 July and 13 May (Figure 17.5b). As *A. ocellaris* and *A. clarkii* inhabit the subtidal nearshore zone, they tolerate a wide range of temperatures. Low water temperatures are critical in limiting the distribution ranges of tropical anemonefish, leading to local adaptation to temperate waters (Clark et al. 2021), where host anemones for specialists *A. ocellaris* are not distributed (Fautin and Allen 1997).

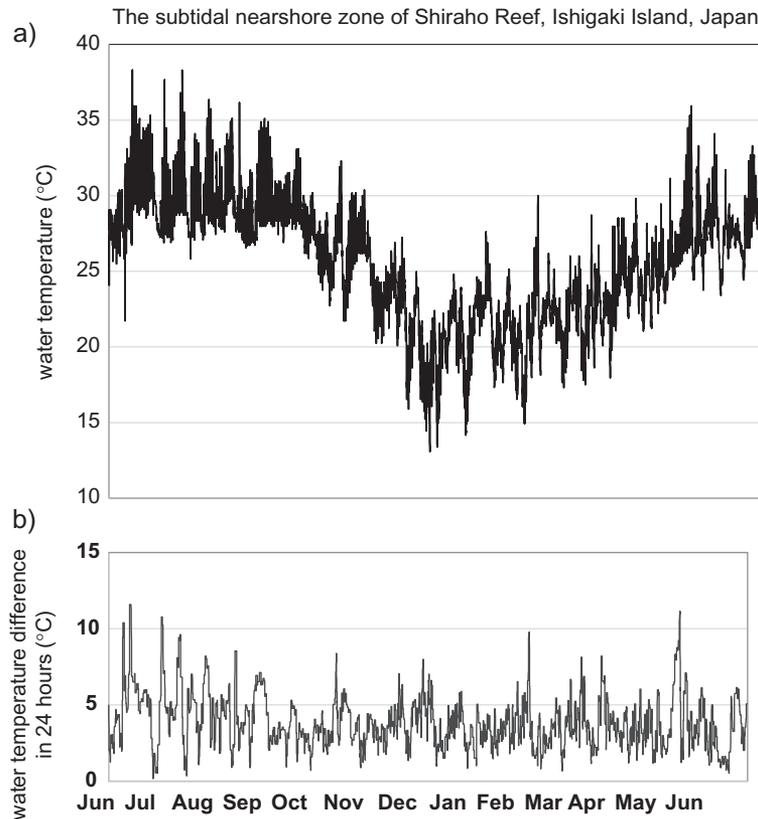


FIGURE 17.5 Change of water temperatures in the subtidal nearshore zone (not intertidal pool; at a depth of about 20 cm approximately 30 m from the shoreline at the lowest tide) of Shiraho Reef in the 12-month period 21 June 2005 to 20 June 2006. a) Water temperatures in every 30 min. b) Ranges of water temperatures (max–min in 24 h) for every 30 min. Water from intertidal pools may influence the water temperature at the subtidal nearshore zone.

17.3.3 DISTRIBUTION OF *ENTACMAEA QUADRICOLOR* ON A LARGE FRINGING REEF

Entacmaea quadricolor are widely distributed and can reproduce both sexually and asexually (Dunn 1981). They tend to form colonies, or clonal assemblages, comprising small individuals in shallow sites or large individuals in deep sites (Dunn 1981; Scott and Harrison 2007). They are not rare in the outer reef slope down to around 20 m deep and can even be distributed to 60 m deep (Bridge et al. 2012). Since larger individuals tend to be found in habitats suitable for large animals (Sebens 1982; Steen 1988), the shallow sites may be unsuitable for *E. quadricolor*.

At Shiraho Reef, Hattori and Kobayashi (2007) and Hattori (2017) plotted *E. quadricolor* onto aerial images in 2001 and 2014 (Figure 17.3d). After the infamous bleaching occurred in 1998, bleaching of *E. quadricolor* was found again in 2007 (Harii et al. 2014). This anemone was most abundant at sites from 10 to 60 cm deep and less abundant at sites deeper than 120 cm (Hattori and Kobayashi 2007). No individuals were found in the intertidal zone or the subtidal nearshore zone. The number of anemones increased from 821 in 2001 to 864 in 2014 but the number of clonal assemblages decreased from 93 to 67 (Hattori 2017) in the same period. Surviving *E. quadricolor* in 2007 increased

in number by 2014. Statistical analysis of the original data obtained by Hattori and Kobayashi (2007) in 2001 revealed that neither total tentacle-crown surface area ($r=0.05$, $t_s=0.5$, $P=0.58$, $n=93$) nor size of an assemblage was related to water depth ($r=0.11$, $t_s=1.1$, $P=0.25$), but the two features were significantly correlated ($r=0.795$, $t_s=12.5$, $P<0.000001$). *Entacmaea quadricolor* is thought to multiply in empty spaces, where bleaching caused coral mortality, and then surviving *E. quadricolor* increased in number. The number of *E. quadricolor* in nine quadrats (area of a quadrat was 50 m × 63 m) was correlated to the area of 3D small patchy reefs detected in aerial images, excluding bare flat substrates (Hattori and Kobayashi 2007; Hattori 2017). While anemonefish depletion reduces survival of *E. quadricolor* (Frisch et al. 2016), bleached *E. quadricolor* may be recovered by resident anemonefish, as evidenced by bleached *H. magnifica* recovered by resident *A. chrysopterus* (Cortese et al. 2021).

Entacmaea quadricolor are inhabited by 16 species of anemonefish (Fautin and Allen 1997). However, in the coral reefs of the Ryukyu Islands, Japan, only members of extreme specialist *A. frenatus* occupy this anemone, although it is inhabited by only the generalist *A. clarkii* in the temperate rocky reefs of southern Japan (Hattori 2011; Clark et al. 2021). In the Manado region, Sulawesi,

Indonesia, individuals in deep sites (> 9 m deep) are all inhabited by generalist *A. clarkii*, and those in shallow sites are used by the specialist *A. melanopus* or the extreme specialist *A. biaculeatus* (Ricciardi et al. 2010).

These distribution patterns of *E. quadricolor* can be explained by two things: (1) drifting larva use a large range of water depth, unlike *S. gigantea* and *H. crispa* (Figure 17.4); (2) if they settle in reefs with many crevices and deep holes, they reproduce asexually to occupy many narrow vacant sites, but if they settle in reefs with large holes or large vacant sites, they do not reproduce asexually because larger body sizes produce more eggs. As *H. magnifica* also reproduce both sexually and asexually (Dunn 1981) but do not adhere to crevices or deep holes, they multiply asexually in open spaces facing open water at shallow sites around 50 cm deep (Fricke 1979), or at deep sites without high coral coverage up to 40 m deep (Brolund et al. 2004), where spaces are sufficient for multiple large animals, unlike *E. quadricolor*.

Larvae of *H. magnifica* and *E. quadricolor* might use deeper water on average than those of *S. gigantea* and *H. crispa*; and *E. quadricolor* has been shown to inhabit a larger range of water depth (0.5 to 60 m deep, Bridge et al. 2012). Speculated depth distributions of anemone larvae (Figure 17.4) remain to be investigated.

17.4 GEOMORPHIC ZONE AND STRATEGY OF HABITAT USE

Water depths of host anemones and their distances from shore are often used by researchers in the analysis of habitat selection by anemonefishes (Chapter 16; Hayashi et al. 2021). However, these data have different meanings in the context of the 3D structure of coral reefs because each geomorphic zone has a unique depth profile and environmental characteristics (see Figure 17.1).

The outer reef slope is characterized by a wide range of water depths and wave exposure and hard substrates. Suitable hosts for anemonefish, *E. quadricolor*, *H. crispa*, *H. magnifica*, *S. gigantea*, and *S. mertensii*, are all found in this zone, because of the availability of hard substrates and stable water temperatures. Here, both specialist and generalist species may be found. In this zone, interspecific competition should be potentially intense and cohabitation by two anemonefishes may be temporarily found (see Chapter 18 and Chapter 16). The two largest host species, *S. mertensii* and *H. magnifica*, are mostly distributed in this zone. Ricciardi et al. (2010) reported that (probably beyond the reef edge) in the Manado region, Sulawesi, Indonesia, generalist *A. clarkii* and specialist *A. sandaracions* use *S. mertensii*, and specialist *A. perideraion* use *H. magnifica* and *H. crispa*, while *A. clarkii* use these all-host species (though 3D information is unavailable). *Amphiprion sandaracions* and *A. perideraion* may be superior competitors because each species often cohabits with *A. clarkii* but occupy different host species (see Hayashi et al. 2021). *Amphiprion clarkii* may avoid interspecific competition after temporary

cohabitation (see Hattori 2002). The width of this zone is measurable. In the large fringing reef (Figure 17.3), for instance, the width of the outer reef slope zone was calculated as 116.6 m (assuming 60 m deep and 100 m wide measured in aerial image), which is larger than the subtidal nearshore zone (100 m) or the reef flat zone (100 m) but may be smaller than the backreef zone (300 m, although about half of the backreef zone is a sandy sea bottom).

The subtidal nearshore zone must be large in large fringing reefs and characterized by shallowness, a very large fluctuation of water temperatures and unstable sandy bottoms (shapes of seagrass beds change over several years). This zone may not be distinct in small fringing reefs. It provides a unique habitat for specialist *A. ocellaris* with *S. gigantea*, which may have high thermal change tolerance. Although *A. clarkii* was sometimes found with *S. haddoni* in this zone, this generalist does not reproduce there because it lives without hard substrates and cannot move small shells, unlike specialist *A. polymnus* (Moyer and Steen 1979). In contrast, *A. ocellaris* reproduce at some *S. gigantea* in this zone, as mentioned earlier. Reproducing in this zone needs unique abilities for anemonefishes. The area of potential habitats for *S. gigantea* in this zone is measurable with image analysis software (Hattori and Kobayashi 2009).

The backreef may be the largest zone in large fringing reefs (see Figure 17.3). This zone consists of sandy bottoms, patchy reefs, and continuous reefs connected to the reef flat. Clonal assemblages of *E. quadricolor* are most abundant in this zone. Hattori (2017) compared two indicators of the backreef habitats for *E. quadricolor* and *A. frenatus*: total area of dark-colored patch reefs detectable in an aerial image with image analysis software, and total area of tall patch reef (> 1.5 m in height) detectable in stereoscopic aerial images with a stereoscope (SOKKIA, Mirror Stereoscope, Model MS27). Unexpectedly, the total area of dark-colored patch reef was the better indicator for habitation. As many crevices and holes in reefs are recognizable as blackish colors in aerial images, we can estimate the total area of 3D rugose reefs, excluding barren flat substrates. Rugose reefs in this zone provide major habitats for *E. quadricolor* and inhabitants *P. biaculeatus*, *A. melanopus*, *A. ehippium*, and *A. rubrocinctus*, as well as *A. frenatus*, which are specialists or extreme specialists. These species should have high thermal change tolerance.

Reef flats provide scarce habitat for host anemones because these seem to be intertidal flat pavement reefs in aerial images. However, deep channels cutting through the reef flat provide suitable habitats for host anemones, like the outer reef slope zone. In small fringing reefs, the reef crest and upper reef slope connect and are difficult to distinguish, and the edge zone provides habitats for host anemone and anemonefish (see Figure 17.2).

In conclusion, information regarding geomorphic zones is crucial to a valid discussion of interspecific competition and host selection strategies by anemonefishes. In overlapping geographic ranges, where several competing anemonefish species prefer one host species, specialists and extreme

specialists should be abundant in a particular zone, often adapting to a particular habitat. Since generalists should have high mobility with broad environmental tolerance, they must be found ubiquitously, avoiding interspecific competition, which may complicate the determination of host selection and cohabitation patterns by anemonefishes.

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