Research article

Hydrodynamics rather than type of coastline shapes self-recruitment in anemonefishes

Authors

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Abstract
Many marine species have a pelagic larval phase that undergo dispersal among habitats. Studies on marine larval dispersal have revealed a large variation in the spatial scale of dispersal and self-recruitment. However, few studies have investigated the influence of types of coastline (e.g., bay vs. open coast) on marine larval dispersal. Bays or lagoons generally enhance the retention of larvae, while larvae are more likely to be flushed by strong currents in open coasts. To examine associations between larval dispersal, coastline type, and hydrodynamics, we compared fin-scale dispersal patterns, self-recruitment, and local retention of two anemonefishes (*Amphiprion frenatus* and *A. perideraion*) between a semi-enclosed bay and an open coast in the Philippines combining genetic parentage analysis and biophysical dispersal modelling. Contrary to our expectations, parentage analysis revealed lower estimates of self-recruitment in the semi-closed bay (0%) than in the open coast (14–15%). The result was consistent with dispersal simulations predicting lower local retention and self-recruitment in the semi closed bay (0.4% and 19%) compared to the open coast (2.9% and 38%). Dispersal modelling also showed that cross-shore currents toward offshore were much stronger around the semi-closed bay and were negatively correlated with local retention and self-recruitment. These results suggest that stronger cross-shore currents around the semi-closed bay transport anemonefish larvae to the offshore and mainly contributed to the lower self-recruitment. Our results highlight importance of hydrodynamics on larval dispersal and difficulty in predicting self-recruitment from coastline type alone.

Keywords: Bay, Biophysical model, Coral reef fish, Larval dispersal, Open coast, Parentage analysis,

Introduction

Many marine species have life cycles with a pelagic larval phase that undergoes dispersal among habitat patches, and a benthic adult phase that occurs in discrete habitat patches after larval settlement (Jones et al., 2009). Marine larvae are subjected to oceanographic processes that transport them at varying distances from their original birthplace (Cowen and Sponaugle, 2009). Additionally, their behavior affects the success of dispersal and settlement (Paris and Cowen, 2004). Quantifying the dispersal patterns of marine species is essential for predicting population dynamics and managing marine populations.

The application of genetic parentage analysis to marine systems has contributed significantly to clarifying dispersal patterns of coral reef fishes (e.g., Jones et al., 2005; Saenz-

Agudelo et al., 2011; D'Aloia et al., 2013). Comparisons of marine dispersal estimates using this method revealed a large variation in the spatial scale of dispersal in coral reef fishes. For example, estimates of dispersal distance ranged from less than 50 m to 35 km for *Amphiprion spp.*, and from 1 to 48 km for *Chaetodon vagabundus* (Saenz-Agudelo et al., 2012; Abesamis et al., 2017). Marine dispersal studies have also shown a rapid decline in the probability functions of dispersal success within the first few kilometers especially for *Amphiprion* (Buston et al., 2012; Saenz-Agudelo et al., 2012). Larval recruitment to the natal patch is often measured in two ways: self-recruitment and local retention (Nanninga et al., 2015). Self-recruitment denotes the fraction of all incoming recruits to a specific patch produced at that patch, whereas local retention describes the fraction of all larvae produced at a focal patch returning to that patch (Fig. S1) (Botsford et al., 2009). Because of the inherent nature of what is measured using parentage analysis (i.e., the fraction of all recruits that have been produced by local parents), empirical studies typically report estimates of self-recruitment, ranging from 0 to 65% for coral reef fishes (Saenz-Agudelo et al., 2011; D'Aloia et al., 2013; Nanninga et al., 2015). At the same time, it is difficult to inform population persistence from self-recruitment because it contains no information about replacement of adults by recruitment (Burgess et al. 2014). For population persistence, a single local population will persist if each adult, on average, is replaced by one self-recruit or immigrant during its lifetime. Calculating such a replacement measure is useful to inform population persistence and MPA designs.

Although seascape patchiness is known to be an important factor for predicting the self-recruitment of marine larvae (Pinsky et al. 2012), types of coastline (e.g., open coast vs. bay) and associated water circulation can also influence larval transport and dispersal patterns in marine organisms. Bays or lagoons generally have restricted connections to the open sea and exhibit long residence times of water (Kjerfve and Magill, 1989; Sponaugle and Cowen, 2002), which may enhance the local retention and self-recruitment of larvae. Meanwhile, pelagic larvae are flushed by strong currents and can be easily dispersed or transported far away along open coasts (Swearer and Shima, 2010; Huebert et al., 2011). This leads to a simple prediction that the local retention and self-recruitment are expected to vary between the distinct types of coastline, whereas such a prediction may be an oversimplification due to interactions of complex topography and hydrodynamics in coastal areas.

Hydrodynamic models verified using oceanographic data have been used as a basis for larval dispersal simulations (Cowen et al., 2007; Werner et al., 2007; Cowen and Sponaugle, 2009). Recent dispersal models integrate biological characteristics of larvae such as larval mortality, competency period, and migration behavior (Cowen et al., 2006; Nanninga et al., 2015; Treml et al., 2015). Such models are especially effective for exploring larval dispersal processes when combined with field/empirical methods (Werner et al., 2007). Meanwhile, most studies have used genetic differentiation measures as empirical estimates of larval dispersal (White et al.,

2010; Nakajima et al., 2014; Hawkins et al., 2019), but such measures indicate averaged population connectivity across generations over evolutionary timescales. In contrast, genetic parentage analysis enabled us to clarify fine-scale patterns of larval dispersal over ecological time scales, whereas there are still few integrations of this approach with hydrodynamic model (but also see, Nanninga et al., 2015, Bode et al., 2019). Comparing the modeling and empirical results of ecological measures of larval dispersal, both consistencies and mismatches between them provide insights into the mechanisms influencing larval dispersal.

In this study, we compared the dispersal patterns, self-recruitment, replacement measures, and local retention of two anemonefishes (*Amphiprion frenatus* and *A. perideraion*) between a semi-enclosed bay and an open coast located using genetic parentage analysis and biophysical modeling. Anemonefish have been widely used as model species for genetic parentage analysis, mainly because they are easily located and can be caught underwater through use of SCUBA as well as their relatively short pelagic larval duration makes it easy to elucidate local dispersal patterns (e.g., Planes et al. 2009; Sato et al. 2017). Sato et al. (2017) showed the dispersal patterns and self-recruitment of the two species on the open coast of the Philippines. The present study empirically estimated the dispersal patterns and self-recruitment in the semi-enclosed bay in the same country for comparison. Biophysical models were then developed to simulate larval dispersal and calculated local retention and self-recruitment of the two anemonefishes in the two sites. The following questions were addressed: (1) Is there variation in self-recruitment estimates of parentage analysis between a semi-enclosed bay and an open coast? (2) Does the larval dispersal simulation using a biophysical model confirm empirical estimates of parentage analysis? (3) How is hydrodynamics related to larval dispersal patterns?

Materials

Study species and study sites

Our target species were the tomato anemonefish (*Amphiprion frenatus*) and the pink anemonefish (*A. perideraion*), which occur throughout the eastern Indian Ocean to the western Pacific Ocean. The two study sites are situated on fringing reefs around Puerto Galera (13°30’N, 120°57’E) in the Verde Island Passage and around Laguindingan (8°38’N, 124°28’E) in the southern Bohol Sea, Philippines (Fig. 1) (Sato et al., 2014a, 2017). Puerto Galera has a semi-enclosed bay, which connects to the passage via two channels, that is, the Manila Channel in the northwest and the Batangas Channel in the northeast, while Laguindingan has an open coast facing the Bohol Sea. The study area of both sites is part of a marine protected area (MPA) that is strongly protected against fishing activity (Honda et al. 2016, Sato et al., 2014a, 2017).

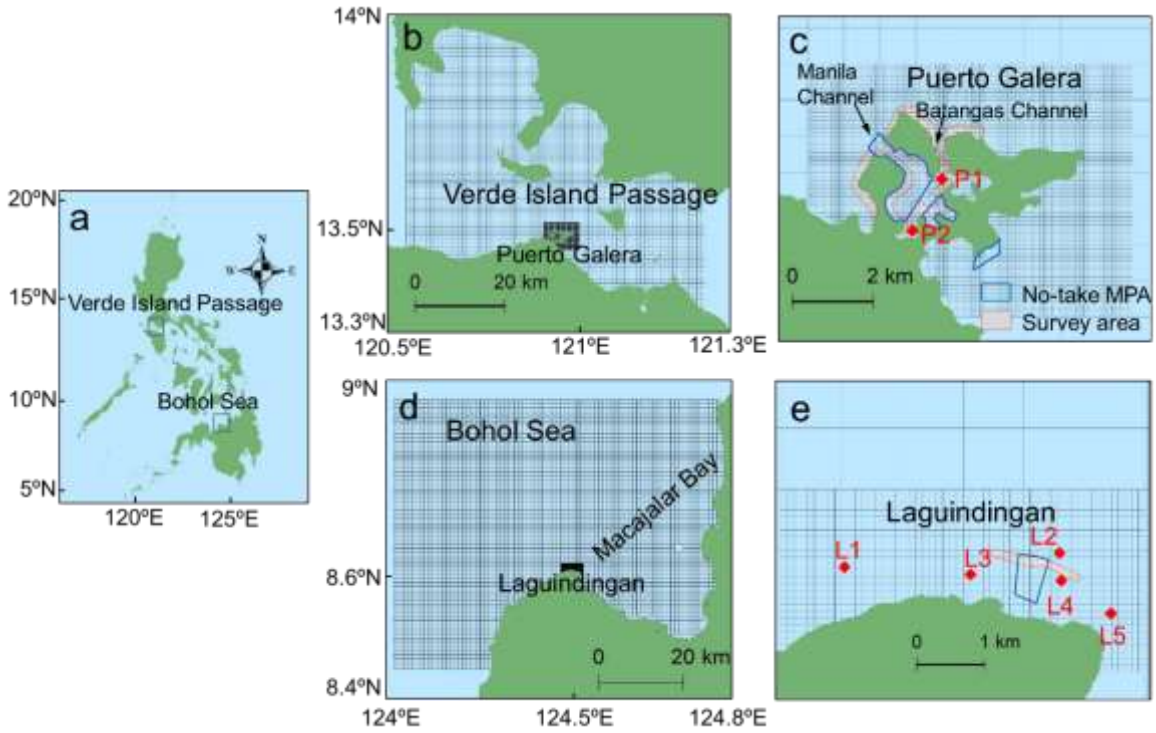

Fig. 1 **a** Map of the Philippines. **b**–**c** Modeled domains of the Verde Island Passage and semi-enclosed bay of Puerto Galera (meshed grids) with sensor array locations (red diamond: P1 and P2). **d**–**e** Modeled domains of the Bohol Sea and open coast of Laguindingan (meshed grids) with sensor array locations (red diamond: L1–L5). The outer and inner domains of both models have a cell size of 900 m and 100 m, respectively. The locations of MPAs, survey areas, prominent embayment, and channels are also indicated.

Field collection of genetic samples

A previous study estimated the larval dispersal and self-recruitment of the target anemonefishes in the open coast of Laguindigan (Sato et al. 2017), whereas the present study investigated their dispersal patterns in the semi-closed bay of Puerto Galera for comparison (Fig. 1). In June 2012, we conducted a preliminary survey by snorkeling on coral reefs in Puerto Galera to record the location of anemonefish and host anemones (Sato et al., 2014). A GPS device (Garmin eTrex 30) was used to determine the locations. On the basis of the location data, we captured anemonefish using hand-nets and clove oil and measured their TL to the nearest mm underwater using SCUBA in September 2012. We basically targeted a pair of the two largest fish in each habitat whose total length (TL) was longer than the minimum mature size of each species (≥80 mm for *A. frenatus* female and ≥46 mm for its male, ≥57 mm for *A. perideraion* female and >39 mm for its male; Hattori, 1991, 2000) as "breeders". When only the one largest fish reached the mature size in a habitat, we also collected the individual as "a single breeder". This resulted in the prevalence of single breeders in our samples, but we retained such breeders because there

is a possibility that we might miss their reproduction pair due to its death. Anemonefish were fin clipped using scissors and then released back into the same host sea anemone. Individuals <30 mm TL (≤30 mm TL) were also targeted as "juveniles" for both species and those that were too small to be fin clipped (<30 mm) were collected. To avoid the danger of boat strikes, we did not collect the samples within the eastern cove of Puerto Galera Bay, which was utilized as a yacht harbor. Based on the classification described above, we sampled 48 juveniles and 134 breeders from 86 host anemones for *A. frenatus* as well as 17 juveniles and 69 breeders from 51 host anemones for *A. perideraion* in the study area of Puerto Galera (863,053 m^2) in September 2012 (Fig. 2, Table 1). This practice resulted in 94.4% and 95.8% of breeder pairs, 100.0% and 92.3% of single breeders as well as 100.0% and 94.4% juveniles collected within the study area of Puerto Galera for the respective species. A previous study estimated that 30 mm *Amphiprion* are approximately three to four months old, respectively (Ochi, 1986). Therefore, the collected juveniles (<30 mm) were predicted to disperse from May to September mainly during the Southwest monsoon.

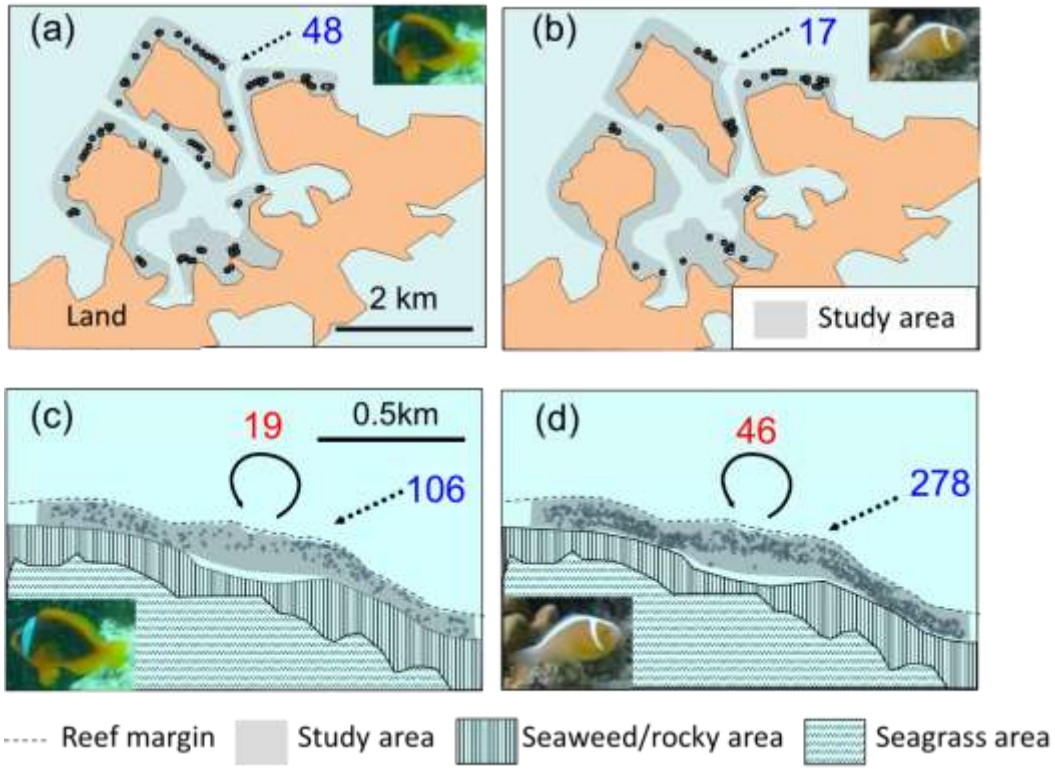

Fig. 2 **a-d** Maps showing the location of host anemones of **a** *Amphiprion frenatus* and **b** *A. perideraion* in the study area of Puerto Galera and that of **c** *A. frenatus* and **d** *A. perideraion* in the study area of Laguindingan. Dispersal tracks of self-recruits and its individual number are shown by an arrow and red number, while immigrants from the outside and its individual number are shown by dashed arrows and blue numbers. The maps of Laguindingan were modified from Sato et al. (2017).

Also, we briefly describe the field collection of genetic samples in Laguindingan (Sato et al. 2017). A preliminary survey was conducted by snorkeling in November 2012 to record the location of anemonefish and host anemones. On the basis of this location data, we collected a total of 125 juveniles and 251 breeders for *A. frenatus* and 324 juveniles and 548 breeders for *A. perideraion* in the study area of Laguindingan (139,019 m^2) during the field survey from May to July 2013 (Fig. 2, Table 1).We prioritized collecting breeder pairs and juveniles, a practice that resulted in 97.4% and 99.2% of breeder pairs, 65.3% and 48.4% of single breeders as well as 96.9% and 94.7% juveniles collected within the study area for the respective species (Table 1). We predict that the collected juveniles (<30 mm) in Laguindingan dispersed in both Northeast (February to April 2013) and Southwest Monsoon (May to July 2013) seasons.

To estimate the pelagic larval duration of each species, lapilli otoliths were dissected from the subsamples of 5 juveniles per species in Puerto Galera. The pelagic larval duration of each fish was determined by counting the number of daily increments of the otolith using an otolith measurement system (Ratoc System Engineering Inc.; www.ratoc.com). Pelagic larval durations were estimated to be 7–14 days for *A. frenatus* and 8–15 days for *A. perideraion* (n = 5 for each).

Table 1. Survey area, individual number of collected anemonefish, density, proportion of collected individuals, self-recruitment, and replacement measures for two anemonefish species (*Amphiprion frenatus* and *A. perideraion*) at Puerto Galera and Laguindingan.

Site	Species	Survey area (m^2)	Density of anemonefish (ind./100m^2)	Proportion of collected breeder pairs (%)	Proportion of collected single breeder (%)	Proportion of collected juveniles (%)	Self-recruitment of juveniles (%)	Self-replacement	Immigrant-replacement	Source
Puerto Galera	*A. frenatus*	863053	0.02	94.4	100	100	0 (0/48)	0 (0/134)	0.36 (48/134)	This study
	A. perideraion	863053	0.01	95.8	92.3	94.4	0 (0/17)	0 (0/69)	0.25 (17/69)	This study
Laguindingan	*A. frenatus*	139019	0.33	97.4	65.3	96.9	15.2 (19/125)	0.08 (19/251)	0.42 (106/251)	Sato et al. (2017)
	A. perideraion	139019	0.87	99.2	48.4	94.7	14.2 (46/324)	0.08 (46/548)	0.51 (278/548)	Sato et al. (2017)

Parentage analysis

We extracted genomic DNA, amplified fragments, and sequenced and scored them according to Sato et al. (2014b). The individuals were genotyped using same 14 microsatellite loci for *A. frenatus* and 15 loci for *A. perideraion* with Sato et al (2017) (Table S1, see Supplemental Information). We conducted a genetic parentage analysis for Puerto Galera samples to identify self-recruits of each target species using the program COLONY v. 2.0.6.4 (Jones and Wang, 2010). This program implements a full-likelihood parentage analysis method and defines the priori probability that the true parent is present in the samples. COLONY is robust to uncertainty in the sampling rate of true parentage and has been shown to outperform other programs (Harrison et al. 2013). We used 0.10 as a sampling proportion for both species as in Sato et al. (2017). Other settings for the analysis in COLONY were also same with Sato et al. (2017) as follows: full-likelihood method, medium run length, medium probability precision, no inbreeding, and assumed monogamy for both sexes. We informed our COLONY runs with allele frequencies estimated from the sampled individuals. To assess the information sufficiency of our markers for the accurate reconstruction of parental assignment, we also used the simulation module in COLONY (see Supplemental Information).

Parentage analyses were run to test the pool of juveniles (n = 48 for *A. frenatus* and n = 17 for *A. perideraion*) against candidate mothers (n = 68 for *A. frenatus* and n = 28 for *A. perideraion*) and fathers (n = 66 for *A. frenatus* and n = 41 for *A. perideraion*), with a mistyping rate of 1 % to account for genotyping errors. We only accepted parentage assignments with a probability of > 0.9 (Sato et al. 2017).

Once the assignment was made, we regarded assigned juveniles as self-recruits in the study site, and remaining juveniles as immigrants from outside of the study site, calculating the self-recruitment as follows:

$$\text{Self-recruitment} = \frac{S}{S+I}$$

where S was the number of settlers assigned to breeders in the study site (self-recruits) and I was the number of settlers not assigned to the breeders (immigrants) (Fig. S1). According to Burgess et al (2014), we also calculated replacement of breeders by self-recruits as self-replacement to infer self-persistence of the target populations as follow:

$$\text{Self-replacment} = \frac{S}{P}$$

where P was the number of breeders at the populations (Fig. S1). Based on the same idea, immigrant-replacement was also defined as replacement of breeders by immigrants and reported to infer population persistence though immigration as follow:

$$\text{Immigrant-replacment} = \frac{I}{P}$$

Because all collected juveniles were younger than four-month-olds, self-replacement and immigrant-replacement indicate replacement of breeders by juveniles over four-month period.

Hydrodynamic model

Using Delft3D-Flow, a 3D-capable hydrodynamic simulation program (Deltares, 2014a), we developed two hydrodynamic models, i.e., the Puerto Galera model extending from 13.38 to 13.93 N and from 120.62 to 121.26 E, and the Laguindingan model extending from 8.41 to 8.99 N and from 124.07 to 124.78 E (Fig. 1). Both models were comprised of two computational domains using one-way nesting technique to properly incorporate the effects of the complicated topographic setup and tidal fluctuation. For the Puerto Galera model, the Verde Island Passage

area was an outer domain with a cell size of 900 m and the Puerto Galera domain with a cell size of 100 m was the inner domain. For the Laguindingan model, the Bohol Sea area was an outer domain with a cell size of 900 m, and the Laguindingan area with a cell size of 100 m was the inner domain. Thirteen and fifteen vertical Z-layers were used for Puerto Galera and Laguindingan models, respectively. The General Bathymetric Chart of the Oceans (GEBCO: http://www.gebco.net/) data were supplemented with the past bathymetry data and echo sounder measurements in both areas, where coral reefs make topography highly variable. Open water boundaries for both models were forced with tidal variation derived from the PH model (Pokavanich 2009) and with salinity and water temperature from JCOPE2 (Miyazawa et al., 2009) and Hybrid Coordinate Modeling System analysis data (HYCOM GLBu0.08) (https://hycom.org/dataserver/glb-analysis). The water surface was forced with a spatially uniform wind, ocean heat exchange, and precipitation.

The Puerto Galera model simulation was run with the forcing conditions from February 1 to September 30, 2012, with a spin-up period of one month while the Laguindingan model was simulated from January 1 to July 31, 2013, with the same spin-up period. The time step was set to 6 s for both models. Details of the hydrodynamic models and evaluation of model performance were provided in Supplemental Information (Figs. S2, S3, and Table S2).

Larval dispersal simulation

We performed larval dispersal simulations for anemonefish at the two sites using Delft3D-PART (Deltares, 2014b). PART computed the position of every individual particle by advection and diffusion, and simulated transport processes by means of a particle-tracking method using flow data from the FLOW module. The processes were assumed to be deterministic except for a random displacement of the particle at each time step. Time step for the particle-tracking calculation was set to 30 minutes. PART simulated larval dispersal from the study site and external surrounding sources into the focal area of the study site in each model domain. The main model output of interest was local retention (the fraction of all released particles from the study site that settled back to there) and self-recruitment (the proportion of settling particles that are derived from study site) for each study site (Fig. 1).

Based on the spawning biology of *Amphiprion* and the expected hatching period for the collected juvenile (<30 mm) in both sites, we started the particle releases on the day of spring tide four months prior to the sample collection (9 spring tides for Puerto Galera and 11 spring tides for Laguindingan). Based on the distance at which 90 % of anemonefish larvae recruit (17.6 km) as estimated by Catalano et al. (2021), we utilized the 20 km radius to set source sites around each study site. In the Puerto Galera model, a total of 75,600 particles were released from 84 locations (100 particles × 9 spring tides × 84 locations) along the shore within a radius of 20 km from the anemonefish survey area in Puerto Galera. Meanwhile, in the Laguindingan model, we released 33,000 particles from 30 locations (100 particles × 11 spring tides × 30 locations) along the shore within a radius of 20 km from the survey area of Laguindingan.

Because biological traits of larvae affect dispersal, we assessed the model's sensitivity to different biological parameter inputs according to Nanninga et al. (2015). Six parameters were examined for their effect on local retention and self-recruitment: larval duration [11 (±4) days], competency [6 days (±2)], horizontal sensory zone [1 (+1/–0.5) km radius], larval mortality [half-life of 6 (±2) days], number of particle releases from the study site [100 particle releases (+100 particles/–50 particles) per source location], and vertical migration behavior (passive and empirical). Biological input values of anemonefishes were derived from the literature, and the measurement of target species or closely related species (see, Supplemental Information).

Comparisons of hydrodynamic characteristics between Puerto Galera and Laguindingan

To compare hydrodynamic characteristic between Puerto Galera and Laguindingan, we made boxplots of the velocity magnitude, East–West (E–W), and North–South (N–S) velocities of modeling results in each site in the same season (from May to July). The velocity magnitude, as well as the E–W and N–S velocities were averaged for the period from each date of particle releases (day 0) to start of settling (day 6) in the same season at all the grids of each inner domain. Then, these values were averaged over these grids and used for making the plots [n = 6 (6 spring tides) for Puerto Galera and n = 5 (5 spring tides) for Laguindingan]. We also compared local retention and self-recruitment values of the original scenario for particle releases during the period from May to July between Puerto Galera [n =18 (6 spring tides × 3 replicates)] and Laguindingan [n =15 (5 spring tides × 3 replicates)]

Influences of hydrodynamics on local retention and self-recruitment

To examine influences of hydrodynamics on local retention and self-recruitment, a multiple regression analysis was conducted using the simulation results of Delft 3D-flow and Delft3D-PART. We calculated 6 days-averaged residual velocity of vertically averaged flow at all grids in the inner domains of the Puerto Galera and Laguindingan models (9 spring tides for Puerto Galera and 11 spring tides for Laguindingan) (Figs. 1, S4, and S5). Then, those values were averaged over the all grids, and the North-South (N-S) and East-West (E-W) components were utilized for this analysis. We assessed the local retention and self-recruitment in relation to the mean N-S and E-W velocities using a generalized linear model. The local retention and self-recruitment for each date of particle release in the original simulation scenario of Delft3D-PART were utilized as dependent variables (9 spring tides × 3 replicates for Puerto Galera and 11 spring tides × 3 replicates for Laguindingan). For the analysis, a mixture of binomial and gamma distributions, which is called a gamma hurdle model," was used for both local retention and self-recruitment as in previous studies (Sato et al. 2021) because these values are continuous and contain zero values. We used BIC weight to average each model parameter found within the model set (Burnham and Anderson, 2004). This model averaging framework was adapted to estimate robust parameters (Johnson and Omland, 2004). We also obtained the relative importance of each variable by summing the BIC weights over all of the models in which the parameter of interest appears. All statistical analyses were performed using RStudio version 2023.03.0+386 (R version 4.2.2) with several packages.

Results

Parentage analysis

The parentage analysis of COLONY revealed that no *A. frenatus and A. perideraion* juveniles were assigned to breeders within the study area of Puerto Galera (Fig. 2) (Table 1). This result indicates that the percentages of self-recruitment in Puerto Galera was 0 % for both species (zero self-recruit/48 juveniles for *A. frenatus*; zero/17 juveniles for *A. perideraion*). Self-replacement was also 0.00 (zero self-recruit/134 breeders for *A. frenatus*; zero/69 breeders for *A. perideraion*) for both species, but immigrant-replacement was 0.36 and 0.25 (48 immigrants/134 breeders for *A. frenatus*; 17/69 breeders for *A. perideraion*) for respective species. *Sato et al.* (2017) showed that self-recruitment in Laguindingan were 15.2% (19 self-recruits/125 juveniles) for *A. frenatus* and 14.2% (46 self-recruits/324 juveniles) for *A. perideraion.* Based on these data, we calculated self-replacement as 0.08 (19 self-recruits/251 breeders for *A. frenatus*; 46/548 breeders for *A. perideraion*) for both species and immigrant-replacement as 0.42 and 0.51 (106 immigrants/251 breeders for *A. frenatus*; 278/548 breeders for *A. perideraion*) for respective species.

Comparisons of hydrodynamic characteristics between Puerto Galera and Laguindingan

During all the periods, the hydrodynamic model predicted strong northward and westward flows were in the eastern side and offshore of Puerto Galera, respectively, whereas flow speed was gradually reduced to the shallower waters of the inner domain (Fig. S4). On the contrary, strong eastward flows were predicted in the offshore of Laguindingan for the periods of May 25–31 and Jun 9–15, and relatively weak flows were found there for the remaining periods (Fig. S5). Flow speed was reduced to the shallower waters of the inner domain of Laguindingan as in the Puerto Galera model.

The magnitude and N-S velocity were higher in Puerto Galera than in Laguindingan during the same seasonal period, whereas the mean E–W velocity was higher in Laguindingan (Fig. 3a). Time-series water level had a bit of time gap, but the tidal amplitude was not so different between the two sites (Fig. 3b).

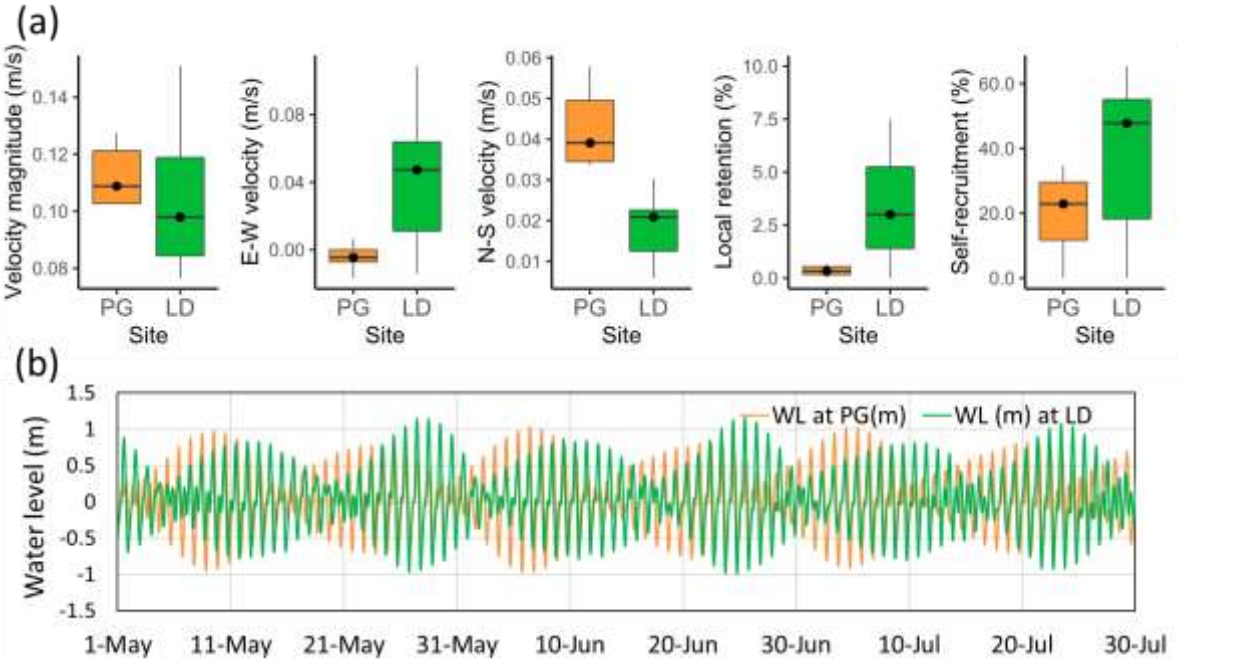

Fig. 3 (a) Boxplots of local retention, self-recruitment, velocity magnitude, East–West (E–W), and North–South (N–S) velocities as well as (b) time-series water level at Puerto Galera (PG) and Laguindingan (LD) from May to July in 2012 and 2013, respectively. These values were obtained from hydrodynamic and larval dispersal simulations of Delft3D-Flow and-Part.

Larval dispersal model

Larval dispersal simulation showed that local retention and self-recruitment were markedly higher in Laguindingan than in Puerto Galera. In the original simulation scenario (n = 3), the levels of local retention were 0.4 ± 0.1 % (mean ± SD) in the Puerto Galera model and 2.9 ± 0.2 % in the Laguindingan model, and those of self-recruitment were 19.0 ± 2.7 % and 37.9 ± 1.6 %, respectively. The Puerto Galera model predicted that only a small number of the particles from Puerto Galera were retained (17.9/4500), while a larger number of particles from the western side settled to Puerto Galera (71.9/30600), mainly contributing to a lower self-recruitment there (19.0 %) (Fig. S6 and Table S3). The Laguindingan model predicted that there were relatively a large number of particles from Laguindingan locally settled there (32.2/1100)

compared to those from the east (48.6/16500) and west (4.1/15400) (Fig. S7 and Table S3). This resulted in a higher self-recruitment [32.2 / (32.2+48.6+4.1) = 37.9 %] in Laguindingan than in Puerto Galera [17.9 / (17.9+4.4+71.9) = 19.0 %] during all the periods. This result was similar for the comparisons during the same month period (Fig. 3).

Individual parameter perturbation of biological traits had variable effects on simulated levels of local retention in Puerto Galera and Laguindingan (Table 2). Changes to settlement competency, sensory zone, mortality rate, or vertical migration led to variations in local retention. Combination of parameters that yielded the maximum level of local retention provided almost five-and two-times estimates (2.1 % and 5.3 %) of the original values (0.4 % and 2.9 %) in Puerto Galera and Laguindingan models, respectively; while that yielded minimum level did half and one fourth (0.2 % and 0.8 %) of the original estimates in respective models. Predicted self-recruitment in both models also varied largely through changes in the number of self-recruits and imports from surrounding sources according to different competency periods, sensory zones, number of particle releases from the study site, and vertical migration behavior (Table 2). Combination of parameters that yielded the maximum level of predicted self-recruitment provided about 2.5 and 1.5-times estimates (45.9 % and 57.0 %) of the original values (19.0 % and 37.9 %) in Puerto Galera and Laguindingan models, respectively; while that yielded minimum level did approximately a half and three fifth (8.9 % and 21.6 %) of the original estimates in respective models.

Table 2 Effects of individual parameter perturbation (IPP) on predicted local retention (LR) and self-recruitment (SR) at Puerto Galera and Laguindingan.

	Original value	IPP range	Negative IPP (%)			Positive IPP (%)		
				LR	SR		LR	SR
Puerto Galera (PG)								
Larval duration	11 day	±4day	7 d :	0.4	20.5	15 d :	0.4	20.0
Competency	6 day	±2day	4 d :	2.1	33.5	8 d :	0.2	17.5
Sensory zones	1km	+1 km/-0.5 km	0.5 km :	0.3	33.4	2 km :	0.6	21.3
Mortality	6 day	±2day	4 day :	0.3	20.4	8 day :	0.5	20.5
Vertical migration	Empirical migration	Passive migration	Passive :	0.4	45.9			
Number of particles*	100 particles	+100 particles/-50 particles	50 particles :	0.3	8.9	200 particles :	0.5	34.9
Parameter combination	n/a	Max/min retention potential	Min:	0.2	8.9	Max:	2.1	45.9
Laguindingan (LD)								
Larval duration	11 day	±4day	7 d :	2.9	39.0	15 d :	2.9	37.7
Competency	6 day	±2day	4 d :	5.3	26.7	8 d :	1.7	41.0
Sensory zones	1km	+1 km/-0.5 km	0.5 km :	2.8	63.3	2 km :	3.0	33.2
Mortality	6 day	±2day	4 day :	2.1	37.9	8 day :	3.5	37.7
Vertical migration	Empirical migration	Passive migration	Passive :	0.8	21.6			
Number of particles*	100 particles	+100 particles/-50 particles	50 particles :	2.8	22.7	200 particles :	3.2	57.0
Parameter combination	n/a	Max/min retention potential	Min:	0.8	21.6	Max:	5.3	57.0

To test model sensitivity, biological parameters of the Delft PART simulations were systematically perturbed for PG and LD models. Original values of LR at PG and LD were 0.4 ± 0.1 % and 2.9 ± 0.2 %, respectively, while those of SR at respective site were 19.0 ± 2.7 % and 37.9 ± 1.6 %. *We only perturbed number of particles releases from the focal areas in PG and LD. Refer to text for parameter descriptions.

Influences of hydrodynamics on local retention and self-recruitment

Multiple regression analysis indicated the continuous (gamma) portion of the mean E-W and N-S velocities, site factor, and the interaction term between the N-S velocity and site have high relative importance (RI > 0.50) for predicted local retention and self-recruitment (Table 3). The model averaging results showed that the local retention and self-recruitment were higher in Laguindingan than Puerto Galera and increased with increasing the mean E-W. Although there was no overlap in the N-S velocity between the two sites (-0.001−0.030 m/s in Laguindigan; 0.033−0.058 m/s in Puerto Galera), the analysis detected that the slopes of the relationship between the local retention or self-recruitment and the mean N-S velocity differed between the sites (Fig. 4). The local retention and self-recruitment decreased with increasing the N-S velocity in Laguindigan whereas the local retention almost unchanged and self-recruitment increased with increasing the N-S velocity in Puerto Galera.

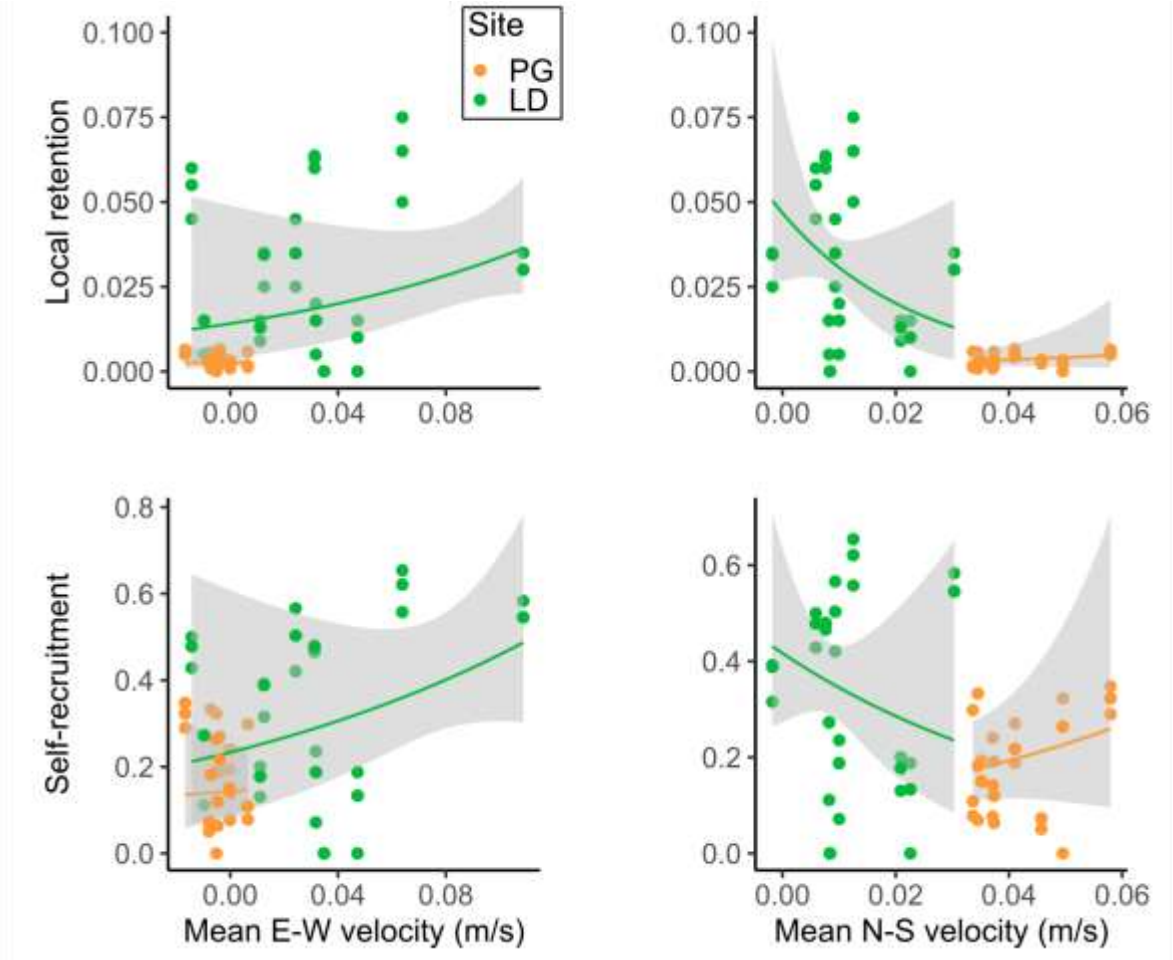

Fig. 4 Predicted local retention and self-recruitment in relation to mean E-W and N-S velocities based on larval dispersal and hydrodynamic simulations in Puerto Galera (PG) and Laguindingan (LD). The black line and gray shaded area (95% confidence interval) were estimated by averaging the model results and represents a strong relationship in which the variable showed high relative importance (>0.5).

Table 3 Model averaging results showing the averaged coefficients, standard errors (SE), and relative importance (RI) of parameters for the Gamma hurdle models, which examined the relationships between the predicted local retention or self-recruitment and current velocity measures.

Variables	Coefficient	SE	RI
Local retention			
Intercept[a]	-3.19	0.22	-
E-W velocity[a]	8.71	6.66	0.73
N-S velocity[a]	-42.20	31.26	0.75
Site (PG)[a]	-3.22	1.00	0.99
E-W velocity:Site (PG)[a]	-7.51	21.73	0.17
N-S velocity:Site (PG)[a]	60.33	47.09	0.68
zi(Intercept)[b]	-2.30	0.61	-
zi(E-W velocity)[b]	2.02	7.18	0.16
zi(N-S velocity)[b]	-2.43	17.06	0.14
zi(Site (PG))[b]	-0.39	292.57	0.20
zi(E-W velocity:Site (PG))[b]	2.25	7990.14	0.00
zi(N-S velocity:Site (PG))[b]	2.88	6706.82	0.00
Self-recruitment			
Intercept[a]	-0.98	0.17	-
E-W velocity[a]	6.76	5.83	0.72
N-S velocity[a]	-18.84	22.92	0.61
Site (PG)[a]	-1.38	0.81	0.96
E-W velocity:Site (PG)[a]	-3.28	12.04	0.14
N-S velocity:Site (PG)[a]	35.35	37.60	0.51
zi(Intercept)[b]	-2.30	0.61	-
zi(E-W velocity)[b]	-0.41	643.74	0.15
zi(N-S velocity)[b]	2.02	7.18	0.13
zi(Site (PG))b	-2.43	17.02	0.18
zi(E-W velocity:Site (PG))b	2.61	13433.61	0.00
zi(N-S velocity:Site (PG))b	3.24	14322.87	0.00

[a]Gamma portion of parameters. [b]Hurdle (binomial) portion of parameters.

Discussion

Using a combined approach of genetic parentage analysis and biophysical modelling, we investigated larval dispersal patterns of two anemonefishes in a semi-enclosed bay of Puerto Galera and open coast of Laguindingan in the Philippines. Although we expected higher self-recruitment in the semi-enclosed setting than in the open coast, results of genetic parentage analysis showed lower self-recruitment in the former than in the latter for two anemonefish species. This was qualitatively consistent with larval dispersal simulations by the biophysical model, which predicted lower local retention and self-recruitment in the semi-enclosed bay than in the open coast. Although our empirical and theoretical estimates of larval dispersal were inferred for about a half year, both results indicate that it is difficult to predict self-recruitment from coastline types (i.e., open coast vs. bay) alone and information of hydrodynamics is critical for it.

Genetic parentage analysis

Many empirical studies have estimated larval dispersal patterns and self-recruitment in coral reef fishes (Catalano et al., 2021; D'Aloia et al., 2013; Planes et al., 2009), but studies comparing dispersal patterns between different geographic sites are limited. We conducted genetic parentage analysis to compare larval dispersal patterns and self-recruitment between a semi-enclosed bay and open coast in the Philippines. Although we expected higher self-recruitment in the semi-enclosed bay of Puerto Galera than in the open coast of Laguindingan, our study obtained an opposite result: self-recruitment in Laguindingan (14–15 %) was higher than that in Puerto Galera (0 %) for two anemonefishes. Our previous research found no effect of patch isolation (mean distance from other anemones) on abundance of the two anemonefishes within the same area of Puerto Galera (Sato et al. 2014a). Present study confirmed that those results were due to no dispersal connectivity within the study area.

The study suffers from some weaknesses. First is the low sample size of collected samples at Puerto Galera. Since anemonefish density was quite lower at Puerto Galera than at Laguindingan (Table 1), we could not collect similar number of juveniles between the two sites (i.e., 48 *A. freanatus* and 17 *A. perideraion* juveniles at Puerto Galera; 125 and 324 juveniles at Laguindigan). Due to the small sample size in Puerto Galera, there can be uncertainty for the estimate of self-recruitment there. Nevertheless, we consider lower self-recruitment at Puerto Galera was not likely to be due to incomplete sampling of anemonefish there because we collected the genetic samples of the 95 % breeder pairs and 100 % single breeders in the study area (Table 1) even though we could not cover the eastern cove area of the bay. Second is the differences in the sampling timing and predicted larval dispersal periods between the sites (May to September for Puerto Galera and February to July for Laguindingan). Although the results of parentage analysis should be treated with some caution, comparisons of larval dispersal simulations for the same seasonal period (May to July) confirmed that predicted local retention and self-recruitment were also higher in Laguindingan than in Puerto Galera (Fig. 3). Our hydrodynamic simulation also showed the velocity magnitude and N-S velocity around Puerto Galera were higher than those off Laguindingan in the same season. Therefore, we infer that the general oceanographic features, which may be derived mainly from the local topography (e.g., strait, channel, and reef structure) rather than distinct types of coastline (open coast or bay), contributed to the contrasting self-recruitment values between them. Such a result was consistent with previous studies that showed that local oceanography was one of the most important determinants of self-recruitment and local retention (Treml et al., 2012).

Larval dispersal simulations

To examine whether the limited self-recruitment in Puerto Galera relative to Laguindingan is a result of low rates of larval retention or possibly due to an attenuation of self-recruitment estimates via high levels of larval imports from external habitats, we implemented a high-resolution biophysical dispersal model. Our larval dispersal simulations predicted a considerably lower proportion of larvae retained in Puerto Galera (local retention = 0.2–2.1%) than in Laguindingan (0.8–5.3%) under all parameters (Table 2). This lower value of local retention in Puerto Galera can be the main factor for the lower self-recruitment in Puerto Galera (8.9–45.9%) than in Laguindingan (21.6–57.0%). Multiple regression analysis showed that predicted local retention and self-recruitment were higher in Laguindingan than Puerto Galera and these values generally decreased with increasing the N-S velocity (Fig. 4). Northward currents face to the offshore in our study sites, and the stronger cross-shore flow may transport anemonefish larvae to the offshore. This would generally contribute to lower local retention in Puerto Galera, which had stronger N-S velocity (0.033−0.058 m/s) than Laguindingan did (-0.001−0.030 m/s). In Puerto Galera, however, the local retention almost unchanged and self-recruitment increased within its N-S velocity range. This is probably because a tiny proportion of larvae was consistently trapped in the Puerto Galera Bay irrespective of the N-S velocity, and larval imports from the external sources decreased with increasing this velocity (Fig. S6). This regression analysis also found predicted local retention and self-recruitment increased with increasing the E-W velocity, which is the along-shore directions in our sites. Stronger eastward currents around Laguindingan may transport larvae released from Laguindingan to the east, but they may be retained within the Macajalar bay and can come back to Laguindingan (Fig. 1).

We also must consider other possible factors creating the variation in self-recruitment between Puerto Galera and Laguindingan. Larval dispersal simulations found that relative number of recruits from the surrounding locations was higher in Puerto Galera (76.3 recruits from external sources vs 17.9 from internal sources) than in Laguindingan (52.7 vs 32.2) (Table S3), which also led to lower self-recruitment in the former. This patten could be derived if relative number of the external to internal sources was higher in Puerto Galera than in Laguindingan. However, an actual ratio of the number of external to internal sources was lower in Puerto Galera [(45 + 34)/5 = 15.8] than in Laguindingan [(15 + 14)/1 = 29.0]. Therefore, the ratio of the external to internal sources was not responsible for the variation in self-recruitment between the two sites. Also, a previous study showed that the size of the focal habitat patch had positive effects on self-recruitment (Treml et al., 2012), providing a possibility that variation in sink patch size between Puerto Galera and Laguindingan can affect estimates of self-recruitment. However, our observed patterns were opposite to the prediction of Treml et al. (2012) that there would be higher estimates of self-recruitment in Puerto Galera than in Laguindingan, because the sink patch size was larger in the former. This possibility could be thus excluded, and we conclude that oceanographic feature shapes contrasting patterns of self-recruitment between Puerto Galera and Laguindingan.

Meanwhile, we should not overlook the discrepancy between the simulated and empirical estimates of self-recruitment (original simulation value of 19 % and empirical value of 0–2 % in Puerto Galera; 38 % and 14–15 % in Laguindingan). For both sites, we defined release locations along the shore within a radius of 20 km from the survey area based on the estimated distance at which 90 % of anemonefish larvae recruited (17.6 km) in a previous study, but it also indicated a certain proportion of the larvae dispersed more than 20 km (1–10 %) (Catalano et al., 2021). Therefore, our release locations limited within a radius of 20 km may increase the self-recruitment of larval dispersal simulations. In addition, because this study did not measure anemonefish density around the surrounding regions, we set a similar density of particle releases in the study site and surrounding region. Additional monitoring of anemonefish density

will increase the accuracy of simulated prediction for self-recruitment. Another possibility is that larval dispersal simulation without detailed settlement process might overestimate the local retention and self-recruitment. Our dispersal simulation records settlement when an individual gets in contact with a sensory zone after the competency period. In reality, the larva would still have to actually reach the reef and successfully settle into the benthic habitat.

We assessed the influences of different biological parameter inputs on local retention and self-recruitment estimates in both models. As in the previous study, perturbations of individual parameters had variable effects on the estimates of local retention. Although the number of particle releases had a negligible effect in both models and the effect of vertical migration was only apparent in the Laguindingan model, competency period, mortality rate, and sensory zone remarkably affected estimates of local retention in both models. Indeed, the importance and effects of these parameters are consistent with other studies (Cowen et al., 2006; Nanninga et al., 2015; Treml et al., 2012). We also found effects of competency period, sensory zones, vertical migration, and number of particle releases from the focal areas on the estimates of self-recruitment. The effects of sensory zones and larval mortality had similar trends to a previous result (Treml et al., 2015). However, the importance and effect of the competency period were somewhat different from it. Treml et al. (2015) showed that increasing the start of the competency period decreases the self-recruitment, but an opposite pattern was observed in the results of our Laguindingan model. In addition, passive migration scenario decreased self-recruitment in Laguindingan but increased it in Puerto Galera. Therefore, the effects of these parameters on self-recruitment can be site dependent.

Implications for management

Based on the results of genetic parentage analysis, we reported simple replacement measures (i.e., self-replacement and immigrant-replacement) to infer population persistence and MPA designs for anemonefish (Burgess et al. 2014), which is an iconic symbol of coral reefs but highly targeted by ornamental fishing (Shuman et al. 2005). Burgess et al. (2014) admitted that the calculation of replacement measures over a single time is simplistic, and it is necessary to collect the data about survival from recruitment to maturity and variation in number of self-recruits and immigrants over time for actual predictions. Nevertheless, we reported the replacement measures because they can better inform issues of population persistence than self-recruitment (Burgess et al. 2014). In closed systems, where a higher proportion of larvae are expected to stay in the area and larval imports from outside are limited, a large fraction of their area is designed as an MPA to ensure population persistence (Jessopp and McAllen, 2007). However, present study showed that anemonefish populations in Puerto Galera were maintained by supply from outside populations (self-replacement = 0.00 for both species; immigrant-replacement = 0.36 for *A. frenatus* and 0.25 for *A. perideraion*). This indicates that even in closed systems, depending on the characteristics of current velocity and direction, protecting several external sources or extending an MPA to beyond the bay may be required to enhance larval imports and population persistence. On the contrary, a large MPA is expected to be necessary for self-sustaining in open systems as larvae disperse widely. In fact, immigrants from the external sources may mainly contribute to population persistence in Laguindingan (immigrant-replacement = 0.42 for *A. frenatus* and 0.51 for *A. perideraion*), but replacement by self-recruits (self-replacement = 0.08 for both species) was also likely to occur despite the small area. This result suggests that population persistence could be enhanced by establishing small local MPAs even in open coasts where currents are weak. According to Weeks et al. (2010), which analyzed 985 MPAs in the Philippines, 90% of MPAs in the Philippines have a total area of <1 km^2. In the Philippines, the different autonomy of each island and sea area,

the narrow range of movement of fishers, and practical consideration of governance, make it difficult to set up large MPAs. This is generally the case in many developing countries with coral reefs, especially where communities rely heavily on these reefs for livelihoods (Ban et al., 2011). When considering the design of MPAs, not only type of coastline but also hydrodynamics (current velocity and direction) should be taken into account to determine the placement of small no-take MPAs to ensure the conservation and management of fish populations.

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Conflict of Interest
None declared.

Author contribution
MS, KH, YNakamura, and MN planned the study, and MS, KH, YNakamura, and KOB collected genetic samples of anemonefish with support from MDF. LCB, TY, ECH, WU, and KN designed and conducted ocean current measurements with support from MDF. MS, YNakajima, and CL contributed to genetic work. MS developed the biophysical model with support from LCB and KN. MS analyzed the data and wrote the paper with assistance from all others. All authors approved the final submitted manuscript.

Data availability statement
Data and R codes are available at https://github.com/Masa1986T/LO_anemonefish_dispersal.

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