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Anemonefish musical chairs and the plight of the two-band anemonefish, *Amphiprion bicinctus*

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Abstract Anemonefishes' obligatory mutualism with sea anemones dictates their occurrence in marine habitats. We examined whether the spatial distribution, number, and size of the host anemones *Heteractis crispa* and *Entacmaea quadricolor* affected the settlement, habitat usage, and survival of the two-band anemonefish, *Amphiprion bicinctus*. In a 200 × 50 m study site off the coast of Israel in the Gulf of Eilat, we followed the fish and anemone populations initially in 13 censuses from October 1996 to August 1997 and follow-up censuses from 1998 to 2015. Based on size, anemonefish were categorized as adults, juveniles, or settlers. Settlers tended to cluster together but displayed significantly dispersed distributions in relation to adult individual fish and breeding pairs. Adult and juvenile anemonefish associated more with, and exhibited higher survival in, *E. quadricolor*. Settlers primarily inhabited *H. crispa,* with similar survival rates in the two anemone species. *H. crispa* was less occupied compared to *E. quadricolor*, but 95 % of the 233 anemones hosted fish during at least one census. From 1997 to 2015, anemone and anemonefish numbers plummeted by 86 % and 74 %, respectively. In 2015, all 27 remaining anemones were occupied, with most *E. quadricolor* inhabited by adults. The anemones left at the study site, on average, hosted more fish per anemone than those in the original population. This saturated habitat could hinder new anemonefish individuals from settling. These results indicate that if the anemone population does not recover, the anemonefish could face local extinction.

Keywords Clownfish · Coral reef · Sea anemone · Symbiosis · Red Sea

Introduction

Adult forms of many coral reef fish are relatively sedentary and have limited dispersal capability within or between reefs. Furthermore, some coral reef fish reside within a single coral head (Fishelson 1964; Fishelson et al. 1974) and limit their movements to around that coral. Consequently, not only the number of potentially inhabitable corals but also the spatial proximity of these corals may determine the number of coral dwelling fish, their movements, and their interaction with conspecifics. Similar to coral dwelling fish, anemonefish (Family Pomacentridae) form obligate mutualisms with sea anemone hosts and rarely venture far from their host anemones (Fautin and Allen 1997).

Anemonefish associate with 10 host anemone species, but most anemonefish species exhibit some level of host specificity or preference by associating with only a few anemone species (Fautin and Allen 1997; Srinivasan et al. 1999; Elliott and Mariscal 2001). An anemone host can be inhabited by two anemonefish

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species (Hattori 2002), or by an adult breeding pair cohabitating with non-breeding juveniles of the same anemonefish species (Ross 1978a; Fricke 1979; Fautin 1991; Hattori 1991; Fautin and Allen 1997). In these cases, anemonefish group size can increase with anemone size (Ross 1978a; Fricke 1979; Fautin 1992; Buston 2003; Elliott and Mariscal 2001), but anemonefish aggressively defend their territory from conspecifics as host anemones approach their carrying capacities (Elliott and Mariscal 2001; Fricke 1979; Buston 2003). Conversely, in other anemonefish species, adults and juveniles segregate into different individual anemones or even species of anemones (Fishelson et al. 1974; Chadwick and Arvedlund 2005).

Since anemonefish restrict their movements to the immediate proximity of sea anemones, the number, depth distribution, and size of sea anemone hosts influence recruitment and anemonefish population dynamics (Fautin and Allen 1997; Richardson 1999; Srinivasan et al. 1999; Buston 2003; Chadwick and Arvedlund 2005; Shuman et al. 2005). Although the dispersal ability of the larvae affects anemonefish recruitment (Jones et al. 2008; Planes et al. 2009; Pinsky et al. 2012; Madduppa et al. 2014a), the existing adult anemonefish in the population may prevent conspecific recruitment (Ross 1978a; Fricke 1979; Fautin 1991; Hattori 1991; Elliott et al. 1995; Fautin and Allen 1997; Buston 2003). Adult anemonefish may also evict smaller individuals (Buston 2003; Huebner et al. 2012) and this competition for space may extend to other nearby anemones (Moyer 1980; Huebner et al. 2012). Therefore, in addition to the number and size of anemones, anemonefish population dynamics may be influenced by the spatial distribution of both the host sea anemones and the existing anemonefish in the population (Sato et al. 2014).

To investigate the influence of the location of host anemones and conspecific anemonefish on anemonefish population dynamics, we followed the spatial distribution of a population of *Amphiprion bicinctus* and newly settled individuals over time. The two-band anemonefish, *A. bicinctus* is one example of an anemonefish species where the adults are most often segregated from the juveniles (Fishelson et al. 1974; Chadwick and Arvedlund 2005). This species is endemic to the Red Sea, Gulf of Aden, and the Chagos Archipelago, and associates with five species of host sea anemones within this range: *Entacmaea quadricolor*; *Heteractis aurora*; *H. crispa*; *H. magnifica*; and *Stichodactyla gigantea* (Fautin and Allen 1997).

In the northern part of the Gulf of Eilat, Red Sea, *A. bicinctus* only inhabits *E. quadricolor* and *H. crispa* (Chadwick and Arvedlund 2005). In this area, adult *A. bicinctus* normally occupy *E. quadricolor* host anemones, either singly or as breeding pairs and only occasionally associate with juveniles in the same anemone (Fishelson et al. 1974; Chadwick and Arvedlund 2005). Juvenile *A. bicinctus* reside in both host anemone species and can form groups that cluster within a single anemone, normally *H. crispa*, until the fish reach 30–50 mm in length, when they move to the *E. quadricolor* anemones (Fishelson 1970; Fishelson et al. 1974; Huebner et al. 2012). Due to its thin tentacle morphology, *H. crispa* may not provide sufficient protection from predators as the anemonefish grow larger (Chadwick and Arvedlund 2005; Huebner et al. 2012), but no studies have characterized survival rates of different *A. bicinctus* size classes between the two host species. Additionally, sea anemone and anemonefish population studies have not taken into account the spatial location of inhabited and uninhabited anemones (e.g., Chadwick and Arvedlund 2005; Huebner et al. 2012).

We monitored the populations of both host anemones and anemonefish over a 19-year period. As climate change and anthropogenic disturbances continue to impact coral reefs worldwide (Hoegh-Guldberg et al. 2007; Munday et al. 2008), long-term monitoring efforts will aid in projecting how these systems change over time and respond to disturbances, and in determining if current protection and conservation efforts are effective (Day 2008; Friedlander and Beets 2008; Cardini et al. 2015). For coral dwelling fish, for example, the demise of coral heads due to habitat destruction and global climate change leads to drastic declines in the associated fish populations (Jones et al. 2008; Munday et al. 2008; Lönnstedt and Frisch 2014). Sea anemones and their associated fish may also demonstrate such a pattern (Shuman et al. 2005; Hobbs et al. 2013).

Materials and methods

Study site and initial populations of sea anemones and anemonefish

The study site encompassed a 200 m × 50 m area (10000 m^2), from 0 to 15 m depth, in the Gulf of Eilat (Aqaba) near the Interuniversity Institute for Marine

Sciences in Eilat, Israel (29° 30′ N, 34° 56′ E). This area included scattered small patch reefs separated by rock, rubble and sand (Chadwick and Arvedlund 2005) and to the north and south were large expanses of sand. In October 1996, all potential host sea anemones (*E. quadricolor* and *H. crispa)* were tagged and identified. While an anemone was expanded, the oral disc diameter was measured by placing a plastic ruler across the long axis of the oral disk. The anemones spatial location and depth within the study site was noted. Distances between each anemone and every nearest anemone neighbor within 360° were measured using compass headings which were incorporated into a map of the study site's anemone population (Fig. 1).

The presence or absence of *A. bicinctus* within each sea anemone was noted, and the size of each anemonefish was recorded. Total lengths of the fishes were determined using the technique described in Pfister and Goulet (1999) as well as estimating from underwater fish models and taped demarcations on a dive slate. Based on total length, anemonefish were placed into size categories: adult (> 75 mm), juvenile (45–75 mm), or settler (< 45 mm). Due to nearly a month between censuses, the settler category included the smallest fish in the population, including the new recruits that appeared sporadically. Given life history data (Fishelson et al. 1974; Fricke 1974), two adult fish occupying the same anemone were assumed to be a breeding pair, which in most cases was confirmed by the presence of eggs during the study. The anemonefish present in the October 1996 census period constituted the original population.

Sea anemone and anemonefish censuses

The initial census (C1) was followed by 12 additional ones (C2 – C13), with an average of 22.25 days between censuses, until August 1997. In each census, the presence or absence of anemones in the study site was noted. The number of anemonefish in each anemone was recorded, and the fish ascribed to one of the three size classes. Anemonefish that appeared in the population in these subsequent census periods were termed immigrants. The percentage of time anemones were inhabited or uninhabited was calculated. Furthermore, we determined whether immigrants settled more often into inhabited or uninhabited anemones.

In the C1 – C13 censuses, anemonefish abundance was investigated in relation to anemone species, its size, and depth. For depth analyses, the study site was divided into three depth ranges (shallow: 0–5 m, mid: 5.1–10 m, and deep: 10.1–15 m). Patterns of turnover of anemonefish inhabitants were explored by noting the number of anemonefish associating with each anemone of both host species through the 13 census periods. Although fish were not tagged, it was possible to track individuals because: 1. Fish had unique and recognizable color patterns. 2. The number of anemonefish occupying an anemone was low (range 1–4) making it easy to count and identify the anemonefish. 3. The average distance between the nearest anemones was 2.9 m, which severely limited anemonefish movement. 4. Anemonefish, especially those less than 45 mm, were rarely observed to move to another anemone if it was further than 50 cm away (Mazeroll and Goulet unpublished data). 5. After each census, the number and size of each anemonefish in each anemone were compared with the previous censuses. This analysis showed a clear pattern of residency by the anemonefish, even as they grew into the next size class. Furthermore, the size and number of anemonefish at the nearest anemones were examined to help determine if an anemonefish was a new settler or had moved from another anemone.

Survival percentages of both original and immigrant anemonefish were calculated by dividing the number of days a particular fish was observed by the total number of days remaining until the end of the 13th census from the time they were first observed and multiplying the ratio by 100. For example, if an anemonefish was first observed in C4 and survived for 244 days through the end of C13, it would be recorded as having 100 % survival. Furthermore, the survival rate of anemonefish within a size class was based upon the size class of a given fish the first time it appeared in the census. Since the study site was surrounded by sand, with large distances between any potential anemones, if an anemonefish disappeared for two censuses, it was assumed that the fish had died and not emigrated. The survival of the original fish and immigrants was examined within and between anemone species.

Additional one-time censuses were conducted in 2001, 2009 and 2015 and data was extracted from a study at the same research site (McVay 2015) for 1998, 1999, 2000, 2013, and 2014. In the 2001 census and the McVay (2015) data, the overall number of anemonefish, breeding pairs, and sea anemones were counted while in the 2009 and 2015 censuses, the number of anemonefish in each size class, the number of breeding pairs and sea

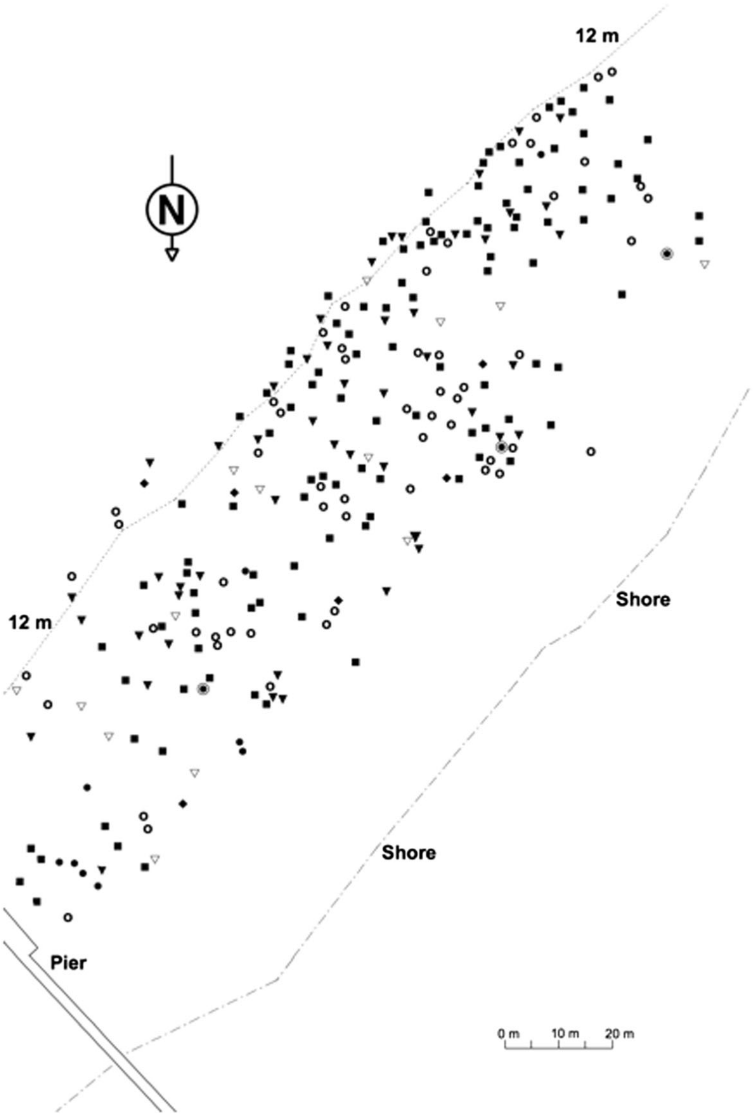

Fig. 1 Map detailing the locations of sea anemones found in the 200 m × 50 m study area during the 1996–1997 censuses. The sea anemones hosted either single adults (●), breeding pairs (♦), juveniles (▼), settlers (■), mixed groups of adults and juveniles or settlers (⦿), mixed groups of juveniles and settlers (▽), or no fish (○)

anemones were recorded. The anemone and anemonefish populations recorded in the August 1997 census (C13) were compared to the populations in the subsequent censuses from our data and McVay (2015) to determine how the anemone and anemonefish populations changed over time.

Average nearest neighbor analysis

Anemone and anemonefish distributions and fish settlement patterns were examined in ArcMap (Esri). Position data of anemones were imported into blank map layers in ArcMap, and each layer was exported as a shapefile (.shp). Shapefiles representing the anemonefish size classes were generated for each census by plotting only the anemones hosting an anemonefish of a particular size class (e.g., a shapefile only plotting anemones hosting adult fish). These shapefiles were then analyzed using the spatial statistics tools package. The Average Nearest Neighbor Analysis tool within ArcMap was run to determine if each of the anemonefish size classes displayed a clustered, dispersed, or random distribution in the study area. Clustered or dispersed distributions referred to instances when the average distance between the points on a map (e.g., anemones hosting adult fish) and their nearest neighbors were significantly smaller or larger, respectively, than would be expected under a random distribution. In addition, the distribution of the settlers was analyzed in relation to that of the fish in the other size classes using the nearest neighbor distances obtained by joining the settler size class layers to the layers of the other size classes. For example, distances between settlers and their nearest adult neighbors were calculated, and significance was determined as above.

Statistical analyses

Based on the data type, different statistical tests were performed using R (v. 3.1.2) (R Development Core Team 2014). Student's t-tests were used to compare oral disk diameters, the percent of unoccupied anemones, the number of consecutively unoccupied anemones, and the number of anemonefish between the two anemone species. Linear regressions were used to examine anemone depth, the number of anemonefish (in each anemone species and both species combined), the number of anemonefish in each size class within each anemone species, and the number of immigrant fish anemones received, all in relation to anemone diameter. To meet the assumptions of normality, the number of adult anemonefish were square root transformed prior to determining their relationship to anemone diameter. One-way ANOVAs were used to compare the number of immigrant anemonefish observed in each depth category and the number of anemonefish observed in C13, 2009, and 2015. A 2-way ANOVA was used to compare the number of anemonefish of each size class observed in the two anemone species. Tukey HSD post-hoc tests were employed, where appropriate, to determine the source of the significance obtained from the ANOVAs. Significance of the distribution patterns was determined by calculating a Z score whereby scores ≤ -1.96 or ≥ 1.96 are significantly clustered or dispersed, respectively.

When data violated the assumptions of the parametric tests listed above, non-parametric tests were used. Kruskal-Wallis and Mann-Whitney U tests were used to compare the survival rates of the three size classes of anemonefish within each host anemone species in addition to the survival rates of the size classes of the original and immigrant anemonefish within each anemone species. Tukey and Kramer (Nemenyi) post-hoc tests were used to determine the source of the significance in the Kruskal-Wallis tests. G-tests were employed to determine if the number of anemones and anemonefish (total and within each anemone species) was independent of depth, while a Cochran-Mantel-Haenszel test was used to test if the number of anemonefish in each size class was independent of depth.

Results

Sea anemone population

During the October 1996 census a total of 205 anemones, 96 *E. quadricolor* and 109 *H. crispa,* were tagged at the study site. Anemones can contract their tentacles and recede within the reef structure making them hard to spot (Godwin and Fautin 1992; Porat and Chadwick-Furman 2004). Consequently, in the subsequent censuses (C2 – C13) an additional 10 *E. quadricolor* and 18 *H. crispa* were located, tagged, and monitored. During the initial 13 censuses, anemone mortality occurred, resulting in a loss of 19 *E. quadricolor* and 15 *H. crispa*. By August 1997, 199 anemones, 87 *E. quadricolor* and 112 *H. crispa*, remained in the study area. Anemone size, as determined by oral disk diameter, of *E. quadricolor* and *H. crispa* ranged from 4-50 cm and 6–40 cm respectively, and the oral disk diameter of *H. crispa* ($\bar{x}$ = 20.58 cm) was significantly larger than that of *E. quadricolor* ($\bar{x}$ =17.72 cm; Student's t test: $t_{[194]} = 2.651$, $p = 0.009$).

E. quadricolor and *H. crispa* occupied depth ranges of 1.1–13.4 m and 1.1–14.4 m, respectively, with abundances of both anemone species decreasing significantly with depth (G test: $G_{[6]} = 101.75$, $p < 0.001$). Most *E. quadricolor* occurred in 0–5 m (shallow, 40.2 %) and 5.1–10 m (mid, 40.2 %) depths with only 19.6 % found between 10.1–15 m (deep, Fig. 2a). Over half of *H. crispa* were found in the shallow depths (56.3 %) with the remaining 31.9 % and 11.8 % residing in the mid and deeper depths, respectively (Fig. 2b). In both anemone species, oral disk diameter changed significantly with depth. The oral disk diameters of *E. quadricolor* displayed a parabolic pattern (Fig. 3a, Quadratic Regression: $R^2_{[2,\ 102]} = 0.135$, p = < 0.001) while in *H. crispa* the oral disk diameters increased with depth (Fig. 3b, Linear Regression: $R^2_{[1,\ 129]} = 0.045$, $p = 0.008$). The average nearest neighbor distance between all anemones in the population was 2.9 m. The distribution of *E. quadricolor* was significantly clustered during the first four censuses (C1 – C4). As additional anemones were found and others disappeared, the distribution became random during C5 –

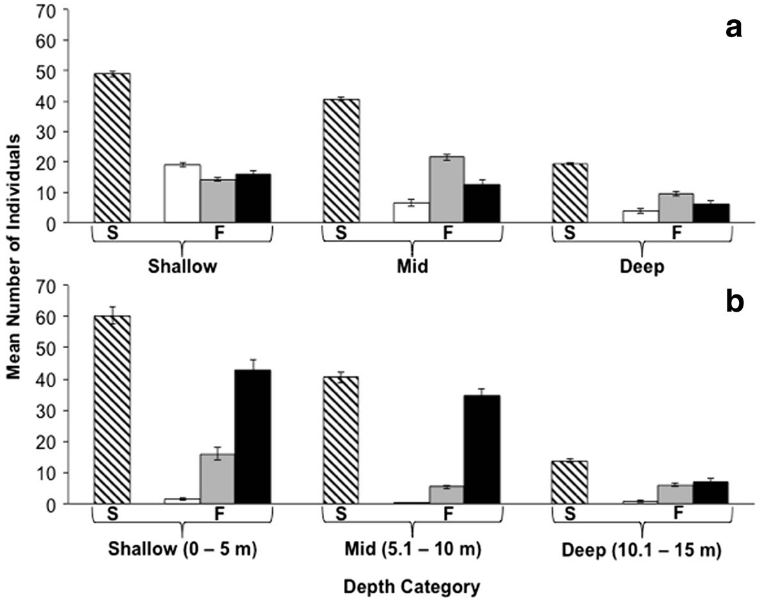

Fig. 2 The mean (±SE) number of sea anemones (S-*hashed bars*) and anemonefish (F) at the study site (10000 m^2) during the 1996–1997 censuses. **a** *Entacmaea quadricolor* and **b** *Heteractis crispa* and *Amphiprion bicinctus* adults (*white*), juveniles (*grey*), and settlers (*black*) bars, respectively, observed in shallow (0–5 m), mid (5.1–10 m) and deep (10.1–15 m) depths

C13. *H. crispa* was randomly distributed during every census except C4 (Online Resource 1).

On average, most (81.8 %) of the anemones in the study area were inhabited by anemonefish at some point during the 13 initial census periods (Student's t test: $t_{[24]} = 57.607$, $p < 0.001$). While almost every anemone (94.9 %) hosted anemonefish during at least one census, only 49.3 % of those were occupied during every census they were observed. Of the unoccupied anemones, significantly fewer *E. quadricolor* were unoccupied ($\overline{x}$ = 10.1 %; Student's t test: $t_{[24]} = 11.16$, $p < 0.001$) and for shorter periods of time ($\overline{x}$ = 0.91 consecutive censuses; Student's t test: $t_{[244]} = 4.572$, p < 0.001) than *H. crispa* ($\overline{x}$ = 24.7 % unoccupied; $\overline{x}$ = 2.54 consecutive

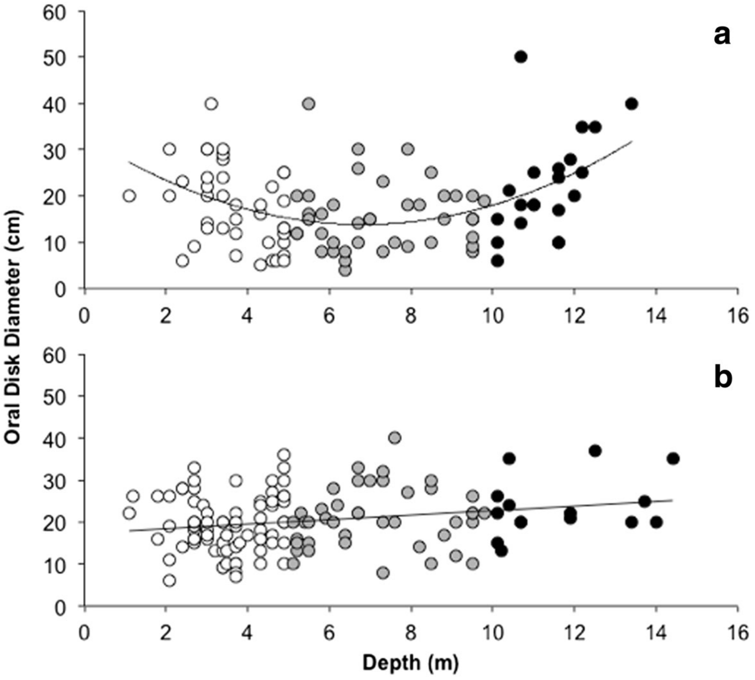

Fig. 3 Oral disk diameter of **a** *Entacmaea quadricolor* and **b** *Heteractis crispa* at the study site during the 1996–1997 censuses. *Black*, *grey*, and *white circles* indicate shallow (0–5 m), mid (5.1–10 m), and deep (10.1–15 m) depths respectively

censuses). Additionally, of the 12 anemones that never hosted anemonefish, only one was *E. quadricolor* while 11 were *H. crispa.* The uninhabited anemones were randomly distributed throughout the study site in every census except C11 when they were clustered (Online Resource 2).

On the other hand, the distribution of uninhabited *E. quadricolor* relative to their nearest neighbor that hosted an adult fish was significantly dispersed in C1, random in C2 and C3, and significantly clustered from C4 – C13 (Online Resource 3). For uninhabited *H. crispa*, the distribution fluctuated between significantly dispersed and random (Online Resource 3). Anemones that lost fish from one census to the next fluctuated between clustered, random, and dispersed distributions in relation to anemones that gained fish. The bulk of the anemones that gained or lost fish were *H. crispa*. In only three censuses was the number of *E. quadricolor* that gained or lost fish greater than that of *H. crispa*. In those censuses when *E. quadricolor* that gained fish outnumbered *H. crispa*, it was only by one or two anemones.

Anemonefish population

The anemonefish population in the initial census (C1) consisted of 197 individuals, 17 adults, which included 5 breeding pairs, 43 juveniles, and 137 settlers inhabiting 159 anemones. The total number of fish increased from the 197 fish in the first census in early October (C1) to a maximum of 261 fish in late December (C5; Fig. 4). This increase in the fish population was driven by settlement. Although recruitment occurred year-round, most recruitment occurred from October – December (C1 – C5) with very little occurring during the spring and summer months (C6 - C13). Due to reduced recruitment in conjunction with mortality, especially of settlers, by mid-August (C13) the anemonefish population size of 195 fish was close to the 197 fish in the C1 census. The 195 anemonefish remaining in C13 consisted of 52 adults, which included 11 breeding pairs, 76 juveniles, and 67 settlers (Fig. 4), inhabiting 149 anemones.

The mean number of anemonefish associating with the two anemone species was not significantly different, with *H. crispa* hosting an average of 115.39 ± 4.27 fish per census while *E. quadricolor* hosted 110.00 ± 1.35 fish per census (Student's t test: $t_{[14]} = 1.202$, $p = 0.249$). On the other hand, fish in the adult, juvenile, and settler size classes inhabited the two anemone species in different ways (ANOVA: $F_{[2,\ 72]} = 99.15$, $p < 0.001$). Group size increased significantly with oral disk diameter in *E. quadricolor* (Linear Regression: $R^2_{[1,\ 101]} = 0.042$, $p = 0.021$) but not in *H. crispa* (Linear Regression: $R^2_{[1,\ 110]} = 0.018$, $p = 0.081$). Adult anemonefish almost exclusively associated with *E. quadricolor* (TukeyHSD: $p < 0.001$), with the mean number of adults increasing significantly with *E. quadricolor* oral disk diameter (Linear Regression: $R^2_{[1,\ 49]} = 0.068$, $p = 0.036$). Juveniles also more frequently associated with

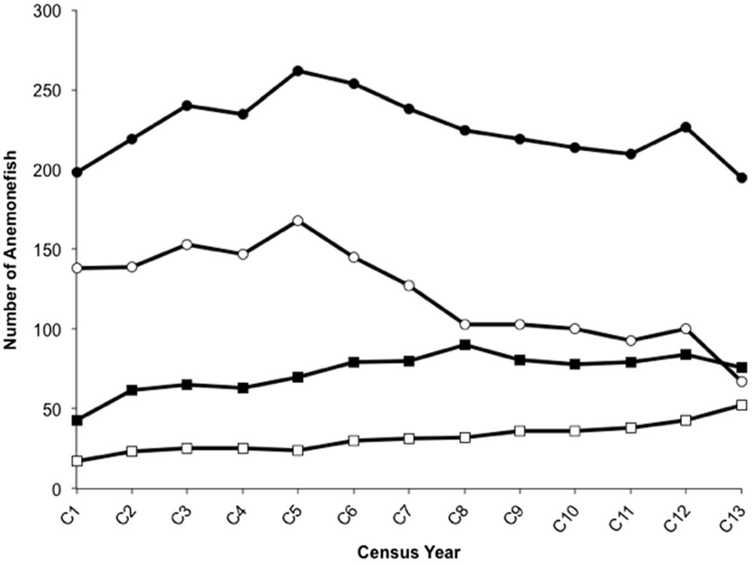

Fig. 4 Number of *Amphiprion bicinctus* during the 13 census periods from October 1996 to August 1997. The total number of anemonefish (●), adults (□), juveniles (■), and settlers (○) are depicted

E. quadricolor, while settlers most often associated with *H. crispa* (TukeyHSD: $p < 0.001$).

Across depths, the average number of fish in each anemonefish size class was significantly different (Cochran-Mantel-Haenszel: *E. quadricolor* $M^2_{[4]} = 108.26$, $p < 0.001$; *H. crispa* $M^2_{[4]} = 98.28$, $p < 0.001$; Fig. 2). The numbers of adults and settlers inhabiting *E. quadricolor* decreased with depth (Fig. 2a). Juveniles associating with *E. quadricolor*, on the other hand, were most abundant in mid depths versus shallow or deep depths. Whilst very few adults inhabited *H. crispa,* those that did were found in shallow waters (Fig. 2b). The numbers of both juveniles and settlers associating with *H. crispa* were highest in shallow waters and decreased with depth (Fig. 2b). Additionally, the number of immigrants that associated with each anemone species decreased with depth, with significantly different numbers in each depth category than expected (Chi-squared Test: $X^2_{[2]} = 8.93$, $p = 0.011$). The number of immigrants that anemones received was not significantly related to the oral disk diameter in either anemone species (Poisson Regression: *E. quadricolor* $z_{[105]} = 0.837$, $p = 0.403$; *H. crispa* $z_{[130]} = 0.375$, $p = 0.708$).

Most adult anemonefish occupied anemones either by themselves or as pairs. In a few instances, single adults or breeding pairs shared an anemone with smaller anemonefish. Single adult fish associated with either a single juvenile or settler in 24 anemones, and with two or three smaller fish in eight and two anemones, respectively. In only four anemones did anemonefish breeding pairs cohabitate with smaller fish. In three of those instances, the additional fish was a settler, and the other involved a breeding pair and a juvenile. Adults or breeding pairs that shared anemones resided in a depth range of 1.1–12.2 m and the anemone oral disk diameter ranged from 6 to 40 cm.

During the first census period (C1), adult anemonefish were significantly clustered (Z test: $Z = -2.450$, $p = 0.014$) relative to one another in anemones in the northern half of the study area. The distribution pattern shifted from clustered to random during the next 8 censuses (C2 – C9), with adults associating with anemones throughout the study site. This distribution change was partially due to some adult mortality but primarily driven by the growth of juveniles into the adult size category. In C10, the fish population dynamics led to a significantly dispersed distribution (Z test: $Z = 2.171$, $p = 0.030$), with a return to a random distribution of adult anemonefish for the remainder of the censuses (Online Resource 4). When only breeding pairs were examined, their distributions throughout the study site were random from C1 – C11. As the number of pairs increased, the distribution changed to significantly dispersed in the C12 and C13 censuses (Z test: C12 $Z = 2.728$, $p = 0.006$; C13 $Z = 2.628$, $p = 0.009$).

Fish in the juvenile size class were randomly distributed in anemones throughout the study site with the exception of the C12 census when juveniles were significantly dispersed (Z test: $Z = 3.588$, $p = 0.003$, Online Resource 4). On the other hand, in the first four censuses, as settler numbers increased, settlers clustered together (Z test: C1 $Z = -3.119$, $p = 0.002$; C2 $Z = -2.571$, $p = 0.010$; C3 $Z = -2.781$, $p = 0.005$; C4 $Z = -2.167$, $p = 0.030$). As recruitment began to taper off and settlers grew into the juvenile size class or disappeared, the distribution pattern of the remaining settlers became random. C11 was the exception with settlers again exhibiting a significantly clustered distribution within the study site. This clustered distribution was probably due to settlement in less isolated anemones (Z test: $Z = -3.099$, $p = 0.002$; Online Resource 4).

The spatial patterns of settlers in relation to neighboring adult or breeding pair fish during C1 – C12 and C1 – C13, respectively were significantly dispersed (Online Resource 5). When settlers were analyzed in relation to their nearest juvenile neighbor, they were significantly dispersed in C1 (Z test: $Z = 6.133$, $p < 0.001$), but were randomly distributed from C2 – C11. In C12 and C13, settlers exhibited a significantly clustered distribution in relation to the juveniles (Z test: C12 $Z = -2.183$, $p = 0.029$; C13 $Z = -2.905$, $p = 0.004$). When the settlers were examined relative to the adults and juveniles combined, a trend towards increasing clustering was evident. During the first census period, the settlers displayed a dispersed distribution (Z test: $Z = 3.624$, $p < 0.001$), but they were randomly distributed during the next five census periods. After C6, the settlers were clustered in relation to the nearest adult or juvenile fish throughout the rest of the census period (Online Resource 5).

Anemonefish survival

Adults and juveniles inhabiting *E. quadricolor* had significantly higher survival rates than those associating with *H. crispa* (Mann-Whitney U Test: Adults $U = 87.5$, $p = 0.017$; Juveniles $U = 1363.5$, $p = 0.046$, Fig. 5). Settler survival rates, on the other hand, did not differ significantly between anemone species (Mann-Whitney

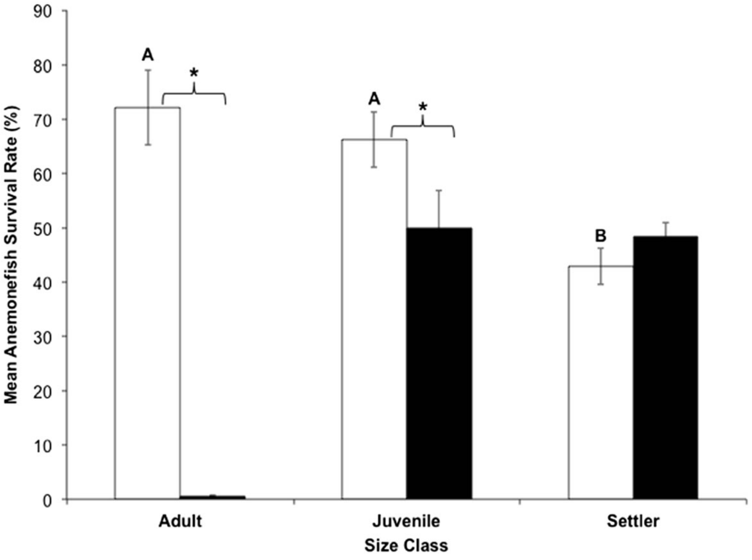

Fig. 5 Mean (±SE) survival rates of *Amphiprion bicinctus* in the sea anemones *Entacmaea quadricolor* (*white*) and *Heteractis crispa* (*black*) during the 13 censuses from October 1996 to August 1997. Significant differences in anemonefish survival between (*) and within (letters) sea anemone species are depicted

U Test: U = 19,981.5, $p = 0.062$). Consequently, mean survival rates of the anemonefish size classes were significantly different in *E. quadricolor* (Kruskal-Wallis Test: $X^2_{[2]} = 20.681$, $p < 0.001$) but not in *H. crispa* (Kruskal-Wallis Test: $X^2_{[2]} = 5.122$, $p = 0.077$; Fig. 5). In *E. quadricolor*, both adult (72.1 ± 6.9 %) and juvenile (66.2 ± 5.1 %) fish displayed significantly higher survival rates than settlers (42.9 ± 3.4 %; Tukey and Kramer (Nemenyi): Adults:Juveniles $p = 0.792$; Adults:Settlers $p = 0.002$; Juveniles:Settlers $p = 0.001$; Fig. 5).

The anemonefish initially at the study site (C1) displayed significantly different survival rates in the three size classes (Kruskal-Wallis: $X^2_{[2]} = 11.36$, $p = 0.003$). Adult (71.4 ± 9.9 %) and juvenile (61.7 ± 5.4 %) survival rates were significantly higher than that of the settlers (44.9 ± 3.2 %; Tukey and Kramer (Nemenyi): Adults:Settlers $p = 0.031$; Juveniles:Settler $p = 0.031$) but not significantly different from one another (Tukey and Kramer (Nemenyi): $p = 0.652$). Adults only inhabited *E. quadricolor,* while the survival rates of juveniles and settlers did not significantly differ between the two host anemone species (Mann-Whitney U Test: Juveniles U 403, $p = 0.097$; Settlers U = 2589.5, $p = 0.121$).

On the other hand, looking at just the immigrant anemonefish, there was no significant difference in the survival rates of the three size classes (Adults: 60.9 ± 1.0 %; Juveniles: 60.2 ± 6.7 %; Settlers: 47.3 ± 2.6 %; Kruskal-Wallis: $X^2_{[2]} = 3.65$, $p = 0.161$). Adult immigrant anemonefish did have significantly higher survival when associating with *E. quadricolor* versus *H. crispa* (Mann-Whitney U Test: U = 39.5, $p = 0.037$). Conversely, survival rates of juvenile and settler immigrants were not significantly different between the two host species (Mann-Whitney U Test: Juveniles U = 278.5, $p = 0.211$; Settlers U = 8281, $p = 0.322$). Even though a greater number of immigrant fish (179 fish) settled onto already occupied anemones than those without fish (162 fish), those fish that settled onto uninhabited anemones had significantly higher survival rates (55.8 ± 3.3 %) than fish settling onto inhabited anemones (44.2 ± 3.2 %; Mann-Whitney U Test: U = 12,318.0, $p = 0.014$).

Follow-up censuses

Overall, the number of anemones at the study site declined sharply throughout the eight follow-up censuses. Although anemone numbers increased in 2013 (McVay 2015) compared to the 2009 census, anemone numbers dipped to only 27 anemones in 2015 (Fig. 6). The anemonefish followed a similar trend. In 1997 there were 195 fish (Fig. 6). In 2000 and 2013 (McVay 2015), the anemonefish population increased compared to the previous census, but overall the anemonefish population declined, and in 2015 there were a mere 52 fish. Unlike the decline in the fish population, the number of anemonefish breeding pairs oscillated between six and 13 pairs throughout the years (Fig. 6; McVay 2015).

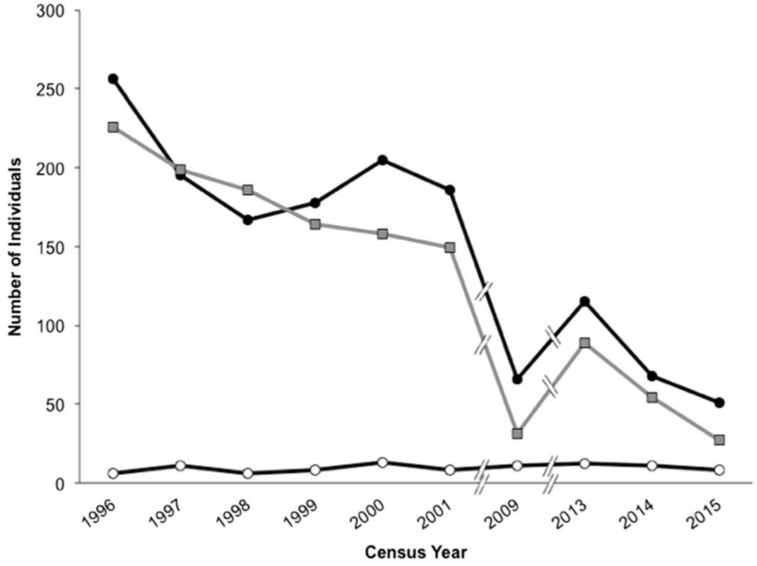

Fig. 6 The total numbers of sea anemone hosts (■), *Amphiprion bicinctus* (●), and anemonefish breeding pairs (○) found at the study site. Data points for 1996 and 1997 correspond to census C5 and C13, respectively; census data includes data from McVay (2015)

Looking at specific examples, compared to the 1997 census, in 2009, the number of host anemones dropped by 76 % with only 24 *E. quadricolor* and 23 *H. crispa* (72.4 % and 79.5 % reductions, respectively) left at the study site (Fig. 6). The anemonefish population plummeted 66 %, with 65 anemonefish inhabiting anemones. In 2009, the anemonefish population consisted of 30 adults (11 breeding pairs), 13 juveniles, and 22 settlers. Unlike in 1997, in 2009 all *E. quadricolor* and 82.6 % of *H. crispa* anemones were inhabited with 41 fish associating with *E. quadricolor* and 24 with *H. crispa*. All of the adult anemonefish inhabited *E. quadricolor*, while only five settlers associated with this species. The remaining 17 settlers resided within *H. crispa*. The juveniles were split between the two anemone species with six fish associating with *E. quadricolor* and seven associating with *H. crispa*.

In 2015, the anemone population further fell to 15 *E. quadricolor* and 12 *H. crispa*. 52 anemonefish inhabited these anemones: 21 adults (eight breeding pairs), 24 juveniles, and seven settlers. The number of anemones declined by 43 % from 2009 and 86 % from 1997 while the number of fish declined by 20 % from 2009 and 73 % from 1997. Consequently, in 2015 there were significantly more fish per anemone compared to the 2009 and 1997 censuses (ANOVA: $F_{[2,\ 269]} = 19.97$, $p < 0.001$). Furthermore, in 2015, every anemone of both species was inhabited. Of the 21 adults, the eight anemonefish breeding pairs and three other adults associated with *E. quadricolor*, while only nine of 24 juveniles and no settlers associated with *E. quadricolor*.

Discussion

In the Gulf of Eilat, the anemonefish *A. bicinctus* obligatorily inhabits the sea anemones *E. quadricolor* and *H. crispa*. At the beginning of the study in October 1996, anemonefish inhabited 88.5 % of *E. quadricolor* and 67.9 % of *H. crispa.* Since most of the uninhabited sea anemones were in a size range that could be inhabited by anemonefish, the sea anemone habitat was not saturated with *A. bicinctus.* Even though there were fewer *E. quadricolor* than *H. crispa,* more adult and juvenile *A. bicinctus* associated with *E. quadricolor* confirming that in the Gulf of Eilat, *E. quadricolor* is the preferred host of *A. bicinctus* (Huebner et al. 2012). Like in previous studies (Chadwick and Arvedlund 2005; Huebner et al. 2012), in our study adult anemonefish, especially breeding pairs, rarely shared an anemone with more than one juvenile or settler. When sharing did occur, the four breeding pairs that associated with an additional juvenile or settler resided in *E. quadricolor* anemones with a minimum of 30 cm oral disk diameter. As opposed to adults and juveniles, the vast majority of settlers associated with *H. crispa*. Unlike anemonefish species such as *A. percula*, which form size hierarchies within host anemones of a breeding pair and smaller anemonefish (Fautin and Allen 1997), smaller *A. bicinctus* tend to aggregate in the less desirable *H. crispa* anemones before attempting to migrate to nearby *E. quadricolor* (Chadwick and Arvedlund 2005; Huebner et al. 2012).

Anemone size may explain why large fish preferentially inhabit one anemone species over another. Larger anemones can host more or larger anemonefish (Ross 1978a; Holbrook and Schmitt 2005; Mitchell and Dill 2005). In our study, the range of the oral disk diameter of the two anemone species overlapped (Fig. 3), concurring with previous data from this site (Chadwick and Arvedlund 2005). Conversely, the mean oral disk diameter in *H. crispa* was significantly larger than that of *E. quadricolor.* Hence anemone size, as reflected by the oral disk diameter, did not explain the anemonefish preference for *E. quadricolor.*

Alternatively, sea anemone morphology may drive *A. bicinctus'* habitat preference. *E. quadricolor* oscillates between bulbous and thick, digitiform tentacle morphs while *H. crispa*'s tentacles are long and thin (Dunn 1981; Chadwick and Arvedlund 2005; Huebner et al. 2012). The *E. quadricolor* digitiform morph has significantly more surface area in their tentacle crowns than *H. crispa* (Huebner et al. 2012), enabling greater concealment, especially for larger-bodied adults. Indeed, in our study, adult and juvenile anemonefish exhibited significantly higher survival rates in *E. quadricolor* than in *H. crispa* (Fig. 5). Settlers had similar survival rates in both anemone species. But, when settlers inhabiting *H. crispa* grow, their survival may increase if they migrate to *E. quadricolor.* Movement from *H. crispa* to *E. quadricolor* may explain the greater observed turnover in *H. crispa* anemones as well as the lack of a consistent distribution pattern of juveniles in our study.

In addition, anemonefish may not inhabit anemones if they are spatially in close proximity to inhabited anemones. An uninhabited 'halo' around inhabited anemones may be a consequence of anemonefish movement and aggression. For example, in large assemblages of *H. magnifica* in the Red Sea, and occasionally in anemones in the Gulf of Eilat, *A. bicinctus* can associate with multiple anemones if they are close, although the fish often retreat to a preferred host when startled or threatened (Brolund et al. 2004; Huebner et al. 2012). In our study, we saw anemonefish moving between two neighboring anemones less than 50 cm apart. Adult anemonefish may defend several adjacent anemones, preventing conspecifics from inhabiting these anemones (Allen 1972; Porat and Chadwick-Furman 2004). As more anemonefish in our study site reached adult size, the number of adults increased, and the distribution of uninhabited *E. quadricolor* became significantly clustered relative to the nearest anemone that hosted an adult fish. The distribution relative to adult-hosting anemone neighbors of uninhabited *H. crispa* fluctuated between significantly dispersed and random. These distribution patterns suggest that adult *A. bicinctus* prevent recruitment not only to the anemones in which they reside but also to the nearby preferred *E. quadricolor* anemones, although *H. crispa* may not be actively protected.

The availability of uninhabited anemones may affect *A. bicinctus'* recruitment. Similar to previous reports of *A. bicinctus* from the Gulf of Eilat (Fricke 1974) and other anemonefish species (Allen 1972; Ross 1978b; Fautin and Allen 1997; Buston 2004) in our 1996–1997 censuses, anemonefish recruited year-round, although the majority of recruitment occurred from October to December (C1-C5). During the first four censuses, settlers were significantly clustered relative to other settlers potentially due to the clustered distribution of the anemone population during C1-C4. Alternatively, the settlers could be attracted to conspecifics. As they settle onto reefs, larvae of the anemonefish *A. percula* are drawn to the olfactory cues of conspecifics (Munday et al. 2009). In fact, more anemonefish settled into inhabited than uninhabited anemones. The potential conspecific attraction in *A. bicinctus* may be confined to settlers attracting settlers. In relation to juveniles, settlers were randomly distributed and clustered only during the last two censuses. Additionally, settlers were significantly dispersed from adult anemonefish in all but the final census, and from breeding pairs in all censuses. Thus *A. bicinctus* settlers could be attracted to the presence of fellow settlers and avoid anemones with adults.

Although settling *A. bicinctus* may be attracted to conspecifics, immigrant anemonefish exhibited lower survival rates in inhabited versus uninhabited anemones. This suggests that stress from aggressive displays or eviction by conspecifics negatively impacts the survival of newcomers. As occurs in many coral reef species, recruits, like other anemonefish or coral reef fish species (Elliott et al. 1995; Buston 2003; Dirnwöber and Herler 2007; Ben-Tzvi et al. 2009), often experience aggression from or are evicted from habitat patches occupied by larger conspecifics (Moyer and Sawyers 1973; Ross 1978a; Fishelson et al. 1974; Elliott and Mariscal 2001; Huebner et al. 2012).

Even with differential mortality of immigrants between inhabited and uninhabited anemones, in the August 1997 census the 195 fish in the population inhabited 149 out of the 199 available anemones. In 2015, the anemone population was a mere 13.6 % of the anemone number in 1997 (Fig. 6), and the contribution of each anemone species to the anemone population switched. In 1997, the anemones at the study site consisted of 43.7 % *E. quadricolor* and 56.3 % *H. crispa* compared to 55.6 % *E. quadricolor* and 44.4 % *H. crispa* in 2015. The sharp decline in sea anemone numbers was echoed in the anemonefish population. Even though in the 2000 and 2013 censuses the number of anemonefish were higher than in the preceding 1999 (McVay 2015) and 2009 censuses, respectively; overall, in nearly a 20-year period, anemonefish numbers dropped by 73 % from the 195 fish found in the August 1997 census to 52 in 2015.

Not only did the fish numbers decline, but the fish population demographics changed. In 1997, 25.1 % of the 195 anemonefish were adults, with the breeding pairs accounting for 5.6 % of the population. In 2015, 40.4 % of the fish population were adults and the breeding pairs comprised 30.8 % of the population. Juveniles accounted for 37.1 % versus 46.2 % in 1997 and 2015, respectively. The largest change occurred in the contribution of the settlers to the population, a drop from 37.4 % in 1997 to only 13.5 % in 2015. These demographic differences could be driven by the available habitat. Because the number of anemones declined by 86 % from 1997 to 2015 while the number of fish fell by 74 %, there were significantly more fish per anemone in 2015 compared to the 1997 census. In addition, in 2015, every anemone of both species was occupied. The absence of empty sea anemone habitat will force settling anemonefish to interact with their larger conspecifics which may result in high settler mortality. Furthermore, our data demonstrate that juvenile anemonefish have significantly higher survival when associating with *E. quadricolor.* Since in 2015 adults dominated this anemone, they may prevent juveniles from migrating to this preferred habitat, also leading to increased mortality.

Since anemonefish obligatorily inhabit sea anemones, anemonefish survival relies on the existence of suitable sea anemone habitats. When sea anemones decline, for example due to collection for the aquarium trade of either the anemones or the anemonefish (Shuman et al. 2005; Madduppa et al. 2014b; Frisch et al. 2016) or anemone bleaching, driven by climate change, occurs (Hattori 2002; Hobbs et al. 2013), anemonefish populations may be adversely affected (Hattori 2002; Hattori 2005). Over the last few decades, the Gulf of Eilat has experienced a decline of reef species alongside increased development and inputs of pollution (Loya 1975; Fishelson 1995; Rinkevich 2005). Additionally, a rise in diving tourism and divers physically damaging corals has negatively impacted the coral reefs (Zakai and Chadwick-Furman 2002). Restoration efforts of rearing *A. bicinctus* or producing host anemones in captivity with the intent of releasing them onto reefs (Maroz and Fishelson 1997; Scott and Baird 2015) do not address the reason for the decline and hence may not prove successful in the long term. Future studies and management efforts should focus on deciphering the causes of the host anemones' demise, potentially eliminating these effects and thereby enabling the recovery of the host anemones *E. quadricolor* and *H. crispa.* Hopefully, *A. bicinctus* recruitment and population growth will follow. Otherwise, the populations of these anemonefish and their sea anemone hosts may face local extinction.

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