# 25 Saving Nemo Extinction Risk, Conservation Status, and Effective Management Strategies for Anemonefishes

Geoffrey P. Jones, Maya Srinivasan, Gemma F. Galbraith, Michael L. Berumen, and Serge Planes

# CONTENTS

Introduction	
Threatening Processes	
25.2.2 Ocean Warming	
25.2.3 Ocean Acidification	
25.2.4 Aquarium Trade	
25.2.5 Coastal Development	
Risk Factors: Life History and Ecological Traits	
25.3.1 Habitat Specialization	
25.3.2 Mutual Dependence	
25.3.3 Low Density	
25.3.4 Low Connectivity	
25.3.5 Small Geographic Range	
25.3.6 Depth Range	
Rarity Traits: Double and Triple Jeopardy	
Conservation Status	291
Effective Management Strategies	291
25.6.1 Marine Reserves	291
25.6.2 Catch Regulations	
25.6.3 Protecting Anemones	
25.6.4 Captive Breeding	
Conclusions	
nowledgements	293
	Introduction

# 25.1 INTRODUCTION

Interest in the extinction risk and conservation of anemonefishes might not have begun in 2003, but the Disney movie *Finding Nemo* sparked an interest in the conservation status of the very small coral reef fishes that continues today. The movie is directly quoted in the titles of numerous papers, including "Finding Nemo" (Ollerton et al. 2007), "Losing Nemo" (Jones et al. 2008), "Not Finding Nemo" (Nanninga et al. 2015), and "Trying to Find Nemo" (Scott and Baird 2015). There is a website dedicated to saving Nemo (www.savingnemo.org) and a documentary film initially titled *Saving Nemo* (Sharkbay Films, 2011), although it was later forced to change its name to *Filmstar Fish: The Struggle for Survival*. The popularity of the movie has no doubt contributed to a huge demand for anemonefish in the aquarium trade and concerns over impacts on wild populations (Jones et al. 2008; Burke da Silva and Nedoskyo 2016). However, at the same time, we have seen an enormous interest in the life history and ecology of anemonefishes, with research focusing on human impacts, extinction risks, and effective management strategies. Almost all of the key papers on threats to anemonefish and their conservation have been published from 2003 onwards, with accelerating interest in recent years (Figure 25.1). So, what does this research tell us about the threat of extinction for anemonefishes? How are we impacting them and what makes them threatened? And



**FIGURE 25.1** Results of a Web of Science search showing the number of publications (histograms) and number of citations (line graph) of papers on human impacts on and conservation of anemonefishes, showing the rapid increase since 2003.

for those that are critically endangered, what can we do about it? That is, how do we go about saving Nemo?

By 2012, a high proportion of species in families represented in the movie Finding Nemo had been assessed by the IUCN (International Union for the Conservation of Nature) and 16% of species had been classified as threatened (McClenachan et al. 2012). However, poor young Nemo himself did not make the cut. As of 2021, no anemonefish species has been placed in any of the endangered species categories on the IUCN Redlist. The United States National Marine Fisheries Service (NMFS) and the National Oceanic and Atmospheric Administration (NOAA) responded to a petition to have Amphiprion percula (aka Nemo) classified as endangered under the US Endangered Species Act (Rauch 2015; Maison and Graham 2016). It was concluded, based on population estimates ranging from 13 and 18 million, that it is not in any danger of extinction either now or in the near future. While this is clearly consistent with the current IUCN criteria, such population estimates are rare and unreliable for marine species. Even if correct, it is questionable whether or not these numbers reflect the actual likelihood of extinction. There is a growing list of suspected and confirmed neo-extinctions of marine fishes (Roberts and Hawkins 1999; Hawkins et al 2000; Dulvy et al 2004), many of which appear to have occurred following catastrophic declines from numbers that were historically much higher than the IUCN thresholds for endangered or vulnerable species.

While there are 28 currently recognized species, the highest biodiversity of anemonefish, like most coral reef

fishes, is concentrated in Southeast Asia and the Western Pacific, where up to 12 species may co-occur in the same area (Figure 25.2). The location of the biodiversity hotspot is unfortunate in the sense that it can be largely overlaid with a high degree of coral reef habitat degradation, a high dependence on marine resources, and numerous problems associated with implementing effective management strategies. Fortunately, many of these species have broad semi-overlapping Indo-Pacific distributions that include places where the impacts are likely to be less severe. Many of the smaller range species lie at the outer limits of the Amphiprion/Premnas distribution, where the level of threat is likely to vary from species to species (McClanahan et al. 2021). Our understanding of anemonefish biodiversity is likely a work in progress, with two new species recently recognized for the Pacific (A. barberi, Allen et al. 2008; and A. pacificus, Allen et al. 2010). Based on the spatial and morphological variation in the region, Drew et al. (2008) suggested that there may be even more species in the Pacific. There are also likely to be more hidden species in the coral triangle (Timm et al. 2008), which will be a conservation concern. One species, A. leucokranos, no longer exists, but only because it was determined to be a hybrid formed when a female A. chrysopterus mates with a male A. sandaracinos (Gainsford et al. 2020). The threat to anemonefish biodiversity requires an assessment, not just of the likelihood of losing one or more of the 28 species, but the extent to which we are losing local populations or seeing a decline in genetic diversity that will affect a species ability to adapt to environmental change.



**FIGURE 25.2** Biodiversity heat map for 28 anemonefish species calculated from overlapping extent of occurrence (EOO km<sup>2</sup>). EOO was estimated as minimum convex hulls: the smallest polygon in which no internal angle exceeds 180 degrees, and which contains all the sites of occurrence (IUCN 2001, 2012, 2019). Hulls were constructed from known occurrence records obtained fishbase.org (Froese and Pauly 2021) and overlaid with a global grid of  $5^{\circ} \times 5^{\circ}$  cells in R 4.1.1 (R Core Team, 2021). Species richness was calculated as the total number of overlapping hulls per cell.

The aims of this chapter are: (1) to assess the main threats to regional and local anemonefish biodiversity as a result of local population declines and possible extinction; (2) to evaluate the life history and ecological characteristics of anemonefishes (and their anemones) that exacerbate the risk of extinction; (3) to quantify relationships among different rarity traits (specialization, geographic range, and depth range) that may expose anemonefish species to double or triple jeopardy; (4) to calculate the actual area of occurrence of anemonefishes within the geographic ranges and assess these in relation to the IUCN endangered species categories; and (5) to consider pre-emptive and effective management strategies that can aid population recovery, protect wild breeding populations into the future, and reduce the likelihood of local or global extinction.

## 25.2 THREATENING PROCESSES

# 25.2.1 ANEMONE BLEACHING

The likelihood of extinction needs to be assessed in the context of the multiple factors having a negative impact on anemonefishes and/or their critical habitats, all of which can be traced back to human activities. Of these, ocean warming and associated bleaching of anemones and their surrounding coral habitat are likely to be the most extreme and largest-scale threats. Almost all anemone symbionts bleach and bleaching can occur across a broad geographic range (Hobbs et al. 2013; Burke da Silva and Nedoskyo 2016) and from shallow to mesophotic reefs (Haguenauer et al. 2021). In some locations, bleaching is now being

observed regularly over multiple years (Hobbs et al. 2013; Hayashi and Reimer 2020). While anemones can recover and fish may survive, numerous papers have observed fewer fish where anemones have bleached (Hattori 2002; Jones et al. 2008). Hattori (2002) found that A. perideraion went locally extinct following bleaching mortality of H. crispa in the 1998 El Nino, while the generalist A. clarkii survived in less preferred hosts. Even if anemonefish survive in bleached anemones, it is known to impair reproductive activity and reduce fecundity (Saenz Agudelo et al. 2011; Beldade et al. 2017), increase metabolic stress (Norin et al. 2018), reduce metabolic rate (Cortese et al. 2021), and disrupt antipredator behavior (Lönnstedt and Frisch 2014), all of which may affect the future persistence of populations. Interestingly, bleaching does not appear to affect nematocysts, so anemones can still defend themselves, which may aid in their recovery (Hoepner et al. 2019).

## 25.2.2 OCEAN WARMING

Ocean warming can have direct negative effects on anemonefish, independent of habitat bleaching, due to thermal sensitivity during the larval and juvenile stages. McLeod et al. (2013) showed that larval *A. percula* take longer to develop and settle at higher temperatures, which may reduce numbers recruiting to the adult population. Nowicki et al. (2012) demonstrated that juvenile *A. melanopus* needed to forage and consume more at higher temperatures, perhaps because of lower energy efficiency. Experiments on *A. melanopus* also show temperature has a strong negative effect on reproduction at 1.5 degrees above current ambient conditions (Miller et al. 2015). On the other hand, future warming may enhance performance in *P. biaculeatus*, which has a higher aerobic scope and potentially higher growth and condition at temperatures slightly above present-day conditions (Donelson 2015).

Fishes may respond to increasing ocean temperatures by shifting poleward, as long as they can find suitable habitat and food resources (Munday et al. 2008). Subtropical anemonefishes with narrow latitudinal ranges are particularly susceptible to increasing temperatures as they may be near upper thermal tolerances. Malcolm and Scott (2017) suggested the Australian endemics *A. akindynos* and *A. latezonatus* have a limited ability to move south, although a small range shift in *A. latezonatus* and its host anemone *E. quadricolor* has been observed at the Solitary Islands, NSW.

#### 25.2.3 OCEAN ACIDIFICATION

Experimental studies on larval and juvenile fishes have indicated numerous effects of elevated pCO<sub>2</sub> on growth, survival, physiological condition, otolith morphology, and sensory behavior (Munday et al. 2019; Munday et al. 2020). This has raised long-term concerns over ocean acidification or the lower predicted pH by mid-to-late this century as a result of increasing  $CO_2$  in the atmosphere. Although controversial, ocean acidification appears to have particularly strong effects on the olfactory and auditory sensory mechanisms of larval anemonefishes (Munday et al. 2009, 2010; Dixson et al. 2010; Simpson et al. 2011; Nilsson et al. 2012). Given that they rely so heavily on olfaction and sound for finding reefs, finding anemones, and avoiding predators, acidification is likely to have a strong negative effect on their settlement and survival. At low pH, A. per*cula* larvae completely lose their ability to discriminate the smell of their host anemone (Munday et al. 2009) and their innate ability to detect predator olfactory cues is impaired, with some larvae actually becoming attracted to predators (Dixson et al. 2010). Anemonefish reproduction also appears to be affected by acidification. Miller et al. (2013) showed that A. melanopus reproduction was stimulated at low pH and females had a higher fecundity, although larvae tended to have smaller yolks. Recently, Holmberg et al. (2018) showed that acidification alters otolith morphology in A. clarkii, with a dramatic negative effect on settlement competency.

The future effects of acidification will occur in combination with rising temperatures, and impacts will depend on how these drivers interact. Nowicki et al. (2012) found temperature had a greater effect on the foraging behavior of *A. melanopus* than low pH, and the interaction between the two caused a reduction in food consumption. Similarly, Miller et al. (2015) showed that the effects of temperature on *A. melanopus* reproduction were much stronger than the effects of acidification, but the negative effect of pCO<sub>2</sub> on offspring quality was more pronounced at higher temperatures.

#### 25.2.4 AQUARIUM TRADE

Anemonefish feature among the most highly sought-after species in the aquarium fish trade and are generally regarded as being at high risk of overexploitation (e.g., Wabnitz et al. 2003; Roelofs and Silcock 2008; Okemwa et al. 2016; Biondo 2018). Their vulnerability can be attributed to popularity, accessibility on shallow coastal reefs, ease of capture, and market value. There is often a higher price for rare species or rare color morphs, which increases pressure on the species and populations that are the most susceptible (Militz et al. 2018). Numerous papers point to significant effects of collecting anemonefish on abundance (Shuman et al. 2005; Jones et al. 2008; Frisch and Hobbs 2009; Madduppa et al. 2014). For example, Shuman et al. (2005) show a large depletion of anemonefish numbers in areas subject to collecting in the Philippines, compared with unfished areas. Similarly, the collecting of A. ocellaris has a huge negative impact on abundance at Spermonde Archipelago (Madduppa et al. 2014). Here there is also a reduced genetic diversity in A. ocellaris that can be attributed to aquarium fish collecting (Madduppa et al. 2018). While depletion of anemonefish numbers can be quite rapid as an industry develops, recovery can be extremely slow, even if there is a complete moratorium on collection (Frisch et al. 2019).

#### 25.2.5 COASTAL DEVELOPMENT

Direct loss of habitat due to coastal development, including increasing sedimentation and nutrient enrichment associated with deforestation, agricultural activities, and marine dredging, represents a major potential threat to coral reef fishes (Wenger et al. 2015, 2017). However, clear evidence for impacts on anemonefishes is hard to find, either for the fish themselves or the anemone habitat. Hayashi et al. (2019a, 2019b) documented the low abundance and diversity of clownfish species directly on the coastline near urban developments in Okinawa. Long-term declines in A. bicinctus and the host anemone Entacmaea in the Gulf of Eilat have been linked to pollution and coastal development (Howell et al. 2016). Anemones may be more resilient to sedimentation than corals (Liu et al. 2015), which may explain why anemonefish-associated anemones can be found in turbid waters. However, direct effects of sedimentation on anemonefishes have been linked to prolonged larval development (Wenger et al. 2014), adverse effects on gill function (Hess et al. 2015, 2017), and altered anti-predator behavior (Hess et al. 2019), all of which may negatively impact on population size.

# 25.3 RISK FACTORS: LIFE HISTORY AND ECOLOGICAL TRAITS

#### **25.3.1 HABITAT SPECIALIZATION**

The multiple human impacts listed here and acting together may pose a risk of extinction for any fish species, but most anemonefishes share life history and ecological traits that exacerbate these threats. The most important of these is their high degree of specialization and obligate dependence on a small range of species of a single habitat-forming organism, the anemones (Allen 1975; Fautin and Allen 1992; Burke da Silva and Nedoskyo 2016). Only ten anemone species are colonized by the 28 anemonefish species and there are eight anemonefish species associated with a single anemone species (Burke da Silva and Nedoskyo 2016). Two species are associated with a particular morph of a single anemone species, with P. biaculatus associated with the solitary morph of Entacmaea and A. melanopus associated with the colonial morph (Srinivasan et al. 1999). The survival of the vast majority of the anemonefish species is dependent on just four to five preferred anemone species. Anemonefishes, perhaps more than any other reef fishes, share the fate of all highly specialized animals. Their distribution and abundance are completely linked to their hosts, and so if the hosts disappear, the fish will disappear too.

## 25.3.2 MUTUAL DEPENDENCE

Another major problem for anemonefishes is that not only are they dependent upon their anemone hosts, but the anemones are just as dependent on them (Fautin and Allen 1992; Burke da Silva and Nedoskyo 2016). Experiments show that when all fish are collected, anemones are often eaten by their predators such as butterflyfish and angelfish, resulting in their death (Bradshaw 1994; Frisch et al. 2016). This is a real problem for the aquarium fish collecting industry, as it is not sustainable unless no anemones are left vacant (Frisch et al. 2016). Anemonefish also appear to be necessary to aid recovery from bleaching (Pryor et al. 2020) but have the ability to avoid bleached anemones if they have the choice (Scott and Dixson 2016). So, anemonefish have a susceptibility that they share with all other obligate mutualists – if one partner goes extinct, the other will go extinct at the same time.

## 25.3.3 LOW DENSITY

For whatever reason, the anemones that host anemonefishes are never particularly abundant on coral reefs. Hence, they almost always have low population densities resulting from naturally low densities of hosts (Srinivasan et al. 1997; Scott and Baird 2015; Steinberg et al. 2020; Hayashi et al. 2019b). Highly specialized species are even more likely to exhibit low abundance when their preferred habitats are rare (Jones et al. 2002; Munday 2004).

#### **25.3.4** Low Connectivity

The emerging evidence is that dispersal distances in anemonefishes can be limited, with a high degree of self-recruitment within populations on isolated reefs (see Chapter 20). Low connectivity may explain slow recovery when local populations are severely depleted or become locally extinct (Bonin et al. 2016; Frisch et al. 2019). This may be a particular problem for endemics that occupy relatively few isolated reefs, with subpopulations being completely dependent on self-recruitment (Steinberg et al. 2016; van der Meer et al. 2012). In this case, local extinction may be a stepping stone to global extinction. However, self-recruitment has its benefits in a stable environment, in terms of promoting local population persistence and local adaptation (Jones et al. 2009; Jones 2015).

## 25.3.5 SMALL GEOGRAPHIC RANGE

A large proportion of anemonefishes have broad Indo-Pacific distributions, and these will only be exposed to global threats such as increasing temperatures or ocean acidification. However, there are also numerous small range species, either endemic to isolated island groups (e.g., A. chagosensis, A. chrysogaster) or with small latitudinal ranges on mainland coasts (e.g., A. omanensis, A. latezonatus) usually near the periphery of the global range of anemonefishes (Figure 25.3). The vast majority of neo-extinctions in the animal kingdom have been species with small ranges or island endemics that have been exposed to habitat loss, exotic pests, and diseases. The few recorded extinctions of marine fishes in recent times have all been small-range species (Roberts and Hawkins 1999; Hawkins et al. 2000; Dulvy et al. 2004). Small-range anemonefishes are clearly susceptible to environmental disturbances that impact the scale of their distribution. They may also be more sensitive than large-range species to global change, especially subtropical species that are likely to be adapted to cooler water environments.

## 25.3.6 DEPTH RANGE

A final risk factor is the narrow and shallow water depth distributions of the majority of anemonefish species (Fautin and Allen 1992). This exposes them to any human impacts that tend to be more severe in shallow water, such as warming water, bleaching, and coastal sedimentation. Some species, such as A. percula are most abundant in water less than 3–4 m in depth. This makes a large proportion of the population completely accessible to aquarium fish collectors, without the need for underwater breathing apparatus. Deep water surveys on the GBR have shown that some species like A. akindynos and A. perideraion can be abundant on mesophotic reefs, suggesting they may have a depth-refuge from shallow water disturbances (Bridge et al. 2012). However, this may not apply to the majority of species which may be much less abundant at depth and appear to be susceptible to deep water warming and bleaching (e.g., A. chrysopterus, Haguenauer et al. 2021).

# 25.4 RARITY TRAITS: DOUBLE AND TRIPLE JEOPARDY

A species with any one of the aforementioned traits would attract conservation attention in an environment that is showing signs of increasing and proliferating threats. The



**FIGURE 25.3** Extent of occurrence (EOO) for the ten anemone fish species with smallest geographical ranges. EOO is plotted as minimum convex hulls; the smallest polygon in which no internal angle exceeds 180 degrees, and which contains all the sites of occurrence (IUCN 2001, 2012, 2019). Hulls were constructed using known occurrence records from fishbase.org (Froese and Pauly 2021) in R 4.1.1 (R Core Team 2021). Occurrence records for *A. chagosensis* were limited to three points on the same axis and therefore a 0.1 decimal degree buffer was applied to calculate an approximate EOO using the package ConR (Dauby et al. 2017, 2020).

problem anemonefish face is that they can have a combination of life history and ecological traits that multiply the risk of extinction. This can be especially true when different aspects of rarity, including small geographic range, low abundance, and high specialization are linked (Rabinowitz 1981; Jones et al. 2002). A species with a combination of any two of these traits is considered to have *double jeopardy* of extinction, and for species exhibiting all three traits, it is triple jeopardy (Jones et al. 2002; Munday 2004). Our analyses show that there are strong relationships among these risk factors in anemonefishes. Using data on geographic range sizes from Fishbase and an index of specialization based on the number of anemones occupied (Fautin 1991; Burke da Silva and Nedoskyo 2016), we show that range size is positively related to decreased specialization (Figure 25.4a). Hence small-range species are exposed to the double risk associated with human impacts on the area in which they live and on the anemone on which they depend. Similarly, depth range declines with increasing specialization on host anemones, so the most specialized species are the most restricted to shallow water (Figure 25.4b). Clearly, some anemonefishes have triple jeopardy. These are the species specialized on a single host anemone which have a small geographic range and also have a narrow depth range. This exposes them to a much greater range of threats than they would have had if they possessed only one of these traits.

Small geographic range and high specialization are also likely to be associated with a low total population size, which would also constitute triple jeopardy for anemonefishes. What little information we have suggests that anemonefish breeding populations are limited by the number of their preferred hosts (see Chapter 18) and they are generally found at low densities. However, the triple jeopardy would only hold if population densities were not related to geographic range. Some evidence suggests that for marine fishes, small-range endemics tend to have higher population densities than their widespread counterparts at the same locations (Hobbs et al. 2010, 2011). This has not been evaluated for anemonefishes, although McClanahan et al. (2021) showed that the endemic A. chrysogaster at Mauritius is moderately abundant, is broadly distributed around the island, and has a large depth range. A complete understanding of extinction risks for island endemics will require a greater effort in estimating population densities and total population size.



**FIGURE 25.4** Relationships between the number of anemone species occupied (Index of Specialization) and a) geographic range as extent of occurrence (EOO, million km<sup>2</sup>) (glm, p=0.017, t=2.56) and b) known depth range (m) (glm, p<0.001, t=4.06) for 27 anemonefish species. Depth range and known occurrence records were obtained from fishbase.org (Froese and Pauly 2021). EOO was calculated as minimum convex hulls constructed from occurrence records. All analyses were performed in R 4.1.1 (R Core Team 2021) using the packages ConR (Dauby 2020), rCAT (Moat 2020), rsq (Zahng 2021), and glmmTMB (Brooks et al. 2017). Generalized linear models were fit with Gaussian error family and identity link. *A. pacificus* is not included in either model as habitat use for this species is not known.

# 25.5 CONSERVATION STATUS

To date, only 15 of the 28 species have been assessed by the IUCN and all have been classified globally as "Least Concern". However, at this stage, this assessment does not include most of the species with the smallest ranges (see Figure 25.3). In terms of regional assessments, the Redlist website lists *A. clarkii* as endangered in the Red Sea, but no data on this assessment is available. Few anemonefish species have been listed as endangered by any country through their national endangered species legislation. As stated earlier, the United States has assessed *A. percula* for its Pacific territories under its Endangered Species Act and it has been considered at no risk of extinction now or in the near future (Rauch 2015; Maison and Graham 2016).

The IUCN criterion that seems most applicable to the real threat of extinction for anemonefishes concerns not just geographic range or extent of occurrence (EOO), but their area of occupancy (AOO) within their geographic range. AOO reflects the fact that a taxon will not usually occur throughout the full area of its EOO, which may contain unsuitable or unoccupied habitats (IUCN 2001, 2012). That is, over what actual area have they been observed. The IUCN considers species with an AOO of less than 10  $km^2$  as Critically Endangered,  $< 500 km^2$  as Endangered, and <2,000 km<sup>2</sup> as Vulnerable (Criterion B2). Using data from Fishbase (Froese and Pauly 2021) on geographic range and confirmed locations, we show the AOOs for the endemic anemonefishes can be extremely small (Figure 25.5). On this basis, three species approach the threshold to be classified as Critically Endangered and as many as 23 species would be classified as Endangered (Figure 25.5). In combination with a small extent of occurrence, low numbers of locations, and estimates of the reef area within these ranges (Allan Coral Atlas 2020), we suggest that these species urgently require an evaluation by the IUCN and by the government agencies of the countries where they are endemic. We acknowledge that accurate estimates of AOO require extensive known occurrence records which is currently problematic for data deficient species. The Fishbase online database we used was the only source of confirmed occurrence data available for all 28 species, but at this stage, these records are not complete. It is noteworthy that the two species with the smallest geographic ranges, *A. chagosensis* (EOO=4,056 km<sup>2</sup>) and *A. mccullochi* (EOO=1,317 km<sup>2</sup>), qualify as Endangered on the basis that their EOOs are less than 5,000 km<sup>2</sup>.

#### 25.6 EFFECTIVE MANAGEMENT STRATEGIES

There are numerous options for protecting anemonefishes that will vary in their effectiveness depending on the species, the location and the most significant threats. The ability to implement effective management will depend on the political will and socioeconomic circumstances that prevail. Here, we will just highlight a few management options that should work, based on the literature or the biology of the species.

# 25.6.1 MARINE RESERVES

Marine reserves or no-take marine protected areas established to protect biodiversity are known to protect anemonefishes where they can be well-managed. Several studies have shown higher numbers of anemonefishes in marine reserves compared to adjacent areas subject to collecting (Shuman et al. 2005; Jones et al. 2008; Madduppa et al. 2014). Scott et al. (2011) showed a long-term increase in



**FIGURE 25.5** Histogram of area of occupancy (AOO, km<sup>2</sup>) for 28 anemonefish species. IUCN Red List threat categories are indicated by dashed lines following Criterion B2 (IUCN 2019) and show: a) five species as Vulnerable (AOO < 2,000 km<sup>2</sup>) and 23 species as Endangered (AOO < 500 km<sup>2</sup>). Inset b) six species with smallest AOO and dashed line to show threshold for IUCN Red List category Critically Endangered (AOO < 10 km<sup>2</sup>). Three species are within 2 km<sup>2</sup> of this threshold. AOO estimates were made using known occurrence records from fishbase.org (Froese and Pauly 2021) at the recommended reference scale of 4 km<sup>2</sup> (2 × 2 km) for occupied cells to assess Red List criterion B2. AOO is taken as the total area of occupied cells in a uniform grid within a given extent of occupancy (EOO) (IUCN 2001, 2012, 2019). Analysis was performed in R 4.1.1 (R Core Team 2021) with the packages rCAT (Moat 2020) and ConR (Dauby 2020).

*A. akindynos* abundance in marine reserves at the Solitary Islands. Bonin et al. (2016) found higher numbers of *A. melanopus* in protected areas at the Keppel Islands, following a long period of historic collecting of anemonefishes. Genetic analyses show that despite protection, the effective population size was extremely small (~750 breeders), so there are questions about how big reserves need to be to protect a population large enough to avoid local extinction. It is important to monitor the success of reserves in protecting anemonefishes, as there can be unexpected outcomes. For example, McClanahan (1994) showed that *A. allardi* thrives in fished areas where it has become associated with high numbers of sea urchins that are thriving due to overexploitation of a triggerfish predator. Where marine reserves were established, the anemonefish went locally extinct.

Studies on self-recruitment in anemonefishes show the benefit of marine reserves as local sanctuaries for species (Almany et al. 2007; Jones et al. 2009). A high proportion of juveniles return to the natal population, ensuring protection that carries through to the next generation (Salles et al. 2016, 2020). This has been recorded for five generations of *A. percula* in a small island reserve in Papua New Guinea; however, this population is largely protected by its remoteness, rather than any effective management actions. Marine

reserves are likely to be an effective first line of defence for endemic species where levels of self-recruitment are expected to be extremely high (van der Meer et al. 2012; Steinberg et al. 2016). However, recovery from past or widespread impacts is likely to be slow (Frisch et al. 2019). Sato et al. (2017) make the point that reserves may be of limited value from the point of view of supporting anemonefish collecting in fished areas through larval dispersal.

Marine reserves will no doubt be more effective for anemonefishes if specific information on their distribution and abundance is taken into account when selecting sites for reserves. There should be a high priority for anem*onefish hotspots* or places where local species diversity is high or a species of concern is unusually abundant. The Solitary Islands marine park is a good example of this, where locations with high anemonefish densities are well protected (Scott et al. 2011). In Kimbe Bay, Papua New Guinea, A. percula is unusually abundant on fringing reefs surrounding small offshore islands, compared to emergent reefs with no islands (Dixson et al. 2011). A marine park planning exercise that prioritized the protection of these reefs because of their habitat diversity could not have been better designed for protecting this iconic species (Green et al. 2009).

#### 25.6.2 CATCH REGULATIONS

In our view, given the likely endangered species status of species with very small areas of occurrence, all collecting should be banned and trade deemed illegal. For species clearly overfished in an area, moratoriums on collecting need to be in place, such as has occurred at the Keppel Islands. Such moratoriums may need to remain in place for the long term for sufficient recovery to occur (Frisch and Hobbs 2009; Frisch et al. 2016), and future catch levels would need to be tightly controlled. In circumstances where catches can be reliably controlled, a ban on catching adult fishes and controlled levels of harvesting juveniles would be extremely effective. Juveniles would be of higher value for the aquarium fish market and limited harvest would not impact the size of the breeding population. However, this could only work for anemonefish species that live in large social groups and not for species that only occur in pairs.

## **25.6.3 PROTECTING ANEMONES**

Marine reserves and other measures that focus on anemonefishes will not protect anemones from extrinsic disturbances such as global warming, sedimentation, and pollution. There is no silver bullet for protecting anemones from these disturbances, and the increasing levels of anemone bleaching are a huge concern. Banning the collecting of anemones that support anemonefishes should be the number one management priority. Studies on how to reduce the impacts of warming water and pollution on anemones should be the number one research priority. The evidence suggests that the reproductive success of anemonefishes is critically linked, not just to anemones, but to anemones at particularly high-quality locations (Salles et al. 2020). There should be a premium on identifying and targeting the protection of these important sources of future generations.

#### 25.6.4 CAPTIVE BREEDING

There is a long tradition of captive breeding and release in terrestrial conservation and it seems a very attractive option for enhancing depleted anemonefish populations. Most species have now been bred in captivity (Olivotto and Geffroy 2017), and juveniles can be readily released in the wild where vacant individuals of preferred anemones can be found. Direct supply of aquarium-reared juveniles has the potential to take the pressure off collecting from wild populations (Burke da Silva and Nedoskyo 2016). This topic has been discussed elsewhere in this book (Chapter 22), but there are many reasons why captive breeding and release of anemonefish should be a last resort. In marine systems, captive breeding does not have a good record in reducing wild catches and there is a lot of potential for conflict when it comes to competing sources of income. For restoring anemonefish populations, the emphasis should really be on breeding and out-planting anemones to restore numbers to historic levels. The methods for propagating anemones exist and there is clearly a huge market for anemones that host anemonefish for the aquarium trade (Fraser et al. 2021). Borrowing from this technology for conservation purposes seems like the best way forward, especially if there is scope for artificial selection for bleaching-resistant strains.

# 25.7 CONCLUSIONS

If we set out to design a fish species that would have a high risk of extinction in an era of rapid environmental change, it would probably look and be like an anemonefish! It would, of course, be so cute that everybody would like to have one, even though it is designed to be rare, so there can never be enough to go around. We would keep coming up with new ways to negatively impact its population size or degrade its environment. We would give it every life-history trait we could think of that would reduce its ability to withstand all of these changes. We would design it to live in a single habitat that we know is highly sensitive to warming water and then crank up the temperature. Perhaps we would put it out on some remote island and hope it can sustain itself there, away from as many human impacts as possible.

The only saving grace to saving Nemo is that we have not seen a species of anemonefish go extinct - yet. That in itself seems like a miracle. We still have 28 species and maybe there are even a few more hidden away for safe keeping. Perhaps this means that they do have a secret for survival that we do not fully understand. Our recent research into larval dispersal shows an incredible ability to navigate their way to suitable habitat, so long as there is some suitable habitat left to find. Perhaps it means that the management actions we have taken for at least some species have been effective. If so, we just need to find ways to expand and tailor these management efforts to all species, whether that is going to be full protection, marine reserves, or sustainable harvest strategies. Or perhaps we have just been lucky that we still have 28 species. One thing the movie Finding Nemo teaches us is that survival always depends on a bit of luck.

## ACKNOWLEDGEMENTS

We would like to acknowledge the College of Science and Engineering and the ARC Centre of Excellence for Coral Reef Studies at James Cook University for logistic support. We also thank the Mahonia Na Dari Research and Conservation Centre and the Walindi Plantation Resort for supporting our research in Papua New Guinea. Nick Murray, Gilles Dauby, Luis Verde Arregoitia, and Justin Moat all provided valuable insights and guidance to our spatial analysis.

#### REFERENCES

- Allen Coral Atlas. 2020. Imagery, maps and monitoring of the world's tropical coral reefs. https://allencoralatlas.org/ (accessed June 28, 2022).
- Allen, G. R. 1975. *Anemonefishes*. Neptune City, NJ: TFH Publications.

- Allen, G. R., J. Drew, and S. Fenner. 2010. Amphiprion pacificus, a new species of anemonefish (Pomcaentridae) from Fiji, Tonga, Samoa and Wallis Island. Aquaculture 16:129–138.
- Allen, G. R., J. Drew, and L. Kaufman. 2008. Amphiprion barberi, a new species of anemonefish (Pomacentridae) from Fiji, Tonga and Samoa. Aqua International Journal of Ichthyology 14:105–114.
- Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316:742–744.
- Beldade, R., A. Blandin, R. O'Donnell, and S. C. Mills. 2017. Cascading effects of thermally-induced anemone bleaching on associated anemonefish hormonal stress response and reproduction. *Nature Communications* 8:716.
- Biondo, M. V. 2018. Importation of marine ornamental fishes to Switzerland. Golbal Ecology and Conservation 15: e00418.
- Bonin, M. C., H. B. Harrison, D. H. Williamson, A. J. Frisch, P. Saenz-Agudelo, M. L. Beruman, and G. P. Jones. 2016. The role of marine reserves in the replenishment of a locallyimpacted population of anemonefish on the Great Barrier Reef. *Molecular Ecology* 25:487–499.
- Bradshaw, E. 1994. Dynamic interactions of the mutualistic association between the spine-cheeked anemonefish Premnas biaculeatus and the host actinian Entacmaea quadricolor. BSc Honours thesis, James Cook University.
- Bridge, T., A. Scott, and D. Steinberg. 2012. Abundance and diversity of anemonefishes and their host sea anemones at two mesophotic sites on the Great Barrier Reef, Australia. *Coral Reefs* 31:1057–1062.
- Brooks, M. E., K. Kristensen, K. j. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9(2):378–400.
- Burke da Silva, K., and A. Nedoskyo. 2016. Sea anemones and anemonefishes: A match made in heaven. In *The Cnidaria*, *Past, Present and Future*, eds S. Goffredo and Z. Dubinsky, 425–438. New York: Springer.
- Cortese, D., T. Norin, R. Beldade, A. Crespel, S. S. Killen, and S. C. Mills. 2021. Physiological and behavioural effects of anemone bleaching on symbiont anemonefish in the wild. *Functional Ecology* 35:663–674.
- Dauby, G. 2020. ConR: Computation of parameters used in preliminary assessment of conservation, status. R package version 1.3.0. https://CRAN.R-project.org/package=ConR (accessed February 2, 2022).
- Dauby, G., T. Stévart, V. Droissart, A. Cosiaux, V. Deblauwe, M. Simo-Droissart, M. S. M. Sosef, et al. 2017. ConR: An R package to assist large-scale multispecies preliminary conservation assessments using distribution data. *Ecology and Evolution* 7:11292.
- Dixson, D. L., G. P. Jones, P. L. Munday, M. S. Pratchett, M. Srinivasan, S. Planes, and S. R. Thorrold. 2011. Terrestrial chemical cues help coral reef fish larvae locate settlement habitat surrounding islands. *Ecology and Evolution* 1:586–595.
- Dixson, D. L., P. L. Munday, and G. P. Jones. 2010. Ocean acidification impairs innate ability of fish to avoid predators. *Ecology Letters* 13:68–75.
- Donelson, J. M. 2015. Development in a warm future ocean may enhance performance in some species. *Journal of Experimental Marine Biology and Ecology* 472:119–125.
- Drew, J., G. R. Allen, L. Kaufman, and P. H. Barber. 2008. Endemism and regional color and genetic differences in five putatively cosmopolitan reef fishes. *Conservation Biology* 22:965–975.

- Dulvy, N. K., J. R. Ellis, N. B. Goodwin, A. Grant, J. D. Reynolds, and S. Jennings. 2004. Methods of assessing extinction risk in marine fishes. *Fish and Fisheries* 5:255–276.
- Fautin, D. G. 1991. The anemonefish symbiosis. What is known and what is not. *Symbiosis* 10(1–3): 23–46.
- Fautin, D. G., and G. R. Allen. 1992. Anemone Fishes and Their Host Sea Anemones. Perth, WA: Western Australian Museum.
- Fraser, N., S. Mangubhai, K. Hall, and A. Scott. 2021. Sea anemones in the marine aquarium trade: Market preferences indicate opportunities for mariculture and conservation Aquatic Conservation. *Marine and Freshwater Ecosystems* 31(12): 3594–3606.
- Frisch, A. J., and J. P. A. Hobbs. 2009. Rapid Assessment of Anemone and Anemonefish Populations at the Keppel Islands. A Report to the Great Barrier Reef Marine Park Authority. Townsville, QLD: Great Barrier Reef Marine Park Authority.
- Frisch, A. J., J. P. A. Hobbs, S. T. Hansen, D. H. Williamson, M. C.Bonin, G. P. Jones, and J. R. Rizzari. 2019. Recovery potential of mutualistic anemone and anemonefish populations. *Fisheries Research* 218:1–9.
- Frisch, A. L., J. R. Rizzari, K. P. Munkres, and J. P. A. Hobbs. 2016. Anemonefish depletion reduces survival, growth, reproduction and fishery productivity of mutualistic anemone-anemonefish colonies. *Coral Reefs* 35:375–386.
- Froese, R., and Pauly, D. (eds). 2021. FishBase.World, Wide Web electronic publication. http://www.fishbase.se (accessed February 2, 2022).
- Gainsford, A., G. P. Jones, J. P. A. Hobbs, F. M. Heindler, and L. van Herwerden. 2020. Species integrity, introgression, and genetic variation across a coral reef fish hybrid zone. *Ecology and Evolution* 10:11998–12014.
- Green, A., S. E. Smith, G. Lipsett-Moore, C. Groves, N. Peterson, S. Sheppard, P. Lokani, et al. 2009. Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx* 43:488–498.
- Haguenauer, A., F. Zuberer, G. Siu, D. Cortese, R. Beldade, and S. C. Mills. 2021. Deep heat: A comparison of water temperature, anemone bleaching, anemonefish density and reproduction between shallow and mesophotic reefs. *Fishes* 6:37.
- Hattori, A. 2002. Small and large anemonefishes can coexist using same patchy resources on a coral reef, before habitat destruction. *Journal of Animal Ecology* 71:824–831.
- Hawkins, J. P., C. M. Roberts, and V. Clark. 2000. The threatened status of restricted-range coral reef fish species. *Animal Conservation* 3:81–88.
- Hayashi, K., and J. D. Reimer. 2020. Five-year study on the bleaching of anemonefish-hosting anemones (Cnidaria: Anthozoa: Actiniaria) in subtropical Okinawajima Island. *Regional Studies in Marine Science* 35:101240.
- Hayashi, K., K. Tachihara, and J. D. Reimer. 2019a. Loss of natural coastline influences species diversity of anemonefish and host anemones in the Ryuku Archipelago. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31:15–27.
- Hayashi, K., K. Tachihara, and J. D. Reimer. 2019b. Low density populations of anemonefish with low replenishment rates on a reef edge with anthropogenic impacts. *Environmental Biology of Fishes* 102:41–54.
- Hess, S., B. J. M. Allan, A. S. Hoey, M. D. Jarrold, A. S. Wenger, and J. L. Rummer. 2019. Enhanced fast-start performance and anti-predator behaviour in a coral reef fish in response to suspended sediment exposure. *Coral Reefs* 38:103–108.

- Hess, S., L. J. Prescott, A. S. Hoey, S. A. McMahon, A. S. Wenger, and J. L. Rummer 2017. Species-specific impacts of suspended sediments on gill structure and function in coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences* 284:20171279.
- Hess, S., A. S. Wenger, T. D. Ainsworth, and J. L. Rummer. 2015. Exposure of clownfish larvae to suspended sediment levels found on the Great Barrier Reef: Impacts on gill structure and microbiome. *Scientific Reports* 5:10561.
- Hobbs, J. P. A., A. J. Frisch, B. M. Ford, M. Thums, P. Saenz-Agudelo, K. A. Furby, and M. L. Beruman. 2013. Taxonomic, spatial and temporal patterns of bleaching in anemones inhabited by anemonefishes. *PLOS ONE* 8:e70966.
- Hobbs, J. P. A., G. P. Jones, and P. L. Munday. 2010. Rarity and extinction risk in coral reef angelfishes on isolated islands: Interrelationships among abundance, geographic range size and specialisation. *Coral Reefs* 29:1–11.
- Hobbs, J. P. A., G. P. Jones, and P. L. Munday. 2011. Extinction risk in endemic marine fishes. *Conservation Biology* 25:1053–1055.
- Hoepner, C. M., C. A. Abott, and K. Burke da Silva. 2019. The ecological importance of toxicity: Sea anemones maintain toxic defence when bleached. *Toxins* 11:266.
- Holmberg, R. J., E. Wilcox-Freeburg, A. L. Rhyne, M. F. Tlusty, A. Stebbins, S. W. Nye Jr, A. Honig, et al. 2018. Ocean acidification alters morphology of all otolith types in Clark's anemonefish (*Amphiprion clarkii*). *PeerJ* 7:e6152.
- Howell, J., T. L. Goulet, and D. Goulet. 2016. Anemonefish musical chairs and the plight of the two-band anemonefish, *Amphiprion bicinctus. Environmental Biology of Fishes* 99:873–886.
- IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge.
- IUCN. 2012. *IUCN Red List Categories and Criteria: Version 3.1.* Second edition. Gland, Switzerland and Cambridge.
- IUCN Standards and Petitions Committee. 2019. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. http://www.iucnredlist.org/documents/RedListGuidelines .pdf (accessed February 2, 2022).
- Jones, A. M., S. Gardner, and W. Sinclair. 2008. Losing 'Nemo': Bleaching and collection appear to reduce inshore populations of anemonefishes. *Journal of Fish Biology* 73:753–761.
- Jones, G. P. 2015. Mission impossible: Unlocking the secrets of dispersal in coral reef fishes. In *Ecology of Fishes on Coral Reefs: The Functioning of an Ecosystem in a Changing World*, ed. C. Mora, 16–27. Cambridge: Cambridge University Press.
- Jones, G. P., G. R. Almany, G. R. Russ, P. F. Sale, R. S. Steneck, M. J. H. van Oppen, and B. L. Willis. 2009. Larval retention and connectivity among populations of corals and reef fishes: History, advances and challenges. *Coral Reefs* 28:307–325.
- Jones, G. P., M. J. Caley, and P. L. Munday. 2002. Rarity in coral reef fish communities. In *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem*, ed. P. F. Sale, 81–101. San Diego, CA: Academic Press.
- Liu, P. J., M. C. Hsin, Y. H. Huang, T-Y. Fan, P-J. Meng, C-C. Lu, and H-J. Lin.2015. Nutrient enrichment coupled with sedimentation favors sea anemones over corals. *PLOS ONE* 10(4): e0125175.
- Lönnstedt, O. M., and A. J. Frisch. 2014. Habitat bleaching disrupts threat responses and persistence in anemonefishes. *Marine Ecology Progress Series* 517:265–270.

- Madduppa, H. H., J. Timm, and M. Kochzius. 2018. Reduced genetic diversity in the clown anemonefish Amphiprion ocellaris in exploited reefs of Spermonde Archipelago, Indonesia. *Frontiers in Marine Science* 5:80.
- Madduppa, H. H., K. von Juterzenka, M. Syakir, and M. Kochzius. 2014. 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.
- Maison, K. A., and K. S. Graham. 2016. Status Review Report: Orange Clownfish (Amphiprion percula). NOAA Technical Memorandum NMFS-PIFSC-52.
- Malcolm, H. A. C., and A. Scott. 2017. Range extensions in anemonefishes and host sea anemones in eastern Australia: Potential constraints to tropicalisation. *Marine and Freshwater Research* 68:1224–1232.
- McClanahan, T. R. 1994. Endemic survives adversity. Coral Reefs 13:104.
- McClanahan, T., V. Munbodhe, J. Naggea, N. Muthiga, and R. Bhagooli. 2021. Rare coral and reef fish species status, possible extinctions, and associated environmental perceptions in Mauritius. *Conservation Science and Practice* 2021:e527.
- McClenachan, L., A. B. Cooper, K. E. Carpenter, and N. K. Dulvy. 2012. Extinction risk and bottlenecks in the conservation of charismatic marine species. *Conservation Letters* 5:73–80.
- McLeod, I. M., J. L. Rummer, T. D. Clark, G. P. Jones, M. I. McCormick, A. S. Wenger, P. L. Munday. 2013. Climate change and the performance of larval coral reef fishes: The interaction between temperature and food availability. *Conservation Physiology* 1:cot024.
- Militz, T. A., S. Foale, J. Kinch, and P. C. Southgate. 2018. Natural rarity places clownfish colour morphs at risk of targeted and opportunistic exploitation in a marine aquarium fishery. *Aquatic Living Resources* 31:18.
- Miller, G. M., F. J. Kroon, S. Metcalfe, and P. L. Munday. 2015. Temperature is the evil twin: Effects if increased temperature and ocean acidification on reproduction in a reef fish. *Ecological Applications* 25:603–620.
- Miller, G. M., S. A. Watson, M. I. McCormick, and P. L. Munday. 2013. Increased CO<sub>2</sub> stimulates reproduction in a coral reef fish. *Global Change Biology* 19:3037–3045.
- Moat, J. 2020. rCAT: Conservation Assessment Tools. R package version 0.1.6. https://CRAN.R-project.org/package=rCAT (accessed February 2, 2022).
- Munday, P. L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* 10:1642–1647.
- Munday, P. L., D. L. Dixson, J. M. Donelson, G. P. Jones, M. S. Pratchett, G. V. Devitsina, and K. B. Døving. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Science* 106:1848–1852.
- Munday, P. L., D. L. Dixson, M. I. McCormick, M. Meekan, M. C. O. Ferrari, and D. P. Chivers. 2010. Replenishment of fish populations is threatened by ocean acidification. *Proceedings of the National Academy of Sciences* 107(29):12930–12934.
- Munday, P. L., D. L. Dixson, M. J. Welch, D. P. Chivers, P. Domenici, M. Grosell, R. M. Heuer, et al. 2020. Methods matter in repeating ocean acidification studies. *Nature* 586:E20–E24.
- Munday, P. L., M. D. Jarrold, and I. Nagelkerken. 2019. Ecological effects of elevated CO2 on marine and freshwater fishes: From individual to community effects. In *Fish Physiology*, *Vol. 37*, eds Grosell, M., Munday, P. L., Farrell, A. P., and C. J. Brauner, 323–368. Amsterdam: Elsevier Inc.

- Munday, P. L., G. P. Jones, M. S. Pratchett, and A. J. Williams. 2008. Climate change and the future for coral reef fishes. *Fish and Fisheries* 9:261–285.
- Nanninga, G. B., P. Saenz-Agudelo, P. Zhan, L. Hoteit, and M. L. Berumen. 2015. Not finding Nemo: Limited reef-scale retention in a coral reef fish. *Coral Reefs* 34:383–392.
- Nilsson, G. E., D. L. Dixson, P. Domenici, M. I. McCormick, C. Sørensen, S-A. Watson, and P. L. Munday. 2012. Nearfuture carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nature Climate Change* 2(3):201–204.
- Norin, T., S. C. Mills, A. Crespel, D. Cortese, S. S. Killen, and R. Beldade. 2018. Anemone bleaching increases the metabolic demands of symbiont anemonefish. *Proceedings of the Royal Society B* 285:20180282.
- Nowicki, J. P., G. M. Miller, and P. L. Munday. 2012. Interactive effects of elevated temperature and CO<sub>2</sub> on foraging behavior of juvenile coral reef fish. *Journal of Experimental Marine Biology and Ecology* 412:46–51.
- Okemwaa, G. M., B. Kaunda-Arara, E. N. Kimani, and B. Ogutu. 2016. Catch composition and sustainability of the marine aquarium fishery in Kenya. *Fisheries Research* 183:19–31.
- Olivotto, I., and B. Geffroy. 2017. Clownfish. In Marine Ornamental Species Aquaculture, First Edition, eds R. Calado, I. Olivotto, M. P. Oliver and G. J. Holt, 177–199. Hoboken, NJ: John Wiley & Sons Ltd.
- Ollerton, J., D. McCollin, D. G. Fautin and G. R. Allen. 2007. Finding NEMO: Nestedness engendered by mutualistic organization in anemonefish and their hosts. *Proceedings* of the Royal Society B 274:591–598.
- Pryor, S. H., R. Hill, D. L. Dixson, N. J. Fraser, B. P. Kelaher, and A. Scott. 2020. Anemonefish facilitate bleaching recovery in a host sea anemone. *Scientific Reports* 10:18586.
- R Core Team. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (accessed February 2, 2022).
- Rabinowitz, D. 1981. Seven forms of rarity. In *The Biological Aspects of Rare Plant Conservation*, ed. H. Synge, 205–217. New York: John Wiley & Sons Ltd.
- Rauch, S. D. III. 2015. Endangered and threatened wildlife and plants; Notice of 12-month finding on a petition to list the orange clownfish as threatened or endangered under the Endangered Species Act. *Federal Register* 80:51235–51247.
- Roberts, C. M., and J. P. Hawkins. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution* 14:241–246.
- Roelofs, A., and R. Silcock. 2008. A Sustainability Assessment of Marine Fish Species Collected in the Queensland Marine Aquarium Trade. Brisbane, QLD: Department of Primary Industries and Fisheries.
- Saenz-Agudelo, P., G. P. Jones, S. R. Thorrold, and S. Planes. 2011. Detrimental effects of host anemone bleaching on anemonefish populations. *Coral Reefs* 30:497–506.
- Salles, O. C., G. R Almany, M. L. Berumen, G. P. Jones, P. Saenz-Agudelo, M. Srinivasan, S. R. Thorrold, et al. 2020. Strong habitat and weak genetic effects shape the lifetime reproductive success in a wild clownfish population. *Ecology Letters* 23:265–273.

- Salles, O. C., B. Pujol, J. A. Maynard, G. R. Almany, M. L.Beruman, G. P. Jones, P. Saenz-Agudelo, et al. 2016. First genealogy for a wild marine fish population reveals multi-generational philopatry. *Proceedings of the National Academy of Science* 113:13245–13250.
- Sato, M., K. Honda, W. H. Uy, D. I. Baslot, T. G. Genovia, Y. Nakamura, L. P. C. Bernardo, et al. 2017. Marine protected area restricts demographic connectivity: Dissimilarity in a marine environment can function as an ecological barrier. *Ecology and Evolution* 7:7859–7817.
- Scott, A., and A. H. Baird. 2015. Trying to find Nemo: Low abundance of sea anemones and anemonefishes on central and southern mid-shelf reefs in the Great Barrier Reef. *Marine Biodiversity* 45:327–331.
- Scott, A., H. A. Malcolm, C. Damiano, and D. L. Richardson. 2011. Long-term increases in abundance of anemonefish and their host anemones in an Australian marine protected area. *Marine and Freshwater Research* 62:187–196.
- Scott, A., K. J. W. Rushworth, S. J. Dalton, and S. D. A. Smith. 2016. Subtropical anemonefish *Amphiprion latezonatus* recorded in two additional host sea anemone species. *Marine Biodiversity* 46:327–328.
- Shuman, C. S., G. Hodgson, and R. F. Ambrose. 2005. Population impacts of collecting sea anemones and anemonefish for the marine aquarium trade in the Philippines. *Coral Reefs* 24:564–573.
- Simpson, S. D., P. L. Munday, M. L. Wittenrich, R. Manassa, D. L. Dixson, M. Gagliano, and H. Y. Yan. 2011. Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biology Letters* 7:917–920.
- Srinivasan, M. 1997. Ecology and Life-Histories of Anemonefishes: A Multi-Scale Study of Patterns and Processes. BSc Honours thesis, James Cook University.
- Srinivasan, M., G. P. Jones, and M. J. Caley. 1999. Experimental evaluation of the roles of habitat selection and interspecific competition in determining patterns of host use in two anemonefishes. *Marine Ecology Progress Series* 186:283–292.
- Steinberg, R., M. van der Meer, E. Walker, M. L. Berumen, J.-P. A. Hobbs, and L. van Herwerden. 2016. Genetic connectivity and self-replenishment of inshore and offshore populations of the endemic anemonefish, *Amphiprion latezonatus*. *Coral Reefs* 35: 959–970.
- Steinberg, R. K., M. H. van der Meer, M. S. Pratchett, L. van Herwerden, and J. P. A. Hobbs. 2020. Keep your friends close and your anemones closer – ecology of endemic wideband anemonefish, *Amphiprion latezonatus*. *Environmental Biology of Fishes* 103:1513–1526.
- Timm, J., M. Figiel, and M. Kochzius. 2008. Contrasting patterns in species boundaries and evolution of anemonefishes (Amphiprioninae, Pomacentridae) in the centre of marine biodiversity. *Molecular Phylogenetics and Evolution* 49:268–276.
- van der Meer, M. H., J. P. A. Hobbs, G. P. Jones, and L. van Herwerden. 2012. Genetic connectivity among and selfreplenishment within island populations of a restricted range subtropical reef fish. *PLOS One* 7: e49660.
- Wabnitz, C., M. Taylor, E. Green, and T. Razak. 2003. From Ocean to Aquarium: The Global Trade in Marine Ornamental Species. Cambridge: UNEP-WCMC.

- Wenger, A. S., K. E. Fabricius, G. P. Jones, and J. E. Brodie. 2015. Sedimentation, eutrophication and pollution: Effects on coral reef fishes. In *Ecology of Fishes on Coral Reefs: The Functioning of an Ecosystem in a Changing World*, ed. Mora, C., 145–153. Cambridge: Cambridge University Press.
- Wenger, A. S., M. I. McCormick, G. G. K. Endo, I. M. McLeod, F. Kroon, and G. P. Jones. 2014. Suspended sediment alters larval development in a coral reef fish. *Journal of Experimental Biology* 217:1122–1128.
- Wenger, A. S., C. A. Rawson, S. Wilson, S. J. Newman, M. J. Travers, S. Atkinson, N. Browne, et al. 2017. Management strategies to minimize the dredging impacts of coastal development on fish and fisheries. *Fish and Fisheries* 18:967–985.
- Zhang, D. 2021. *rsq: R-Squared and Related Measures*. R package version 2.2. https://CRAN.R-project.org/package=rsq (accessed February 2, 2022).

