AN ABSTRACT OF THE THESIS OF Robert M. Ross for the Master of Science degree in Biology presented 19 April 1976.

Title: Reproductive and Territorial Behavior of the Anemonefish *Amphiprion melanopus* Bleeker

Approved: Steven S. Amesbury
STEVEN S. AMESBURY, Chairman, Thesis Committee

Populations of the anemonefish *Amphiprion melanopus* were observed on Guam from November 1974 through March 1976 in order to determine their ecology, display repertoire, reproductive behavior, and territorial behavior. Individuals colonize the anemone *Physobrachia* sp. extensively and almost exclusively. The number and size of fish (measured in terms of total standard length) in each population is closely related to the areal coverage of resident anemones, suggesting that some critical resource (such as food, shelter, or protection) is directly related to the quantity of anemone present. Breeding populations require proportionally more anemone area than non-breeding populations. The mean population size is 3.51 individuals per anemone aggregation (n = 37). Individuals of stable breeding populations have a calculated mean turnover period of approximately 4 years. Both larval recruitment and interpopulation migration may contribute to optimum population size.

The display repertoire (excluding reproductive behavior) consists of some 11 behavior patterns, most of which are either directly or indirectly related to the defense of territory. Other displays, functioning as appeasement or submissive postures, may be related to dominance within the populations.

Nest preparation probably consists of behavior causing anemones to contract (anemone biting) followed by substrate biting. Spawning occurs 2-2.5 hours after sunrise and lasts for approximately 1.5 hours. Egg fanning occurs only during daylight hours and increases in frequency as the eggs mature. Hatching occurs 1-2 hours after sunset on the seventh or eighth day of incubation. Spawning is related to moon phase, with peak activity at -5 and +6 days from the full moon. Hatching peaks correlate strongly with high water heights (high tides) and currents, suggesting that hatchling predation may have been the selective force resulting in the observed rhythmicity. There is no seasonal periodicity in spawning activity.

The experimental introduction of conspecific "intruding" fish shows that both juveniles (as small as 20 mm SL) and adults defend territory. The mated adult female and male defend essentially the same territory, which is considerably larger than the area covered by resident anemones. The mated adult female fish defends territorial peripheries to a significantly greater extent than does the male. Juveniles and subadults, however, defend mutually exclusive areas (subterritories) within the confines of the anemone aggregation defended by the mated adult pair. Consequently, adult-juvenile agonistic encounters are frequent. Large conspecific intruders are attacked more heavily and at greater distances than are small ones. Territorial fluctuations in size, emphasis, and location are related to loss of individuals, changes in nest location, and immigration. Reduced agonistic behavior (resulting in increased immigration and growth of juveniles) in adult fish whose mates are lost may reflect a feedback mechanism whose effect is to stabilize populations at their optimum size. Interspecific territorial behavior is sporadic and appears to be directly related to defense of the nest or eggs rather than defense of feeding areas. Territorial behavior in *Amphiprion melanopus* probably functions to protect some vital resource related to the actiniarian host as well as to increase reproductive success.

REPRODUCTIVE AND TERRITORIAL BEHAVIOR OF THE ANEMONEFISH *AMPHIPRION MELANOPUS* BLEEKER

by

ROBERT MELVIN ROSS

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER IN SCIENCE
in
BIOLOGY

University of Guam

1976

TO THE GRADUATE SCHOOL:

The members of the Committee approve the thesis of Robert Melvin Ross presented April 19, 1976.

Steven S. Amesbury

Steven S. Amesbury, Chairman

James A Marsh, Jr

James A. Marsh, Jr.

Lynn Raulerson

Lynn Raulerson

George J Boughton

George Boughton

ACCEPTED:

James A. McDonough

James A. McDonough
Dean of the Graduate School

ACKNOWLEDGMENTS

I wish to thank the people associated with the Graduate Program in Biology at the University of Guam, the Marine Laboratory staff, and fellow graduate students for their advice, helpful criticism, and assistance.

Dr. Jack T. Moyer of the Tatsuo Tanaka Memorial Biological Station, Japan was kind enough to provide a manuscript prior to publication.

In addition, I would like to thank Dr. Robert May of the Hawaii Institute of Marine Biology for providing literature and comments on spawning data.

TABLE OF CONTENTS

PAGE

ACKNOWLEDGMENTS ii

LIST OF TABLES iv

LIST OF FIGURES vii

INTRODUCTION 1

METHODS 7

- The Study Area 7
- Field Observations 7
- Field Experiments 18

RESULTS 21

- Population Ecology 21
- Display Behavior 28
- Reproductive Behavior and Ecology 35
- Territorial Behavior 50

DISCUSSION 76

- Population Ecology 76
- Display Behavior 78
- Reproductive Behavior and Ecology 80
- Territorial Behavior 84

SUMMARY 87

LITERATURE CITED 89

LIST OF TABLES

TABLE PAGE

1. Some physiographic characteristics of anemone sites supporting breeding populations of *Amphiprion melanopus* at Tumon Bay and Agana Bay, Guam . . . 11

2. Summary of the number of documented *Amphiprion melanopus* individuals inhabiting various sea anemones at several study sites on Guam 22

3. Some population characteristics of anemonefish (*Amphiprion melanopus*) and sea anemones (*Physobrachia* sp.) occurring together at Tumon Bay, Guam 23

4. Summary of the results of correlation analyses performed on the anemonefish/sea anemone population data of Table 3 24

5. Summary of the size of individual populations of anemonefish at the Tumon Bay, Agana Bay, and Pago Bay sites over the course of this study . . 26

6. Frequency distribution of the size of individual *Amphiprion melanopus* observed at Tumon Bay, Agana Bay, Pago Bay, and Cocos Lagoon, Guam . . . 27

7. Frequency distribution of the number of white bars on individual *Amphiprion melanopus* (20 mm SL or larger) observed at Tumon Bay, Agana Bay, Pago Bay, and Cocos Lagoon, Guam 29

8. Summary of observed lost and gained individuals of *Amphiprion melanopus* in Tumon Bay populations with breeding adults and no known human interference 30

9. Summary of observed inter-population migrations . . . 31

10. The relative percent occurrence of displays and behavior patterns observed in *Amphiprion melanopus* individuals during quantitative observation sessions at sites 1B and 1D 37

TABLE PAGE

11. Qualitative analysis of context in observed intraspecific displays and behavior patterns of the anemonefish *Amphiprion melanopus* 38

12. Nest longevity in breeding pairs of *Amphiprion melanopus* observed for at least 5 lunar months 41

13. Macrocharacteristics of the naturally occurring eggs of *Amphiprion melanopus* at successive days of incubation 44

14. Summary of nest-associated behavior in the anemonefish *Amphiprion melanopus* 45

15. Pair fecundity and lunar periodicity of observed egg clutches in the anemonefish *Amphiprion melanopus* 48

16. The number of spawns per lunar month of five breeding pairs of *Amphiprion melanopus* observed for 1 year 51

17. Analysis of the initiators and recipients of agonistic behavior (attack, threat, and raised dorsal) in populations of *Amphiprion melanopus* 53

18. The relationship between size of fish and distance from center of activity at which attack or threat was observed to occur naturally 54

19. The number of attacks per 5 minutes on a conspecific intruder (56 mm SL) by the resident breeding pair of *Amphiprion melanopus* at site 1D (x-axis) 59

20. The number of attacks per 5 minutes on a conspecific intruder (56 mm SL) by the resident breeding pair of *Amphiprion melanopus* at site 1D (y-axis) 60

21. The number of attacks per 5 minutes on a conspecific intruder (56 mm SL) by the resident breeding pair of *Amphiprion melanopus* at site 1J 61

TABLE PAGE

22. The ratio of concurrent female to male attacks on a conspecific intruder by the resident adult pair of Amphiprion melanopus at site 1D (x-axis) 63

23. The ratio of concurrent female to male attacks on a conspecific intruder by the resident adult pair of Amphiprion melanopus at site 1J 64

24. Summary of the total number of attacks by resident adult Amphiprion melanopus on a conspecific intruder for each experimental series, showing both short-term and long-term diminished response to continued exposure 67

25. The effect of size of intruder on both the maximum distance of attack and the number of attacks per 5 minutes by the resident adult pair of Amphiprion melanopus at site 1D 69

26. The number of attacks per 5 minutes by subadult (1J3) and juvenile (1J4) subterritorial fish on a conspecific intruder (38 mm SL) at site 1J 70

27. The number of attacks per 5 minutes by a subterritorial, subadult fish (1J3) on a conspecific intruder (38 mm SL) after removal (on 22 Dec. 75) of a subterritorial juvenile (1J4) from the population 72

28. The number of attacks per 5 minutes on an adult Dascyllus aruanus (46 mm SL) by resident adult Amphiprion melanopus at site 1J 73

29. A comparison of observed aggression rates (number of agonistic encounters per 15 minutes) in the present study with those reported for Amphiprion species elsewhere 75

30. A comparison of predicted water heights 1 hour after sunset on observed peak hatching days with water heights of days 90 degrees out of phase (±7 days) in the lunar cycle 83

LIST OF FIGURES

FIGURE PAGE

1. Map of Guam showing the location of major study sites 8

2. Map of Tumon Bay (West end) showing the location of breeding populations of _Amphiprion melanopus_ 9

3. Map of Agana Bay (near Agana Boat Basin) showing the location of breeding populations of _Amphiprion melanopus_ 10

4. Sketch of anemonefish site 1D 14-15

5. Sketch of anemonefish site 1J 16-17

6. The regressions of total standard length of resident fish on total areal coverage of resident sea anemones for individual populations of _Amphiprion melanopus_ and _Physobrachia_ sp. at Tumon Bay, Guam 25

7. Raised-dorsal display 33

8. Tail-jerking display 36

9. Nest of anemonefish population 1N, photographed at approximately 1000 o'clock on 21 February 1976 40

10. Mean egg-fanning activity at sites 1B, 1D, 1H, 1J, 1L, 1M, and 1N on successive days of incubation 46

11. Frequency distribution of the number of spawns observed in breeding populations of _Amphiprion melanopus_ versus lunar day of spawning 49

12. Preparing a "bagged" anemonefish for territorial experiments at site 1D 55-56

FIGURE PAGE

13. Placing the bagged conspecific fish into test position "0" at site 1D for a 5-minute trial during which the number of attacks on the intruder by both the resident female and male fish are counted 55-56

14. Experimental trial with conspecific intruder at site 1J (position "-61") 57

15. Closeup of the behavior of resident anemonefish at site 1J (position "-61") toward model intruder 58

16. The effect of distance from territorial center on both the total number of attacks (T) and the ratio of female to male attacks (R) on a conspecific intruder at site 1D (x-axis) 65

17. The effect of distance from territorial center on both the total number of attacks (T) and the ratio of female to male attacks (R) on a conspecific intruder at site 1J 66

INTRODUCTION

Studies of reproductive and territorial behavior in pomacentrid fishes have become numerous in recent years. A survey of various works shows that pomacentrids as a group have many similar reproductive behavior patterns. Certain components of courtship, nest preparation, spawning, and egg care are very similar across several genera (Reese, 1964; Myerberg *et al.*, 1967; Albrecht, 1969; Fricke, 1974; Allen, 1975; and Moyer and Bell, in press). Territories among pomacentrids, however, may or may not exist, and, when they occur, vary considerably in form , function, space, and time (Reese, 1964; Rasa, 1969; Clarke, 1970; Low, 1971; Myerberg, 1972; Sale, 1972; Moyer and Sawyers, 1973; Fricke, 1974; Myerberg and Thresher, 1974; and Allen, 1975). The function of territorial behavior, in most cases, is to increase reproductive success (Albrecht, 1969; Rasa, 1969; Clarke, 1970; and Moyer and Sawyers, 1973), though interspecific territoriality necessarily implies protection of resources such as food and space (Rasa, 1969; Low, 1971; and Myerberg and Thresher, 1974).

It has been observed that anemonefish defend sea anemones both in an aquarium and in nature (Mariscal, 1966 and 1970a; Moyer and Sawyers, 1973; and Allen 1975). Whether territories consist of single anemones, several anemones, or large areas surrounding anemones is not always clear, however. Mariscal (1970a) and Allen (1975) used the term "subterritory" to describe the subdivision and occupation of an anemone cluster by several individuals, and this term was applied to *Amphiprion melanopus* populations observed at Enewetak (Allen. 1975).

Though many papers on the adaptive significance of territorial behavior have been published, Hinde (1956) was careful to distinguish consequences from true functions. Recently, Wilson (1975) synthesized much of the work on territoriality in terms of social spacing and treated aspects such as territorial evolution, interspecific territoriality, and population regulation. Erlich (1975) reviewed many aspects of the population biology of reef fishes including reproduction and territoriality.

More specifically, the ethology of fishes was reviewed by Baerends (1957), who discussed the whole spectrum of concepts including fixed action patterns, orientation, instinct, hierarchy, releasing mechanisms, and ritualization. A comprehensive phylogenetic study of reproductive behavior of fishes appears in Breder and Rosen (1966). One of the first detailed analyses of display behavior in fishes is that of Baerends and Baerends-van Roon (1950). Many of the behavior patterns named and described by them are still utilized today in describing the behavior of fishes from many different families.

The first major review of reproductive behavior in pomacentrid fishes is that of Reese (1964). He concluded that pomacentrids characteristically undergo the following phases: (1) establishment of territory, (2) selection of nest site, (3) preparation of nest site, (4) courtship and pair formation, (5) spawning and fertilization, and (6) parental care.

Major works on the genus Amphiprion include a review of territoriality by Mariscal (1966) and a field and laboratory study of the behavior of several species of Amphiprion (Mariscal, 1970a). The most comprehensive study of the genus Amphiprion to date is that of

Allen (1975), who described their taxonomy, ecology, behavior, and growth. Allen's behavior studies concentrated on three species: *A. chrysopterus*, *A. perideraion*, and *A. tricinctus*. The only detailed comprehensive study of the behavior and ecology of a single species of *Amphiprion* is that of Fricke (1974). Fricke's studies with *A. bicinctus* emphasized the importance of the biotope in the evolution of individual and social behavior patterns peculiar to anemonefish.

The anemonefish *A. melanopus* was reported to be host specific for the anemone *Physobrachia douglasi* (= *P. ramsayi*) (Mariscal, 1970a; Allen, 1973; and Allen, 1975). In addition, Allen (1975) reported an average of three *A. melanopus* individuals per anemone cluster (n = 150), though the size range of anemone clusters was not given. Verwey (1930) reported on the appearance of white bands (bars) on newly hatched *A. percula*. The first band appeared 10-12 days after hatching, the second about a week later, and the third band a week after the second. Specimens of *A. melanopus* (ranging from 16-57 mm SL) illustrated by Allen (1975) had one to four white bars. Allen (1975) studied the size-specific growth rates for *A. melanopus* and reported that maturity is reached at an age of 20 months (45-55 mm SL). Allen (1975) also determined the omnivorous nature of *A. melanopus*. Gut analyses showed the food to be 37.5% copepods, 26.7% algae (both planktonic and benthic), and 11.6% other crustaceans (n = 18). Most of these food organisms are planktonic.

Specific works describing displays of *Amphiprion* species include Fishelson's (1965) study of *A. bicinctus*, in which he described lateral displays, attack, trembling, rattling sounds, up-down swimming, tail-wagging, and others. Mariscal (1970a) discussed rocking behavior and play behavior, while Mariscal (1970b) suggested anemone biting may simply serve as a source of food (zooxanthellae algae). Allen (1975) observed tentacle bathing, lateral and parallel posturing, dorsal and ventral leaning, substrate biting, head standing, head shaking, belly touching, tentacle skimming, chasing, clicking, and grunting in three species of *Amphiprion*. Moyer and Sawyers (1973) reported clicking, quivering, and jerking in *A. xanthurus*. Many of these behavior patterns are reported in other genera as well (Myerberg *et al*., 1967 on *Chromis multilineata* and Fishelson, 1970 on *Abudefduf saxatilis*, for example).

A number of papers on reproductive behavior in pomacentrid fish have been published since Reese's (1964) review. Myerberg *et al*. (1967), for example, described reproductive behavior in the polygamous species *Chromis multilineata*. Clarke (1970) observed the reproductive phases of another pomacentrid fish, *Hypsypops rubicunda*. Moyer and Sawyers (1973) found the anemonefish *Amphiprion xanthurus* to be biologically polygamous. Verwey (1930) reported spawning to occur three times a month for 3.5 months in aquarium-held *A. percula*.

The periodicity of breeding behavior in marine animals was reviewed by Korringa (1947). Qasim (1956) related breeding periodicity to plankton productivity peaks and temperature cycles. Randall (1961) looked into the lunar periodicity of surgeonfish spawns and found greatest reproductive activity coinciding with the full moon. Allen (1975) obtained similar results with several *Amphiprion* species and suggested three possible explanations: (1) better nocturnal egg care, (2) a stimulus for larval dispersal, and (3) more food for larvae from other lunar-periodic organisms.

Okuno (1963) experimented with aggressiveness in aquarium-held *Amphiprion* species and found intraspecific rates as high as 24 attacks (chases) per 50 minutes for *A. frenatus* and 0 attacks per 100 minutes for *A. chrysogaster*. Interspecific rates as high as 49 attacks per 50 minutes in *A. frenatus* and 18 attacks per 100 minutes in *A. chrysogaster* were also observed. Fishelson (1965) found male *A. bicinctus* to be more active in guarding the host anemone, while females were more active in patrolling the territory. Clarke (1970) observed that territorial defense in the adult Garibaldi helps to regulate density, but only to limits set by resources. Its primary function, he concluded, is to increase reproductive success. Clarke (1971) observed a ratio of 79 interspecific attacks to eight intraspecific attacks per unit time in the Garibaldi. Sale (1972) found a significant inverse relationship between agonistic behavior and available space in *Dascyllus aruanus* and suggested that such behavior may function to disperse individuals over the reef. Moyer and Sawyers (1973) reported that both male and female *A. xanthurus* defended territories, but female territories were much larger. Male territorial behavior was directed primarily toward the periphery whereas female energy was directed internally. In the defense of nest holes, however, males were more aggressive than females. Immatures and some low-ranking adults did not defend territory.

By correlating kind of food eaten with the extent of agonistic behavior toward various fishes, Low (1971) showed that territoriality in *Pomacentrus flavicauda* functions primarily in the defense of food resources. Myerberg and Thresher (1974) observed that territoriality in the damselfish *Eupomacentrus planifrons* was, in general, inversely related to the phylogenetic distance of the intruder. Size of intruder was not an important factor. Both the intensity of territorial defense and the size of territory varied seasonally, reflecting the reproductive cycle of the fish. Myerberg and Thresher (1974) concluded that the function of territoriality was to protect food resources, spawn, and, perhaps, living space. Sale (1974) discussed mechanisms of coexistence in pomacentrid reef fish in terms of pelagic dispersal, chance openings in the habitat through death, and high success of defending territory once obtained. He implied that all members of the group largely coexisted in the same niche.

The purpose of this study was to observe the ecology, reproduction, and behavior of the anemonefish _A. melanopus_, and to relate these observations to published works on other pomacentrids, particularly other anemonefish. In addition, an attempt was made to relate the part of the habitat being defended to the type of potential intruder against which this defense is directed. These data should permit adequate evaluation of the adaptive significance of such behavior.

METHODS

The Study Area

Field work was carried out on the fringing reef flats surrounding the island of Guam, Mariana Islands (13° 23' N and 144° 45' W). Continuous, frequent observations were made on individuals in two specific areas (primary sites) throughout the course of this study: Tumon Bay off Ipao Beach and Agana Bay adjacent to the boat channel (Figures 1-3 and Table 1). Other areas surveyed or visited include Pago Bay, Apra Harbor, Glass Breakwater, and Cocos Lagoon. All observations were made between November 1974 and March 1976. Observations of *A. melanopus* alone totaled 131 hours. Notes were taken on underwater writing paper with clipboard. Individuals in the primary study sites and at Pago Bay were recognizable after a short time on the basis of their size, number of white bars, and location or center of activity within the anemone aggregation.

Field Observations

Ecological data on distribution, reef-flat density, host requirements (both qualitative and quantitative), size distribution, and white bar frequency distribution were obtained at the primary study sites in order to more fully evaluate the significance of observed behavior. Additional ecological data were collected at the other study sites.

An estimate of the density of *A. melanopus* was obtained at the primary sites by determining, first, the two most distant populations in each area. The distance between these two populations then became

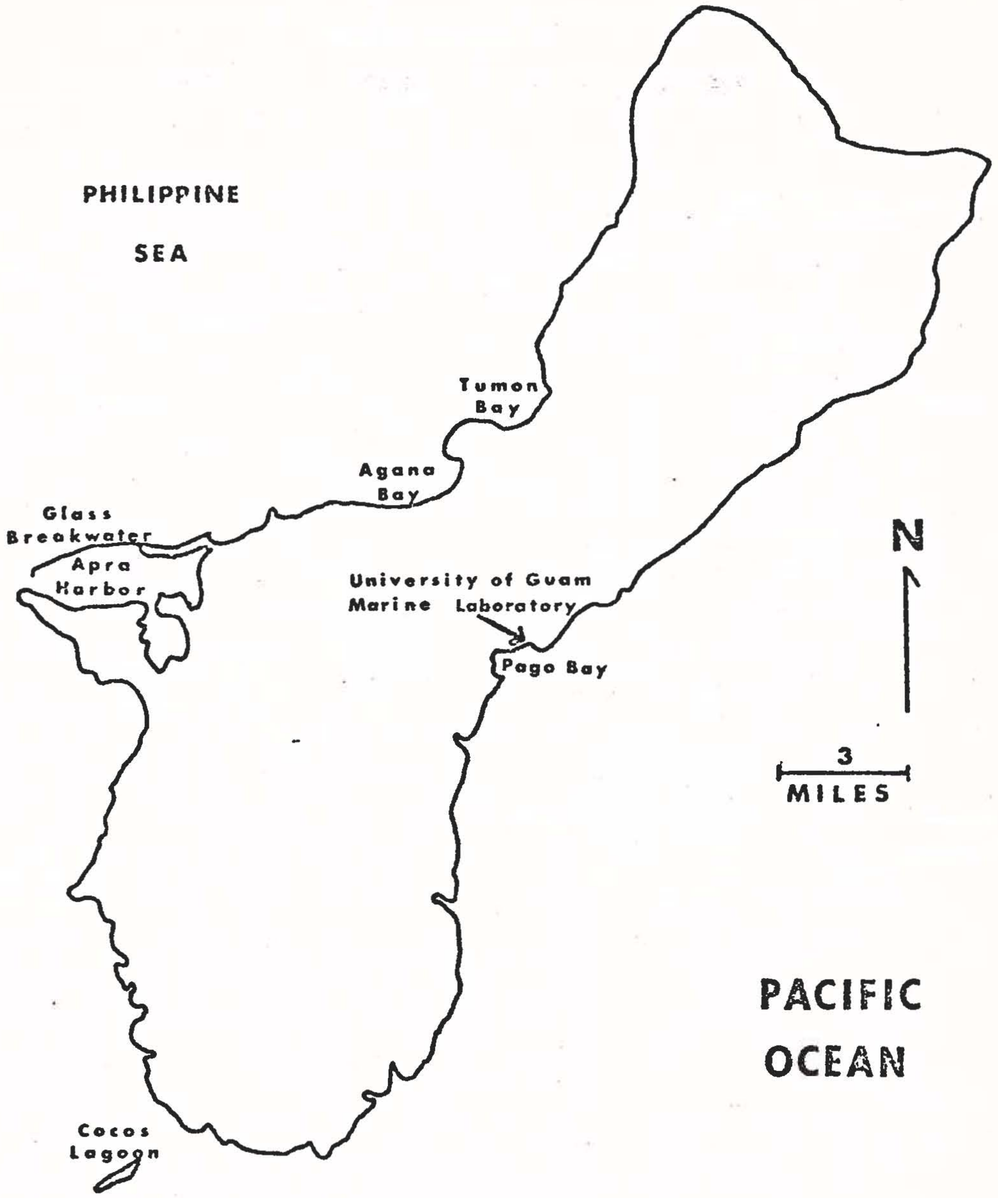


Figure 1. Map of Guam showing the location of major study sites.

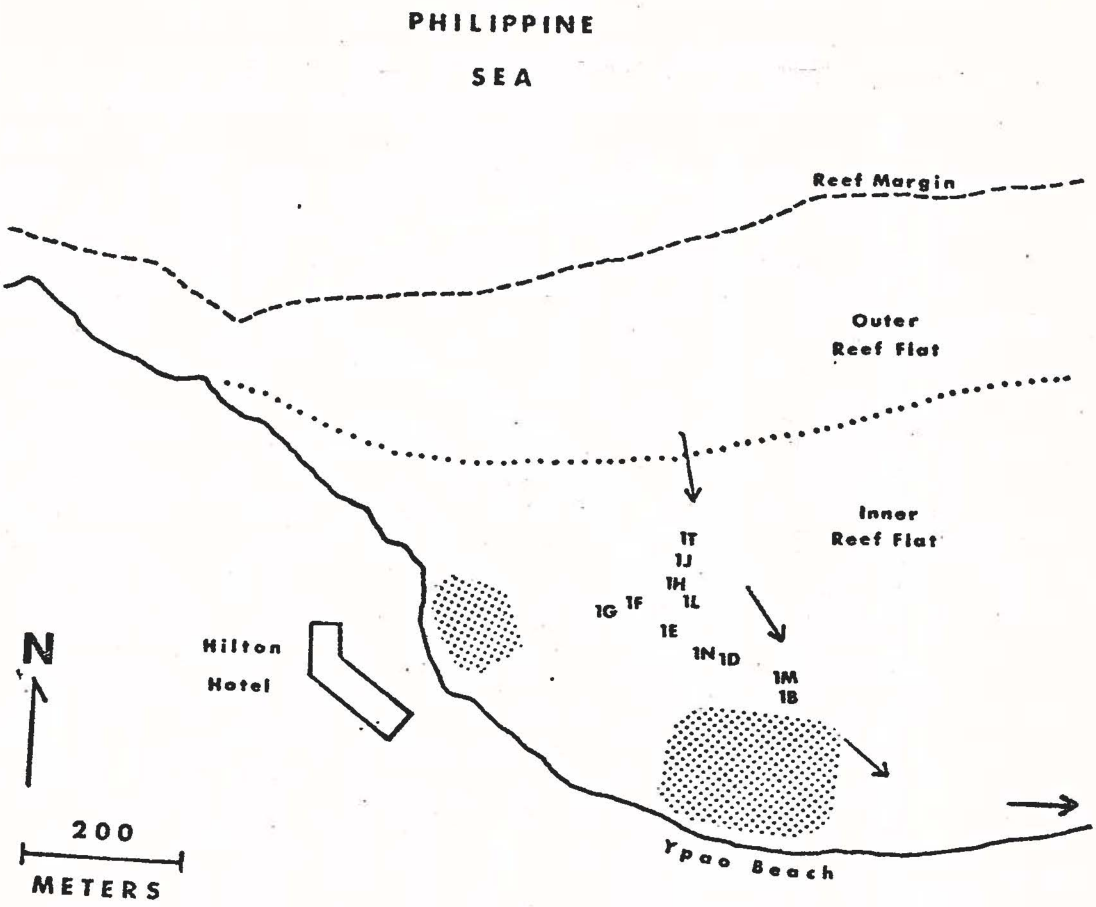


Figure 2. Map of Tumon Bay (West end) showing the location of breeding populations of <u>Amphiprion</u> <u>melanopus</u>. Arrows indicate the direction of water movement. Dredged swimming areas are shaded.

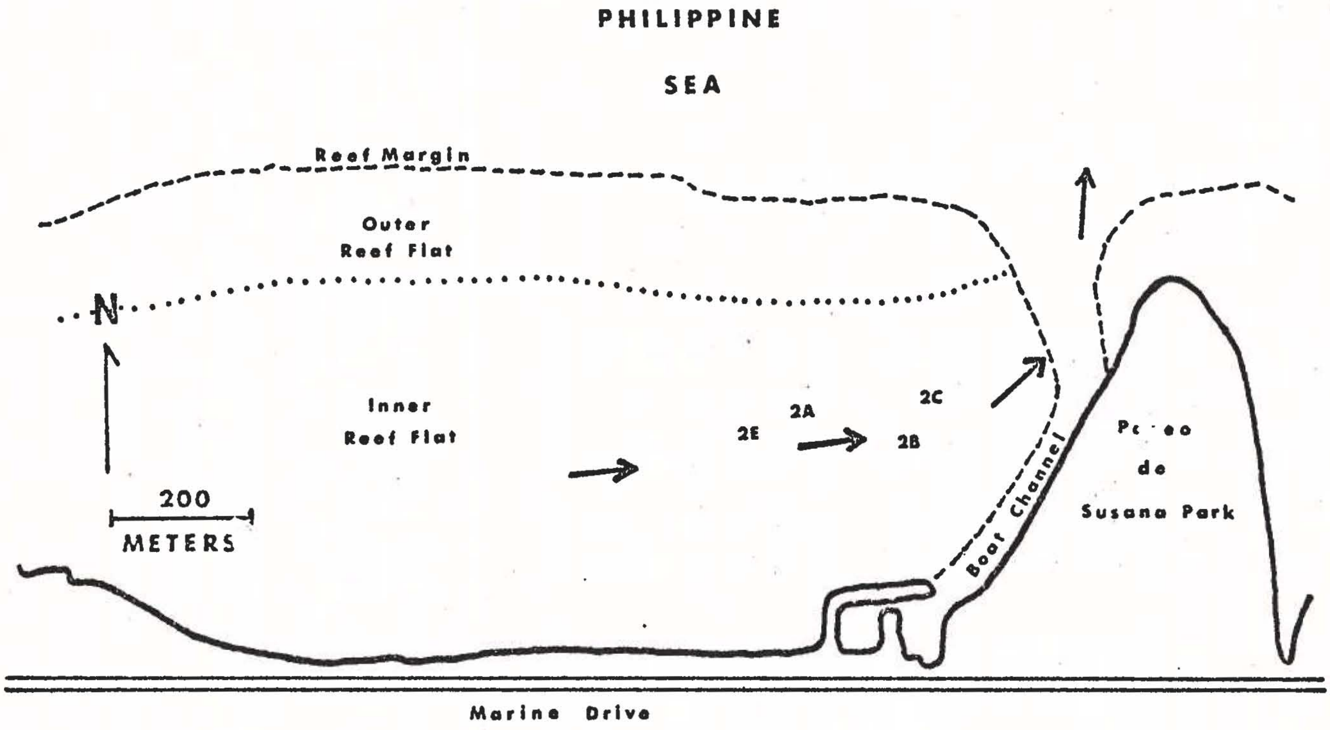


Figure 3. Map of Agana Bay (near Agana Boat Basin) showing the location of breeding populations of _Amphiprion_ _melanopus_. Arrows indicate the direction of water movement.

Table 1. Some physiographic characteristics of anemone sites supporting breeding populations of *Amphiprion melanopus* at Tumon Bay and Agana Bay, Guam.*

Site	Water Depth (m)†	Approximate Dimensions of Coral Head (m)ψ	Living Corals Surrounding Anemones
1B	1.0	1.5 x 1.5 x 0.5	*Porites* sp.
1D	0.5	10.0 x 8.0 x 0.3	*Porites* sp., Pavona sp.
1E	1.0	1.0 x 0.5 x 0.3	*Acropora* sp.
1F	1.0	0.5 x 0.5 x 0.5	None
1G	1.0	2.0 x 2.0 x 0.3	None
1H	1.5	0.5 x 0.5 x 0.3	None
1J	0.5	4.0 x 2.0 x 0.3	*Pavona* sp., *Porites* sp., *Acropora* sp., *Psamocora* sp.
1L	1.0	1.0 x 0.5 x 0.3	*Porites* sp.
1M	1.0	2.0 x 2.0 x 0.3	*Porites* sp.
1N	1.0	2.0 x 1.5 x 0.3	*Porites* sp.
2A	1.0	0.5 x 0.5 x 0.3	*Porites* sp.
2B	1.0	0.3 x 0.3 x 0.3	None
2C	0.5	2.0 x 2.0 x 0.3	*Porites* sp., *Acropora* sp.
2E	1.0	0.5 x 0.5 x 0.3	*Psamocora* sp.

---

*All Tumon Bay and Agana Bay sites were located on the inner reef-flat zone, in areas where scattered coral heads and rock pavement or sandy bottom predominated (see Figures 2 and 3). One Pago Bay breeding site, however, was located on the reef margin.

†Water depth varies considerably with tidal state and surf. These values represent approximate water depth above anemone clusters at mean water height with light to moderate surf.

ψValues are length, width, and height, respectively.

the length of a rectangle large enough to include all other populations in the area. The total number of individuals (>10 mm SL) observed in the area was then divided by the area of the above rectangle to obtain density.

Quantitative host requirements were determined by counting the number of anemones in each cluster and estimating anemone-cluster areal coverage. Areal coverage of anemones was obtained by measuring the diameter of all anemones in their fully distended state. For non-circular anemones, two diameters were obtained and an appropriate intermediate value assigned. Then the total standard length (in mm) of resident anemonefish was determined by placing a metric ruler near each fish and estimating its size by visual comparison.

Display behavior was studied in detail at sites 1B and 1D during quantitative observation sessions from January to April 1975. Maps of both sites showing the major physiographic features and the location of all anemones, nests, and centers of activity were drawn in the field. These maps were overlain with clear plastic, and the location of each observed behavior pattern was recorded on the plastic by marking an "X" with a grease pencil. Depth of occurrence was estimated and recorded at the same time. Maps and overlays (display maps) were photocopied after each observation session and erased for subsequent use.

Display maps were used to evaluate the mean distance from center of activity at which each individual engaged in agonistic behavior (attack, threat, or raised dorsals). The distance from each such display to center of activity was measured on the display map and divided by the scale of the map. Depth of occurrence was then utilized to obtain a right triangle, the hypotenuse of which was calculated to yield an estimate of the actual distance from center of activity at which the display occurred. Analyses of display behavior requiring a knowledge of the limits of each fish's subterritory were based on the known center of activity for each fish and the location of observed border conflicts between fish (see Figures 4 and 5).

The relative percent occurrence of each display observed was also calculated from quantitative observations. Since interspecific aggression was observed occasionally, its rate of occurrence was calculated relative to that of intraspecific aggression. Rates of aggression were expressed on a per-minute basis, whenever possible, for comparison.

Data on reproductive behavior were obtained by observing adult anemonefish and their spawns on a regular basis. Frequent observations of anemonefish spawns resulted in a visual description of the eggs at successive days of incubation. These descriptions, in turn, allowed for the prediction of the date of spawn of any observed egg clutch, based on the eggs' visual characteristics. Predicted spawn dates were probably subject to an error of ±1 day. All primary site nests were checked for eggs at least once a week throughout the period of study. Egg-fanning data were obtained by counting the number of discrete fanning sessions by adult males in 5 minutes (initial 8-minute counts were reduced to an equivalent number per 5 minutes). Egg clutches from several Tumon Bay sites were utilized to obtain these data, and the age of each egg clutch was determined from either observed spawning dates or careful visual inspection of eggs.

Figure 4. Sketch of anemonefish site 1D. Peripheral solid line denotes the physiographic limits of the Porites sp. coral head. Internal solid lines denote depressions in which sea anemones are situated. Approximate subterritorial centers of resident anemonefish are indicated as 1D1, 1D2, etc. Nest location is indicated with an arrow. Dotted line denotes the location of numerous border conflicts between fishes 1D2 and 1D3. Encircled numbers represent positions at which experimental fish were introduced (horizontal numbers lie in x-axis and vertical numbers lie in y-axis).

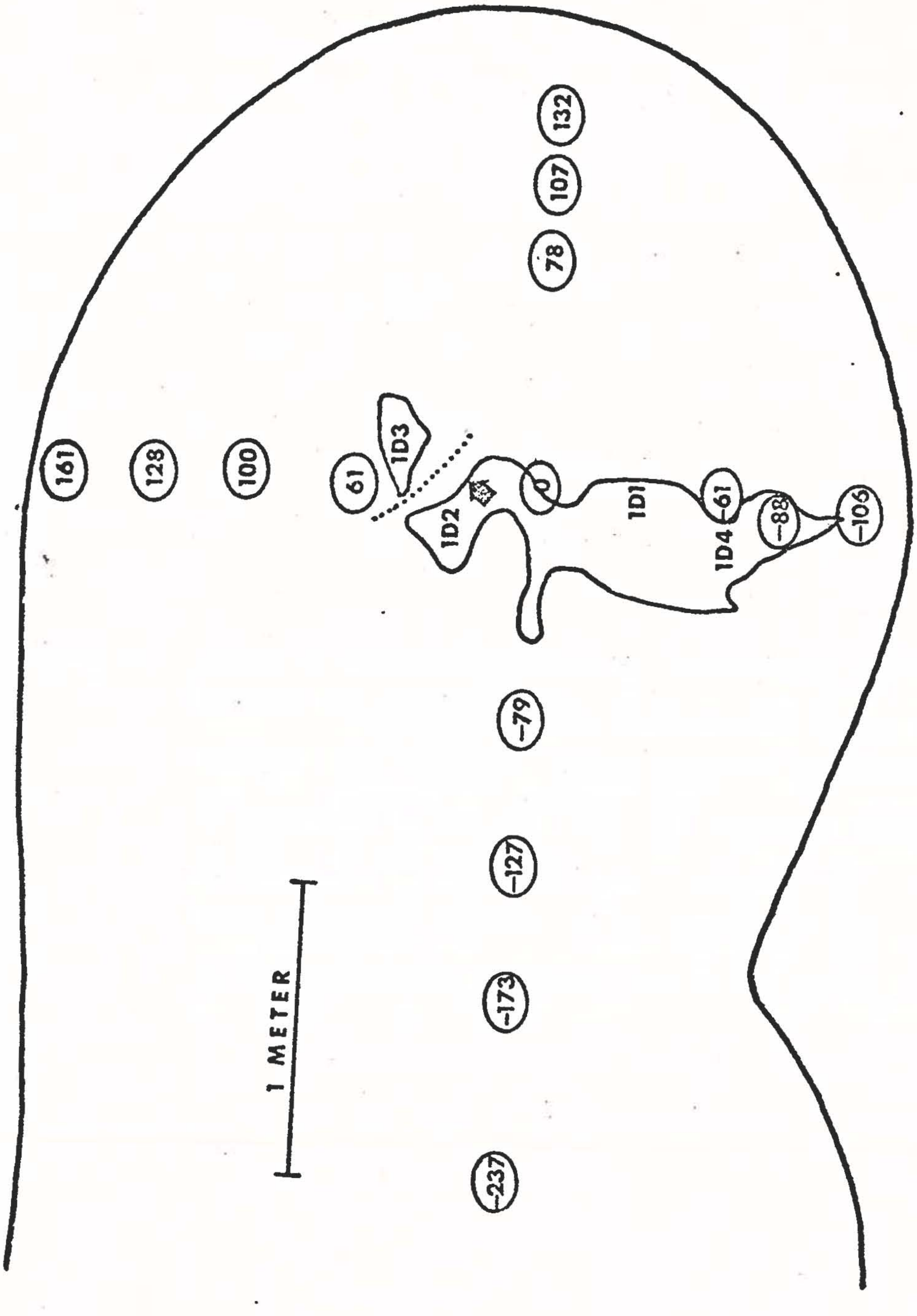
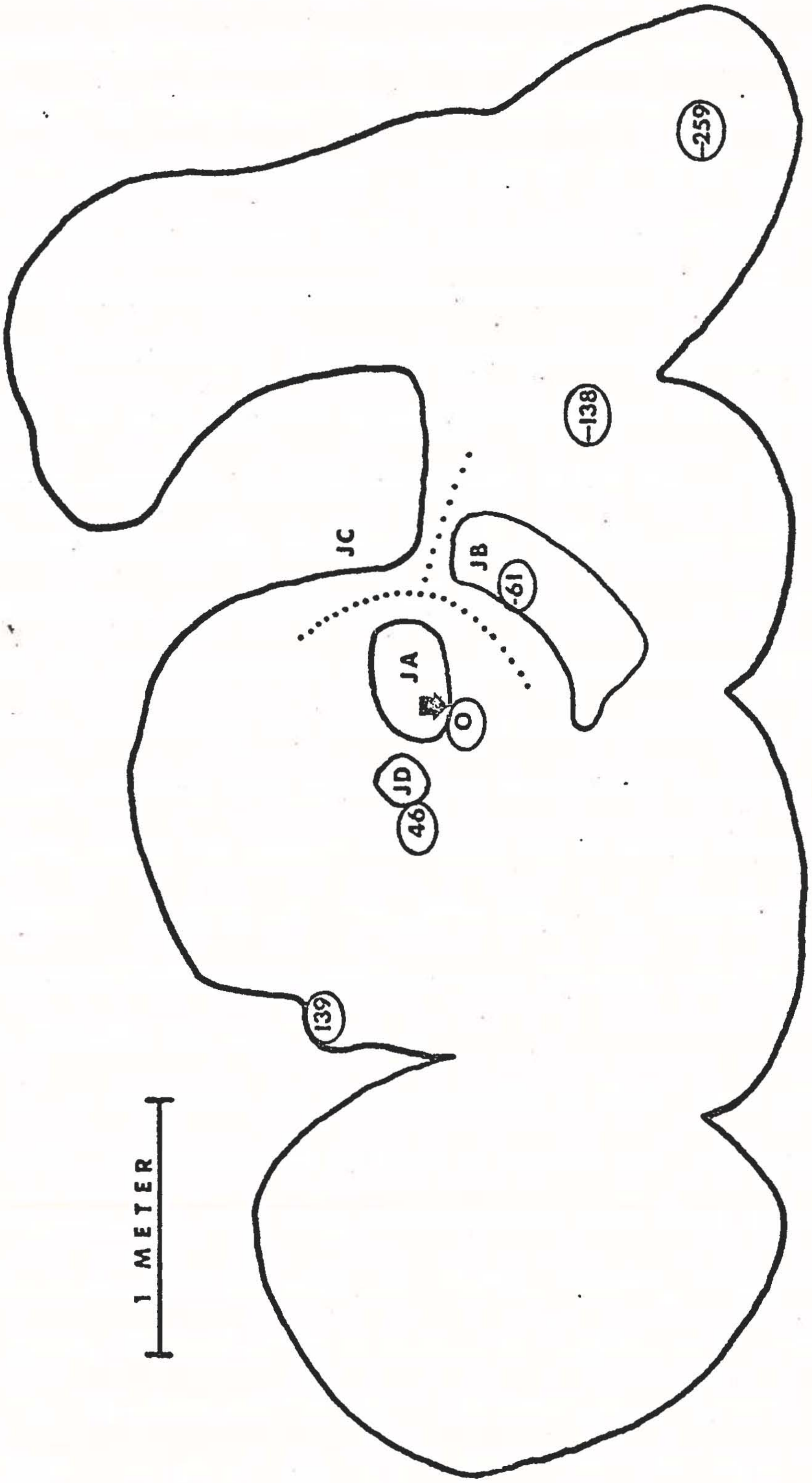

161
128
100
61
1D3
1D2
0
1D1
61
1D4
-88
-106
78
107
132
-79
-127
-173
-237
1 METER

Figure 5. Sketch of anemonefish site 1J. Peripheral solid line denotes the physiographic limits of the coral head, while internal solid lines denote depressions in which sea anemones are situated. Areas strongly defended by specific anemonefish (subterritories) are indicated as JA (defended by 1J1 and 1J2), JB (defended nearly always by 1J3), JC (defended by 1J4 until fish removed), and JD (defended by smallest, least dominant fish). Dotted lines represent subterritorial boundaries at which numerous border conflicts were observed. Nest location is indicated with an arrow. Encircled numbers represent positions at which experimental fish were introduced.


-259
-138
JC
JB
-61
JA
O
JD
46
139
1 METER

Field Experiments

To test the effect of such factors as distance from territorial center and size of intruder on territorial behavior, a method of introducing live fish at specific locations relative to established territories was developed. The method is similar to that employed by Myerberg and Thresher (1974), who placed experimental fish in glass jars and counted the number of attacks (nips or butts) by resident fish in 3 minutes. In this study clear plastic bags (13.5 cm X 30.5 cm) were found to be more practical due to occasional strong water currents. A fish was placed in the bag, a small air bubble was introduced to keep the bag upright, and the open end was twisted shut. Then a rubber band was placed around the twisted end, allowing the bag to be fastened to the substrate with the rubber band. The number of attacks by resident fish in 5 minutes was counted. In all cases 5-minute test periods were preceded by 5-minute control periods during which the number of attacks on an empty plastic bag was counted. In only two cases were there any attacks on control bags. All experimental fish were held in seawater tanks at the University of Guam Marine Laboratory.

In the first set of experiments a 56-mm SL *A. melanopus* individual was introduced at site 1D (Figure 4). The fish was placed at various points along perpendicular axes whose intersection coincided with the adult territorial center. Only one axis (consisting of eight or nine points) was tested on a given day. Each axis therefore required 80 or 90 consecutive minutes of observation. These tests were repeated six times over a period of 6 weeks.

To correct for bias due to habituation for a given series of tests, points were tested in a different predetermined sequence each time. The 1D resident fish consisted of only two individuals, the adult female and male, at the time of these experiments.

The experimental procedure described above was repeated at site 1J (Figure 5) with a few modifications. Site 1J consisted of four individuals including the adult breeding pair, a 60-mm SL (estimated) non-breeding adult or subadult, and a 44-mm SL juvenile. Only attacks by the adult female and male were counted, but notes were taken on the activity of the other two resident fish (1J3 and 1J4, respectively) during test trials. A single axis, consisting of six points, was tested six times over a period of 2 weeks.

To determine the effect of size of intruder on territorial behavior, a modified "maximum distance of attack" (Myerberg and Thresher, 1974) series of experiments were performed at site 1D. Experimental fish were introduced at a distance of 4.5 m from the territorial center and moved into the resident territory (again, using 5-minute control and 5-minute test periods) until attacks by resident fish were observed. Three different experimental fish, a 69-mm SL adult, the 56-mm SL subadult, and a 36-mm SL juvenile, were utilized in this series. Each fish was introduced three times (again, only once on a given day) over a period of 5 weeks.

In order to determine the size of subadult and juvenile territories, new test points were selected at site 1J. These points were selected to coincide with both the known centers of activity of resident fish and points half way between those centers (see Figure 5). In this case, however, only attacks by the subadult and juvenile residents (1J3 and 1J4) were counted, while the activity of the adult pair was noted. A 38-mm SL juvenile fish was employed in this series of experiments. Four separate tests were performed over a period of 10 days. At the conclusion of this series the 44-mm SL juvenile (1J4) was removed from the population to test the effect of loss of a territorial individual on the size and location of remaining territories. After a 5-day equilibration period, the experimental procedure described above was repeated. Only attacks by the 60-mm SL subadult (1J3) were counted but adult activity was noted. Four tests were performed over a period of 10 days.

Finally, to gain some assurance that the results obtained by experimental studies thus far were not due simply to the presence of _any_ fish near established territory, the single-axis series of experiments was performed at site 1J using a non-conspecific fish. A 46-mm SL adult _Dascyllus aruanus_ was chosen because attacks on this species by _A. melanopus_ adults had been observed previously. Four separate tests of adult _A. melanopus_ behavior toward this fish inside established territory were performed over a period of 3 weeks.

RESULTS

Population Ecology

At Tumon Bay a total population density of 0.0021 individuals m^{-2} (57 individuals, 20 mm SL or larger, occupying a rectangle 153 m X 176 m) was observed. At Agana Bay a density of 0.0156 individuals m^{-2} (15 individuals, 20 mm SL or larger, occupying a rectangle 10 m X 96 m) was observed for a smaller area. Ninety-seven percent of all individuals observed were found inhabiting the anemone Physobrachia sp. (Table 2). Furthermore, the number and size of anemonefish (measured in terms of total standard length of resident fish) was found to be directly proportional to the areal coverage of anemones present (Tables 3 and 4). Non-breeding populations were found to require proportionally less anemone area than breeding populations (Figure 6).

The mean population size was 3.51 individuals per anemone cluster (n = 37, s = 3.00, and range = 1-18). The mean size would have been 3.11 individuals per anemone cluster (n = 36, s = 1.75, and range = 1-7) if the extremely large population 3B were omitted (Table 5). In terms of size distribution, the number of individuals occurring in 10 mm increments of standard length above 19 mm is strikingly constant (Table 6). However, individuals estimated to be 35 mm SL or less became increasingly inconspicuous and secretive, so that their numbers were probably underestimated. Sexual maturity in males is estimated to occur at approximately 60 mm SL (about one third of the individuals ranging 60-69 mm SL were observed to be breeding males). Approximately 80 percent of all individuals which were 20 mm SL or larger displayed

Table 2. Summary of the number of documented *Amphiprion melanopus* individuals inhabiting various sea anemones at several study sites on Guam.

	Host Sea Anemone			
Study Site	*Physobrachia* sp.	*Radianthus* sp.	*Stoichactis* sp.	Unknown species
Tumon Bay	60	(0)	(0)	0
Agana Bay	17	(0)	(0)	0
Pago Bay	19	(0)	(0)	0
Cocos Lagoon	33	2	(0)	(0)
Glass Breakwater	8	(0)	(0)	(0)
Apra Harbor	12	0	1	2
Total	149	2	1	2

( ) Indicates that none of these anemones were observed in the area.

Table 3. Some population characteristics of anemonefish (Amphiprion melanopus) and sea anemones (Physobrachia sp.) occurring together at Tumon Bay, Guam.

Population	Number of Anemones	Total Area of Anemones (cm^2)	Number of Fish	Total SL of Fish (mm)	Total Number White Bars on Fish
1Q	1	50	1	35	1
1W	3	21	1	30	3
1R	3	27	1	20	3
1S	6	53	1	40	1
1A	13	250	2	75	5
1P	15	134	1	45	1
1B*	43	2530	4	265	4
1H*	57	765	2	150	2
1D*	73	2838	4	280	4
1M*	82	1393	3	155	5
1N*	97	2322	4	205	6
1J*	103	2001	5	265	7

*Populations with breeding adults.

Table 4. Summary of the results of correlation analyses performed on the anemonefish/sea anemone population data of Table 3.

Correlation Variable x	Correlation Variable y	All Populations n	All Populations r	Breeding Populations n	Breeding Populations r	Non-breeding Populations n	Non-breeding Populations r
Area of Anemones	SL of Fish	12	0.969†	6	0.868*	6	0.957†
Area of Anemones	No. of Fish	12	0.939†	6	0.760	6	0.890*
No. of Anemones	SL of Fish	12	0.849†	6	0.026	6	0.733
No. of Anemones	No. of Fish	12	0.892†	6	0.492	6	0.520

*$p<0.05$

$^{\dagger}p<0.01$

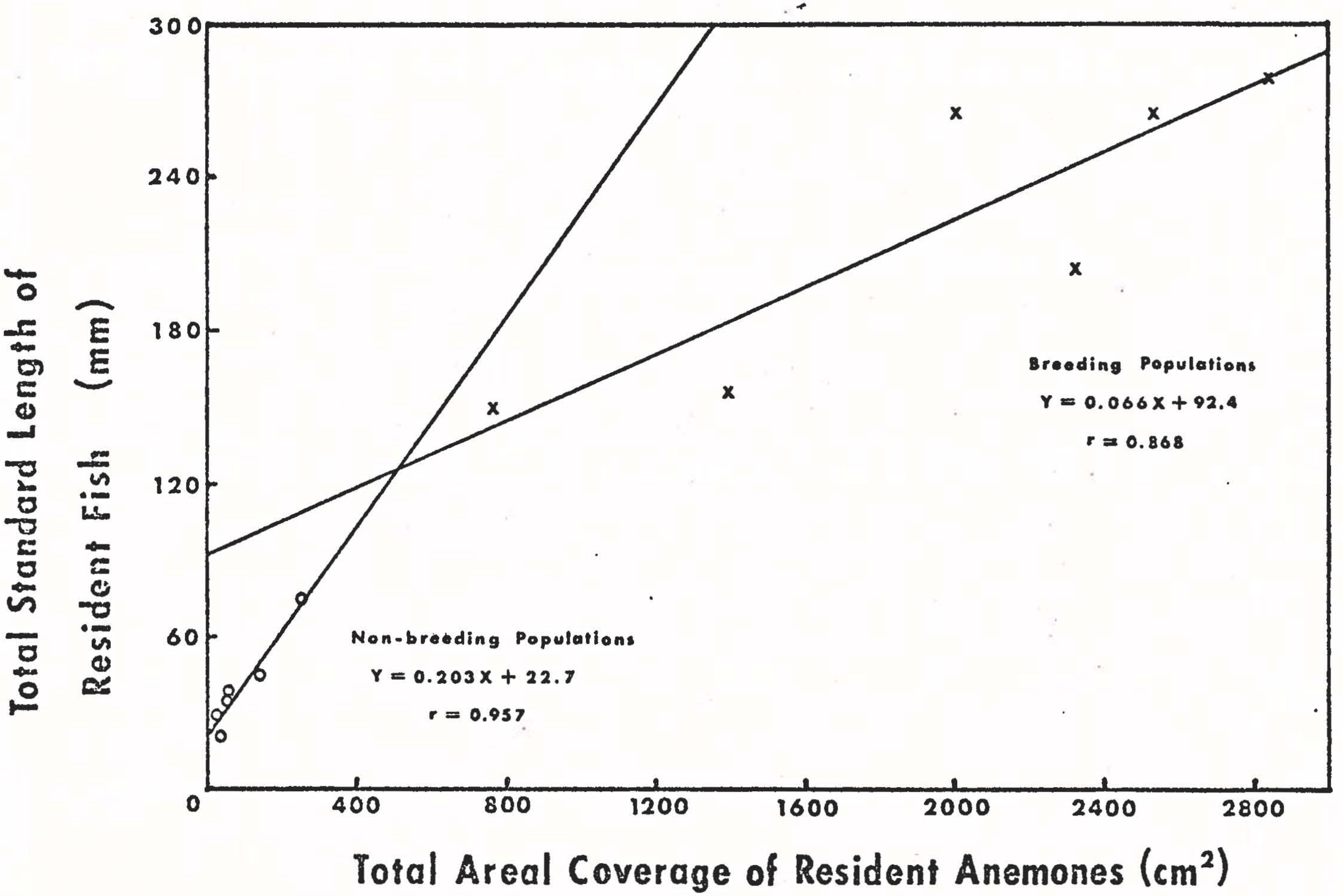


Figure 6. The regressions of total standard length of resident fish on total areal coverage of resident sea anemones for individual populations of *Amphiprion melanopus* and *Physobrachia* sp. at Tumon Bay, Guam.

Table 5. Summary of the size of individual populations of anemonefish at the Tumon Bay, Agana Bay, and Pago Bay sites over the course of this study.

Population	No. Months Observed	$\overline{x}$ No. Visits Per Month	No. Individuals Present		
			High	Low	Most Frequent
1A	14	1.0	2	1	2
1B	14	7.3	4	2	4
1C	3	2.2	1	0	0
1D	14	7.9	4	1	4
1E	13	4.0	5	2	4
1F	13	4.3	2	1	2
1G	10	4.8	5	2	5
1H	12	7.2	3	2	2
1J	12	8.0	6	3	5
1K	4	0.8	2	2	2
1L	12	7.3	4	3	3
1M	11	7.0	3	3	3
1N	11	4.3	4	3	4
1P	9	6.9	1	1	1
1Q	6	0.5	1	1	1
1R	3	1.1	1	1	1
1S	6	0.8	1	1	1
1T	3	6.6	2	2	2
1U	4	0.5	5	4	5
1V	5	2.8	2	2	2
1W	1	4.0	1	0	0
1X	2	1.0	4	4	4
2A	14	0.2	2	2	2
2B	14	1.6	7	5	7
2C	9	2.9	6	5	5
2D	4	2.6	3	3	3
3A	3	1.0	1	1	1
3B	8	1.2	?	?	18*

*Single count only and probably too low, as the population was located at a large aggregation of anemones in a reef-margin surge channel where observation was difficult.

Table 6. Frequency distribution of the size of individual *Amphiprion melanopus* observed at Tumon Bay, Agana Bay, Pago Bay, and Cocos Lagoon, Guam.

Size (mm SL)	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89
No. of Fish	1	20	19	15	19	17	22	18

only one white bar, though undercounting of very small individuals may have resulted in some bias (Table 7). Only individuals less than 40 mm SL were multi-barred. Some individuals as small as 10 mm SL, however, had only one bar.

The most stable populations (those with breeding adults and without obvious interference) lost and gained less than one resident fish per year, a turnover period of approximately 4 years per fish (Table 8). Though difficult to quantify, some inter-population migration was observed (Table 9). Known vacancies, due to removal or loss of territorial individuals, were filled by migrating fish in a mean period of 16 days (n = 2). The fish migrated from small peripheral anemone clusters to large anemone clusters occupied by adults with well-established territories in both cases.

Display Behavior

During the course of this study, nine distinct ritualized displays, in addition to outright attack and escape, were observed in *Amphiprion melanopus* individuals. These do not include various forms of reproductive behavior to be discussed below. A description of each observed behavior pattern follows.

Attack. This form of behavior involves the active, swift pursuit of one fish by another, obviously aggressive, fish. The dorsal fin of the pursuing fish may or may not be erect. Since damage may not be inflicted upon the recipient, this use of the word attack is probably more general than that of other observers (Fishelson, 1965, for example). It probably includes observed forms of behavior such as "chasing" (Fishelson, 1970 and Allen, 1975), "threatening"

Table 7. Frequency distribution of the number of white bars on individual <u>Amphiprion</u> <u>melanopus</u> (20 mm SL or larger) observed at Tumon Bay, Agana Bay, Pago Bay, and Cocos Lagoon, Guam.*

No. of White Bars	1	2	3	4	Total
No. of Fish	106	3	17	4	130
% Composition of Population	82	2	13	3	100

*Partial bars are counted as whole bars. There were many individuals in category "3" with only two full bars.

Table 8. Summary of observed lost and gained individuals of *Amphiprion melanopus* in Tumon Bay populations with breeding adults and no known human interference.

Population	No. Months Observed	Original No. of Individuals	Lost No.	Lost Size*	Gained No.	Gained Size*	Net Change
1B	15	4	1	80	0	30	-1
1D	15	4	3	85	2	15	-1
1E	12	2	0	65	3	35	+3
1F	14	2	1	50	0	30	-1
1H	13	2	0	80	0	20	0
1L	10	4	1	25	0		-1
1M	12	3	0		0		0
All	13	21	6[†]		5[†]		-1

*mm SL, estimated.

[†] Equivalent to the following, calculated from the total number of original fish (21), the number of populations observed (7), and the mean number of months observed (13):

0.79 fishes lost/population/year and
0.66 fishes gained/population/year or
0.26 fishes lost/fish/year and
0.22 fishes gained/fish/year.

Table 9. Summary of observed inter-population migrations.

Documentation	Territorial Fish Lost or Site Open 1D1	 1J4	 1JD*
Last date territorial fish observed at site	26 Oct. 75	22 Dec. 75	unknown
First date territorial fish observed missing	29 Oct. 75	22 Dec. 75†	unknown
Last date migrating fish observed at old site	2 Nov. 75	Origin unknown	27 Dec. 75
First date migrating fish observed at new site	6 Nov. 75	16 Jan. 76	30 Dec. 75
Probable length of time subterritory vacant	7 days	25 days	unknown
Distance traveled by migrating fish	3 m	unknown	4 m
Characteristics of migrating fish	20 mm SL 3 white bars	35 mm SL 1 white bar	30 mm SL 3 white bars

*See Figure 5 for location of this subterritory.

†This fish was captured and taken to the Lab.

(Fishelson, 1970), and "frontal thrusts" (Myerberg _et al_., 1967). Chases up to 1.2 m were observed.

Escape. Essentially the opposite of attack, this form of behavior involves the active, swift retreat of one fish from another aggressive individual.

Threat. This behavior pattern differs from attack only in the velocity of the aggressor. The threatening fish directly faces the recipient and may either remain stationary or move slowly toward the recipient at close range (less than 5 cm). The dorsal fin of the pursuing fish may or may not be erect.

Raised dorsal (Figure 7). This display involves simply the elevated dorsal fin of a fish in any situation, location, or position. Raised dorsal displays were observed concurrently with attack, escape, threat, clicking, and head shaking.

Clicking. Described by Allen (1975) in detail, this audible signal consists of a rapid series of discrete pulses. It was detected only in adult individuals when the observer approached to within one meter of the fish.

Head shaking. Also described by Allen (1975), this display appears to involved the rapid vibration of the entire body of the fish. It was observed in both adults and juveniles and often occurred following attack or threat by another individual, but never before such attack or threat. Head shaking was observed concurrently with raised dorsal, head standing, and dorsal leaning. A variation of this form of behavior, mutual head shaking, involved two individuals simultaneously engaged in head shaking in close proximity.

Figure 7. Raised-dorsal display. Extended pelvic and anal fins are also evident as fish displays in apparent response to the presence of an experimentally introduced conspecific fish.

Anemone biting. A fish aggressively bites off an anemone tentacle and consumes it. This ritualized behavior was observed primarily in juveniles, and only when the observer approached to within approximately one meter of the fish.

Tentacle nibbling. Described by Mariscal (1970a), this display differs from anemone biting in that the tentacle is not bitten off and consumed. In one case the entire length of a tentacle was slid through the mouth of an adult fish, beginning at the base. At other times apparently just the tip of the tentacle was mouthed. This form of behavior was observed only in a pair of breeding adults during spawning, though it may not be restricted to spawning.

Head standing. This behavior pattern, also described by Allen (1975), does not appear to differ appreciably from substrate biting (to be discussed with reproductive behavior). The fish assumes a vertical, head-down posture, touches the substrate, and, perhaps, moves away slightly in an alternating sequence. Only juveniles have been observed to engage in this activity. This display was observed concurrently with head shaking as it was by Allen (1975) in Amphiprion perideraion. Mutual head standing, involving two juveniles, was observed once.

Dorsal leaning. This display described also by Allen (1975), consists of a 30 to 45 degree roll of one fish toward another so that the dorsal fin in the displaying fish is nearest the recipient fish. Observed in both juveniles and adults, this display occurs when there appears to be a high probability of aggressive behavior on the part of another fish, such as when the displayer is inside the territory of another fish. Alternatively, a resident fish may display in this manner when an unknown "intruder," whose behavior cannot be predicted, is within its territory. The display occurs at close range only (less than 10 cm from recipient) and is independent of the size of either the displayer or recipient. Dorsal leaning was observed concurrently with only one other display, head shaking.

Tail jerking (Figure 8). A fish faces away from the recipient at close range, and, pivoting near the pectoral fins, jerks its body, exposing one side, then the other, to the recipient. Jerks occurred between one half and one second apart, and displays of two, four, six, or eight jerks were observed. It appears to be very similar to "side-turning" behavior described by Mariscal (1970a) in *A. xanthurus* and *A. akallopisos*. This display was observed both in juveniles and adults and occurred independently of size of either the displayer or the recipient. It was, however, always observed at territorial borders or well within the territory of another fish.

The relative percent occurrence of the above displays and behavior patterns, determined from quantitative observations at sites 1B and 1D, was calculated (Table 10). In addition, the context of displays and behavior patterns observed throughout the study period was analyzed qualitatively (Table 11).

Reproductive Behavior and Ecology

Variable numbers of observations were made on a total of 19 mated pairs of *A. melanopus* with observed egg clutches. In all confirmed cases (10 in all) the female was larger than the male. Furthermore, no reproducing male fish was estimated to be smaller than 60 mm SL. The largest reproducing female was estimated to be 85 mm SL. There

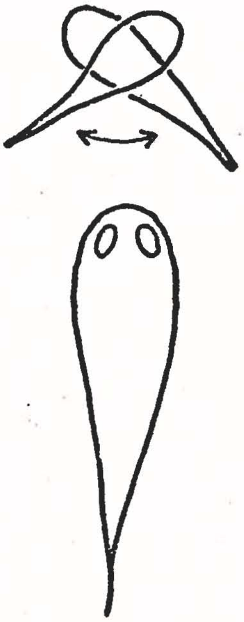


Figure 8. Tail-jerking display. Sketch (view from above) shows a small displaying fish in front of a larger recipient fish.

Table 10. The relative percent occurrence of displays and behavior patterns observed in _Amphiprion melanopus_ individuals during quantitative observation sessions at sites 1B and 1D.

Display or Behavior Pattern	Number of Observations	Relative Percent Occurrence	Concurrence With Other Displays No.	Concurrence With Other Displays %
Attack/Escape (considered as a unit event)	89	38	57	64
Raised dorsal	74	31	66	89
Head shaking	47	20	7	15
Threat	11	5	8	73
Head standing	8	3	5	62
Dorsal leaning	3	1	1	33
Tail jerking	3	1	0	0
Clicking*	0	0	0	0
Anemone biting*	0	0	0	0
Tentacle nibbling*	0	0	0	0
TOTAL	235	100	144	61

*Observed at times other than during the quantitative observation sessions of 28 January 1975 to 10 April 1975 on which these data are based.

able 11. Qualitative analysis of context in observed intraspecific displays and behavior patterns of the anemonefish *Amphiprion melanopus*.

Display or ehavior Pattern	Occurrence Within Subterritory of		Relative Size of Recipient Fish			Concurrent Behavior (If Observed)	Response of Recipient Fish (If Observed)	Type and Number of Observations		
	Displayer	Other Fish	Smaller	Larger	Either			Quantitative Field Obs.*	Additional Field Obs.	Holding Tank/ Aquarium Obs.
ttack (A)	Yes	No[†]	X[ψ]			RD	E, RD, HSh, TJ	89	Many	Many
scape (E)	No	Yes		X[ψ]		RD	-	88	Many	Many
hreat (T)	Yes	No[†]			X	RD	E, HSh, DL	11	>11	0
aised dorsal (RD)	Yes	Yes			X	A, E, T, HSh, C	E, RD, HSh, DL, TJ	74	Many	Many
ead shaking (HSh)	Yes	Yes			X	RD, HSt, DL	HSh, cessation of pursuit	47	Many	Many
ead Standing (HSt)	No	Yes		X		HSh	-	8	1	>1
orsal leaning (DL)	Yes	Yes			X	HSh	-	3	>5	>12
ail jerking (TJ)	No	Yes			X	-	RD, cessation of pursuit	3	9	7
licking (C)	Yes	No		-		RD	-	0	Many	0
nemone biting (AB)	Yes	Yes		-		-	-	0	5	1
entacle nibbling (TN)	Yes	No		-		Spawning	-	0	6	0
TAL	8	7	1	2	5	-	-	323	>37	>21

*Summarized in Table 9.

[†] Exceptions are adult breeding fish inside juvenile subterritory.

[ψ] Occasional exceptions observed, but only once during quantitative sessions.

were no observed instances of polygamy, though no careful observations of multi-adult populations were made.

Of 28 active nests observed (Figure 9, for example), the following characteristics were shared by a majority:

1) Nests were located on the surface of limestone rock (dead coral skeleton).
2) Nests were usually positioned on surfaces that were more vertical than horizontal.
3) The shape of the rock near the nest appeared to provide concealment and protection through concavity, overhang, or similar features.
4) Tentacles of surrounding anemones in a normal (daytime) state of distention covered the nest either partially or completely.

Contracted anemones in the area of the nest were always observed immediately prior to, and sometimes as much as a day prior to, spawning. In addition, at those nests where algal growth was normally observed, there was a striking lack of algal growth immediately prior to spawning. Mutal substrate-biting behavior was observed on one occasion immediately prior to spawning at site 1D.

The mean length of time nests were utilized by 12 adult pairs was approximately 6 months (Table 12). Only two of ten nest changes were obviously related to some particular event. One nest change followed the loss and replacement of an adult male, while the other change followed destruction of part of the coral head where the nest was located.

Figure 9. Nest of anemonefish population 1N, photographed at approximately 1000 o'clock on 21 February 1976. Eggs (located between arrow and fish) were spawned just prior to photograph, and anemones have not yet redistended to cover nest.

Table 12. Nest longevity in breeding pairs of *Amphiprion melanopus* observed for at least 5 lunar months.

Breeding Pair	No. Lunar Months Observed	No. Nests Utilized	$\bar{x}$ Nest Longevity (Lunar Months)
1B	16	2	8.0
1D	10	2	5.0
1E	5	1	5.0
1F	7	1	7.0
1G	9	1	9.0
1H	14	3	4.7
1J	14	1	14.0
1L	14	3	4.7
1M	13	4	3.3
1N	6	1	6.0
2B	5	2	2.5
2C	10	1	10.0
ALL	123	22	5.6

Spawning in four different adult pairs was observed on five separate occasions. In all five cases, spawning was initiated 2 to 2.5 hours after sunrise (0830-0900) and lasted approximately 1.5 hours. The following account of spawning behavior at site 1D on 17 October 1975 is given, as it is the most complete of the five:

> Observation distance was approximately 1.5 m. Anemones in the immediate vicinity of the nest were contracted. White genital structures were quite visible on both the female and male. Close observation of these structures revealed that the female ovipositor was larger than the male urogenital papilla. The female ovipositor was tapered or rounded while the male structure was conical and pointed in shape. Both structures were located approximately half-way between pelvic and anal fins. Behavioral events were observed closely between 0835 and 0900. During this 25-minute period both the female and male spent most of their time at the nest. The female (whose normal center of activity is approximately 0.5 m away from nest) left the nest only 12 times, usually going to her normal center of activity, but only momentarily. The ovipositor was never retracted during such visits. The male, however, whose normal center of activity is the nest itself, came out of the nest site frequently. Male forays were never as far as those of the female. The male genital structure was never retracted during such forays. Both female and male were observed in an upside down position (female most of the time, male part of the time) at the nest, as the nest was located on the underside of overhanging limestone rock. Pectoral fins of the female were observed to flutter rapidly during slow passes over the nest (skimming). It was not certain whether rapid fluttering of pectorals occurred during male passes over the nest. Six times the male was observed to slide its mouth along an anemone tentacle to the tip, once while upside down, and at least twice followed by mouth activity near the eggs (actual mouth contact with eggs was not certain). The anemone tentacles did not contract as a result of this activity. At 0920 the female was spending less time at the nest than the male. At 1030 anemones surrounding the nest had already redistended and eggs were completely covered with tentacles. Both male and female were occupying their normal centers of activity at this time, but the genitalia of both fish were still visible (approximately two thirds retracted).

The incubation period for eggs of A. melanopus was determined to be 7.5 or 8.5 days, based on the following observed hatching schemes: (1) 100% hatched in 7.5 days, (2) n % hatched in 7.5 days and (100-n) % hatched in 8.5 days, and (3) 100% hatched in 8.5 days. Scheme (1) was observed three times, scheme (2) was observed twice, and scheme (3) was observed twice. These determinations are based on several early morning observations and the assumptions that eggs are spawned shortly after sunrise (reported above) and hatched shortly after sunset (reported below).

Based on confirmed spawning days and many repeated observations of eggs in varying stages of incubation, a description of the visual characteristics of eggs at successive days of incubation was obtained. These characteristics are summarized in Table 13.

Several forms of behavior, in addition to egg fanning (to be discussed below), were observed in both the male and female at the nest during the incubation period. With the exception of mutual occurrences, these behavior patterns occurred at greater rates in the male than in the female. Behavior patterns observed include head shaking, mutual head shaking, substrate biting, mutual substrate biting, concurrent head shaking/substrate biting, mutual concurrent head shaking/substrate biting, mutual mouth touching, and egg mouthing. All forms of reproductive behavior occurring before, at the time of, and after spawning are summarized in Table 14.

Egg fanning was the most time-consuming of all reproductive behaviors observed. This activity was performed almost entirely by the male. The data (Figure 10) may not accurately reflect the total time or energy expended by the male, however, as increased numbers of

Table 13. Macrocharacteristics of the naturally occurring eggs of <u>Amphiprion</u> <u>melanopus</u> at successive days of incubation.

Days After Spawning	Description of Eggs
0	Exposed if just spawned; bright orange with small white anterior tip; ovoid; length approximately 2 mm.
1	Orange to red with small white anterior tip.
2	Dark red with small white anterior tip; ellipsoid.
3	Dark red; dark pigmentation in eye region.
4	Dark red; black circular eyes.
5	Dark red; small silver circles on black eyes; elongate.
6	Reduced reddish area; large silver circles on black eyes.
7	Greatly reduced reddish area; transparent areas prominent; large silver or gold circles on black eyes; length approximately 2.5 mm.

Table 14. Summary of nest-associated behavior in the anemonefish *Amphiprion melanopus*.

Behavior	Time of Occurrence Prior to Spawning	 During Spawning	 During Incubation	Number of Observations
Anemone contraction	X			4
Egg fanning			X	Many
Egg mouthing		X	X	6
Head shaking/substrate biting	X		X	5
Mutual mouth touching			X	1
Mutual head shaking			X	1
Mutual head shaking/ substrate biting			X	3
Mutual substrate biting	X			1
Pectoral fluttering		X		Many
Skimming		X		Many
Substrate biting			X	3
Tentacle nibbling		X		6

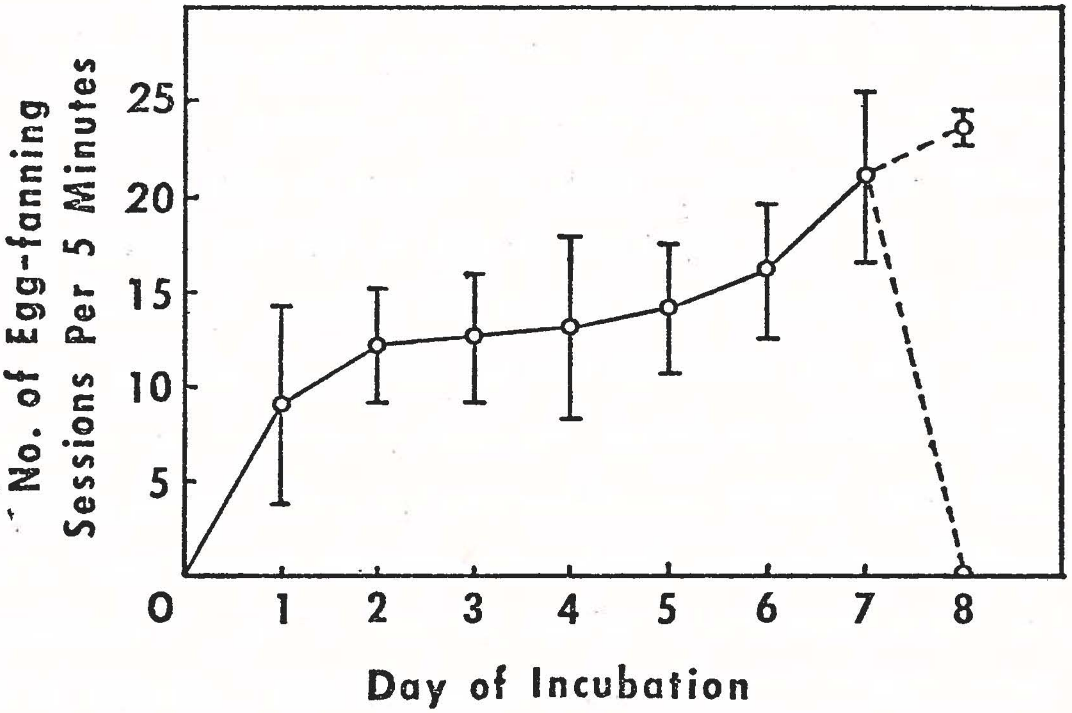


Figure 10. Mean egg-fanning activity at sites 1B, 1D, 1H, 1J, 1L, 1M, and 1N on successive days of incubation. There are four to nine observations for each day of incubation. Dashed lines indicate activity on Day 8 when either all eggs were still present (upper, n = 2) or less than half the eggs were present (lower, n = 4). Error limits are ± 1 standard deviation.

pectoral fin strokes per fanning session were also observed during latter days of incubation. The time spent by male fish fanning eggs during latter stages of incubation appeared to allow for little other activity, including feeding.

Neither egg fanning nor any other form of egg care was observed at night, with the exception of the night of hatching. Furthermore, anemones were observed in a partial state of contraction at night, often exposing the nest and eggs to some extent.

Hatching was observed once at site 1M on 16 March 1976 (full moon). Both the adult female and male (especially the male) remained near the nest and actively fanned and mouthed eggs through the entire hatching period. Nearly all the eggs hatched between 1 and 2 hours after sunset, though the exact time of peak hatching activity was not determined (it was felt that the underwater light might effectively delay hatching). High tide was predicted to occur 1.5 hours after sunset, and there were strong water currents at the time of hatching.

The reproductive cycle was found to be directly related to moon phase (Table 15 and Figure 11). Two spawning peaks (Figure 11), reflecting the usual occurrence of two spawnings per lunar cycle, were observed. Peak centers are considered to be -5 and +6 days from the full moon, based on the apparent peaks, the spread of the data, and the mean number of days between spawnings in multiple-spawn cycles. The latter was found to be 10.9 days (s = 1.6, n = 62, and range = 8-16), indicating a mean "rest period" of 3.5 days for fish spawning two or three times per lunar cycle (assuming a 7.5 day incubation period). Individual pair fecundity is also shown in Table 15.

Table 15. Pair fecundity and lunar periodicity of observed egg clutches in the anemonefish *Amphiprion melanopus*.

Breeding Pair	No. Lunar Months Observed	No. Spawns Observed*	No. Spawns Per Lunar Month		Occurrence of Spawns Relative to Full Moon (Day)	
			$\bar{x}$	Range	$\bar{x}$	Range
1B	13.5	23	1.7	1-3	0	-11 to +11
1D	8.3	14	1.7	1-2	+2	-9 to +11
1E	5.0	7	1.4	1-2	+1	-5 to +4
1F	4.5	4	0.9	0-1	+2	-7 to +11
1G	6.9	12	1.7	1-2	+3	-4 to +10
1H	12.2	19	1.6	1-2	+2	-6 to +12
1J	11.8	21	1.8	0-3	0	-8 to +12
1L	10.0	19	1.9	2-2	+2	-5 to +9
1M	11.0	17	1.6	1-2	0	-8 to +12
1N	5.7	11	1.9	1-2	+2	-7 to +9
1T	2.3	5	2.2	2-2	+1	-6 to +7
2A	2.0	3	1.5	1-2	0	-14 to +14
2B	4.3	7	1.6	1-2	-1	-12 to +6
2C	8.5	12	1.4	1-2	+1	-9 to +7
2E	2.0	3	1.5	1-2	0	-7 to +4
3B1	0.9	1	1.1	-	-4	-
3B2	0.9	2	2.2	-	-5	-6 to -4
3B3	0.3	1	3.3	-	0	-
4A	0.3	1	3.3	-	-2	-
TOTAL	110.4	182	1.6	0-3	+1	-14 to +14

*Though no exact counts of the number of eggs were made, clutches were estimated to contain 200-400 eggs.

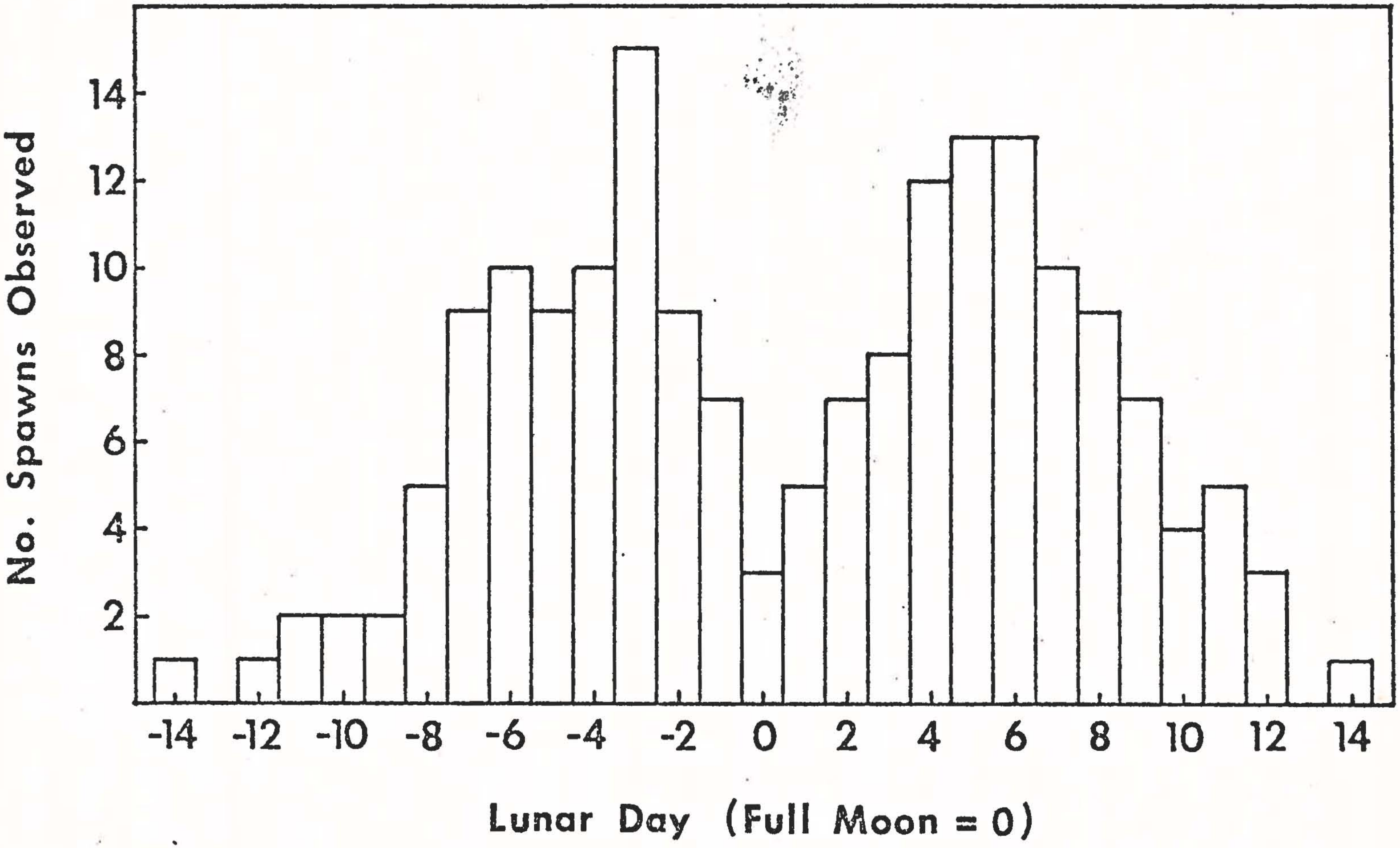


Figure 11. Frequency distribution of the number of spawns observed in breeding populations of *Amphiprion melanopus* versus lunar day of spawning.

There is little evidence for any seasonal change in spawning activity (Table 16). Breeding pair 1J did not spawn in July. However, other noted failures to spawn over an entire month interval were related to changes in nest site. Spawning may have occurred, but I did not discover the new nest site until the following month. Any seasonal reduction in spawning activity not detected in the present study would have to occur between May and July.

Territorial Behavior

General observations have shown that all A. melanopus individuals 20 mm SL or larger utilize a foraging home range that is larger than the area covered by co-resident sea anemones. Individuals less than 20 mm SL, however, were never observed to lose contact with anemones for any appreciable length of time. Only a portion of the home range of individuals 20 mm SL or larger was actively defended against other conspecifics. Each individual was observed to occupy a single anemone or small group of anemones a large portion of the time. Such a position or location is referred to as the "center of activity" in the present study, and, when actively defended against conspecifics by means of attack, threat, or raised dorsal, as the center of territory. Individuals less than 20 mm SL were observed to move freely throughout the anemone cluster without defending territory and without receiving territorial aggression from larger fish. Individuals 20 mm SL or larger, however, defended territory of varying size and with varying levels of intensity. Overlapping territories were observed when both breeding adults and juveniles were present. In such cases adults defended large territories within which subadults or juveniles defended

Table 16. The number of spawns per lunar month of five breeding pairs of *Amphiprion melanopus* observed for 1 year.

Lunar Month	Breeding Pair					Total
	1B	1H	1J	1L	1M	
March 75	2	1	2	2	2	9
April	1	2	1	2	2	8
May*						
June*						
July	1	1	0	0†	0†	2
August	1	2	2	0†	1	5
September	2	1	2	2	1	8
October	2	2	2	2	1	9
November	1	2	2	2	2	9
December	1	2	2	2	2	9
January 76	2	1	3	2	2	10
February	2	2	2	2	2	10
March	1	1	2	1	2	7

*Not observed.

†Probably due to change in nest site and unobserved spawns, rather than to no spawns.

mutually exclusive subterritories (Allen, 1975). Though the total area defended by the mated female and male was essentially the same, their centers of activity were usually separate. There was no aggressive behavior observed between members of the mated pair, at their respective centers of activity, toward each other. The mated male's center of activity coincided with the nest, while the mated female's center of activity was usually some distance from the nest.

A considerable portion of the behavior of A. melanopus consisted of activity related to defense of territory, ranging from the damage-inflicting chase and attack to simple, ritualized threat. Agonistic behavior comprised 74% ($n = 235$) of all displays and behavior patterns observed during quantitative observation sessions (Table 10). Eighty-two percent of this agonistic behavior was initiated by the mated pair; the recipients of agonistic behavior were non-breeding fish in 91% of the observations (Table 17). Field observations also indicated that the area defended was proportional to the size of the fish (Table 18). This was especially obvious in the case of the adult female.

Experimental studies (Figures 12-15) showed that the mated female and male defended essentially the same territory against a conspecific intruder, and that territorial behavior was inversely proportional to distance from the center of territory (Tables 19, 20, and 21). Analysis of variance showed this relationship to be significant at a level greater than 0.001 at site 1D ($F_{6,\ 28} = 7.54$, x-axis, and $F_{8,\ 18} = 21.59$, y-axis) and at a level greater than 0.01 at site 1J ($F_{5,\ 29} = 4.62$).

Table 17. Analysis of the initiators and recipients of agonistic behavior (attack, threat, and raised dorsal) in populations of _Amphiprion_ _melanopus_.*

Population Members Observed	Agonistic Behavioral Events Initiated By No.	 %	 Received By No.	 %
Breeding Adults	93	82	10	9
Other Members	21	18	102	91
Total	114	100	112	100

*Based on quantitative field observations (summarized in Table 10).

Table 18. The relationship between size of fish and distance from center of activity at which attack or threat was observed to occur naturally.*

Individual Anemonefish	Size (mm SL)	Distance of Attack/Threat from Center of Activity (cm)		
		$\bar{x}$	s	n
1B1 (♀)	85	38.6	11.2	40
1B2 (♂)	80	24.5	15.9	7
1B3	60	26.3	10.3	7
1B4	40	14.1	4.5	5
1D1 (♀)	85	30.5	28.4	9
1D2 (♂)	80	21.2	16.4	30
1D3	65	13.6	3.4	2

*Based on quantitative field observations (summarized in Table 10).

Figure 12. Preparing a "bagged" anemonefish for territorial experiments at site 1D.

Figure 13. Placing the bagged conspecific fish into test position "0" at site 1D for a 5-minute trial during which the number of attacks on the intruder by both the resident female and male fish are counted.

Figure 14. Experimental trial with conspecific intruder at site 1J (position "-61"). Adult female (1J1) attacks model intruder while adult male (1J2) remains close by (above intruder). Numbered arrows indicate the following: (1) nest location at edge of area JA, (2) subadult fish 1J3 in area JB, and (3) area JC.

Figure 15. Closeup of the behavior of resident anemonefish at site 1J (position "-61") toward model intruder. Female (left) attacks intruder head-on, while male (right) attacks from behind. Subadult fish (below intruder) remains near anemones in area JB.

Table 19. The number of attacks per 5 minutes on a conspecific intruder (56 mm SL) by the resident breeding pair of <u>Amphiprion</u> <u>melanopus</u> at site 1D (x-axis).

Distance From Territorial Center (cm)	Date of Experiment														
	25 Jul. 75		11 Aug. 75		15 Aug. 75		22 Aug. 75		27 Aug. 75		8 Sep. 75		Total		
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	Both
+132	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2
+107	9	0	3	0	0	0	0	0	0	0	0	0	12	0	12
+78	29	13	41	19	6	2	3	0	0	0	0	0	79	34	113
-79	49	33	55	25	36	25	33	5	4	0	30	22	207	110	317
-127	49	18	49	19	43	15	8	0	30	1	3	2	182	55	237
-173	16	6	24	5	3	0	8	1	1	0	0	0	52	12	64
-237	0	0	20	4	0	0	0	0	0	0	0	0	20	4	24

Table 20. The number of attacks per 5 minutes on a conspecific intruder (56 mm SL) by the resident breeding pair of <u>Amphiprion melanopus</u> at site 1D (y-axis).

Distance From Territorial Center (cm)	Date of Experiment										
	21 Aug. 75		25 Aug. 75		29 Aug. 75		10 Sep. 75		Total		
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	Both
+161	4	2	0	0	0	0	0	0	4	2	6
+128	28	18	0	0	5	2	0	0	33	20	53
+100*	13	13	3	0	0	0	0	0	16	13	29
+61*	5	5	0	0	1	0	0	0	6	5	11
0†	62	30	66	29	47	60	36	43	211	162	373
-60	44	14	19	1	9	5	1	0	73	20	93
-83	28	5	3	0	3	0	1	0	35	5	40
-106	2	0	3	0	0	0	0	0	5	0	5
-154	0	0	0	0	0	0	0	0	0	0	0

*Apparent territorial center of a <u>Eupomacentrus lividus</u> individual. Low levels of <u>A. melanopus</u> attack are due largely to high levels of <u>E. lividus</u> attack on resident <u>A. melanopus</u>.

†Female and male centers of activity are displaced slightly, in this case, in opposite directions from "0" (see Figure 4).

Table 21. The number of attacks per 5 minutes on a conspecific intruder (56 mm SL) by the resident breeding pair of <u>Amphiprion melanopus</u> at site 1J.

Distance From Territorial Center (cm)	Date of Experiment														
	2 Nov. 75		6 Nov. 75		10 Nov. 75		12 Nov. 75		14 Nov. 75		17 Nov. 75		Total		
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	Both
+139	19	17	0	0	8	3	0	0	0	0	29	2	56	22	78
+46	36	30	67	41	44	30	5	6	24	19	30	23	206	149	355
0	46	42	50	55	35	47	1	5	4	13	25	27	161	189	350
-61	32	30	41	27	28	25	1	6	0	4	1	2	103	94	197
-138	*	*	28	18	19	9	10	14	2	0	12	1	71	42	113
-259	0	0	0	0	0	0	0	0	0	0	12	0	12	0	12

*Data lost.

Though mated female and male territories were essentially identical in size, a subtle difference in emphasis was observed and demonstrated experimentally. The ratio of concurrent female to male attacks (R) on a conspecific intruder was observed to increase with distance from center of territory (Tables 22 and 23). These ratios were placed into two groups (territorial center and territorial periphery), ranked, and subjected to the Mann-Whitney *U*-test. The test showed peripheral R's to be significantly greater than central R's at the 0.01 level ($U_{7, 7} = 43$, 1D x-axis, and $U_{14, 8} = 91$, 1J). There were insufficient data, using the criteria footnoted in Table 22, to test 1D y-axis. The relationship between distance from territorial center, the total number of attacks (T), and the ratio of female to male attacks (R) on a conspecific intruder is illustrated in Figures 16 and 17.

Despite attempts to nullify possible habituation effects during experiments with conspecific intruders (by using a different point sequence for each repetition), there is evidence that both a short-term and long-term diminished response to continued exposure to the experimental fish occurred (Table 24). Recovery from the short-term effect was approximately 3 days for both adult pairs tested. Recovery from the long-term effect was not observed; however, it had to have been greater than 10 days. These effects should have biased all analyses performed equally, as each test point was subjected to the same effect on a given day, and the effects were observed in both female and male fish.

Though not well quantified, the size of the conspecific intruder was shown to affect the maximum distance of attack by resident adult

Table 22. The ratio of concurrent female to male attacks on a conspecific intruder by the resident adult pair of _Amphiprion melanopus_ at site 1D (x-axis).*

Distance From Territorial Center (cm)	Date of Experiment						Total
	25 Jul.75	11 Aug.75	15 Aug.75	22 Aug.75	27 Aug.75	8 Sep.75	
+107							13.00
+78	2.23	2.16					2.32
-79	1.48	2.20	1.44	6.60		1.36	1.88
-127	2.72	2.58	2.87		30.00		3.31
-173	2.67	4.80					4.33
-237		5.00					5.00

*For statistical analysis, positions +78 and -79 were taken as the territorial center while positions +107, -127, -173, and -237 were considered the territorial periphery. To reduce the possibility of large bias due to low levels of attack, ratios were calculated only where combined female/male attacks were greater than 10. Where denominators were 0, the ratio obtained by increasing both the numerator and denominator by one was utilized.

Table 23. The ratio of concurrent female to male attacks on a conspecific intruder by the resident adult pair of *Amphiprion melanopus* at site 1J.*

Distance From Territorial Center (cm)	Date of Experiment						Total
	2 Nov.75	6 Nov.75	10 Nov.75	12 Nov.75	14 Nov.75	17 Nov.75	
+139	1.12		2.67			14.50	2.55
+46	1.20	1.63	1.47	0.83	1.26	1.30	1.38
0	1.10	0.91	0.74		0.31	0.93	0.85
-61	1.07	1.52	1.12				1.10
-138		1.56	2.11	0.71		12.00	1.69
-259						13.00	13.00

*Methods of analysis footnoted in Table 22 apply here also. Positions +46, 0, and -61 constitute the territorial center for statistical applications, in this case.

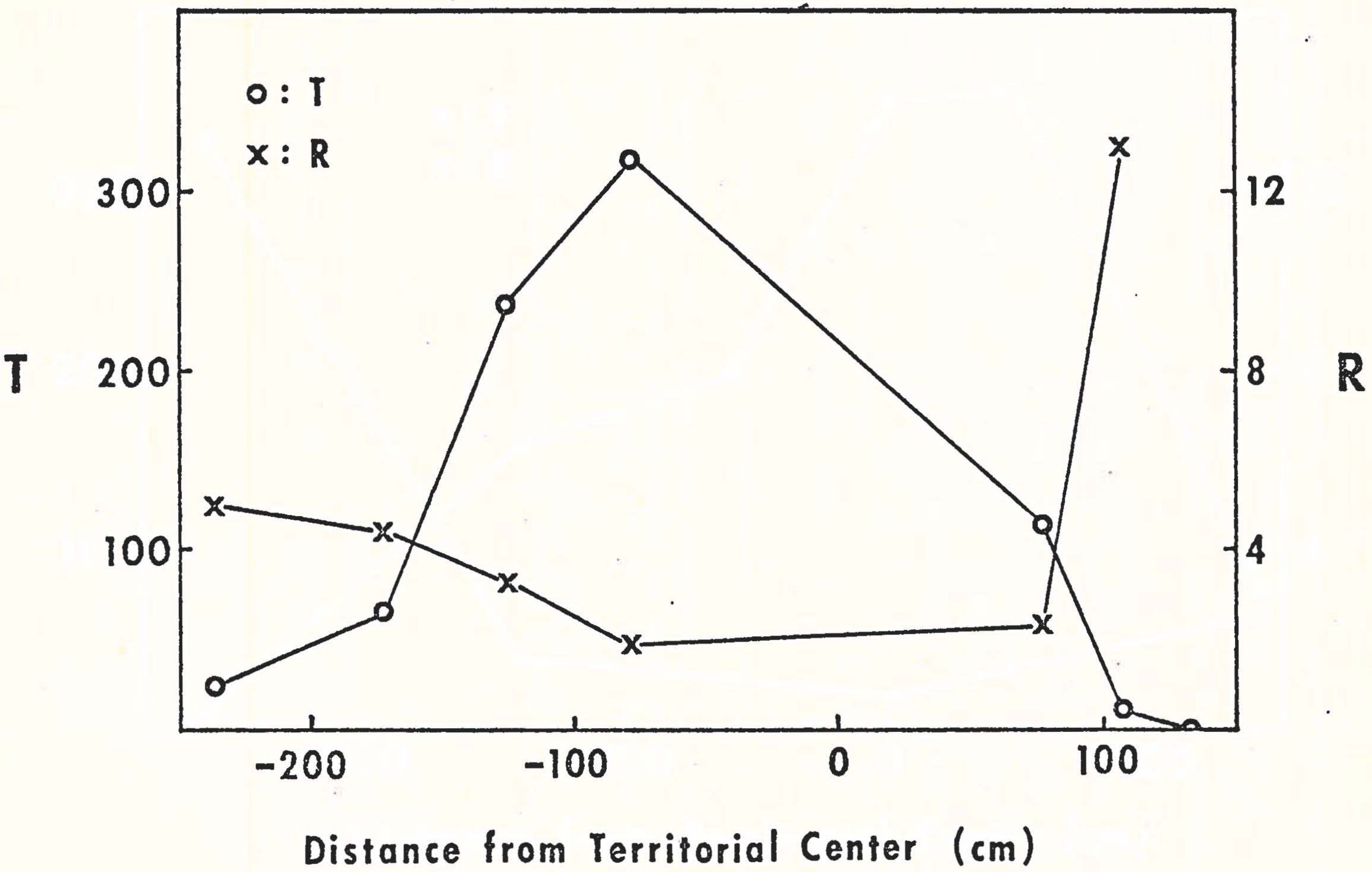


Figure 16. The effect of distance from territorial center on both the total number of attacks (T) and the ratio of female to male attacks (R) on a conspecific intruder at site 1D (x-axis).

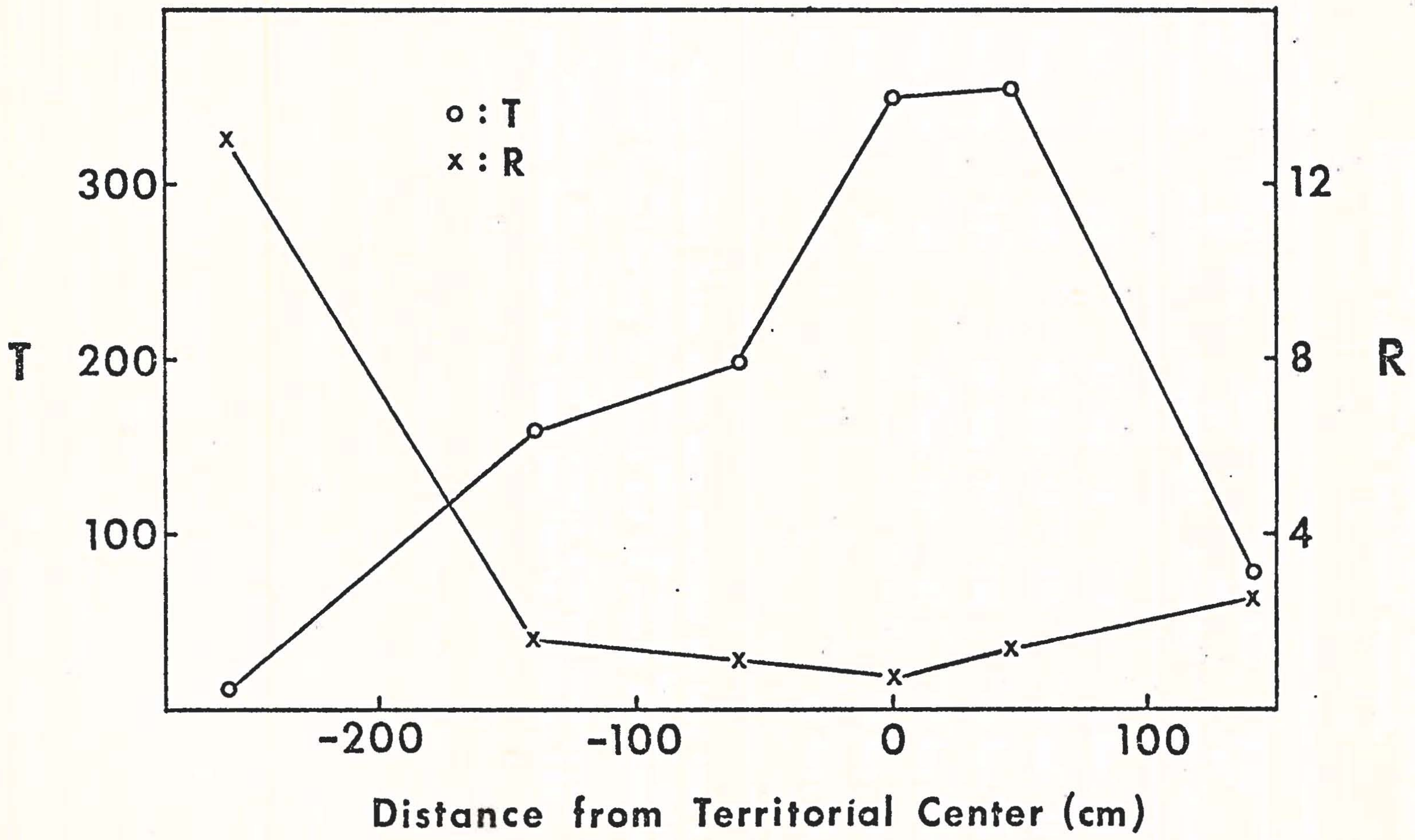


Figure 17. The effect of distance from territorial center on both the total number of attacks (T) and the ratio of female to male attacks (R) on a conspecific intruder at site 1J.

Table 24. Summary of the total number of attacks by resident adult Amphiprion melanopus on a conspecific intruder for each experimental series, showing both short-term and long-term diminished response to continued exposure.

1D x-axis		1D y-axis		1J	
Date of Experiment	Total No. of Attacks	Date of Experiment	Total No. of Attacks	Date of Experiment	Total No. of Attacks
25 Jul. 75	234	21 Aug. 75	273	2 Nov. 75	299[†]
11 Aug. 75	266	25 Aug. 75	124	6 Nov. 75	327
15 Aug. 75	130	29 Aug. 75*	132	10 Nov. 75	248
22 Aug. 75*	58	10 Sep. 75*	81	12 Nov. 75*	48
27 Aug. 75*	36			14 Nov. 75*	66
8 Sep. 75	57			17 Nov. 75	164

*Experimental dates which were preceded by less than a 3-day "rest period" or interval during which no experimental intruder was introduced (considering 1D x-axis and 1D y-axis simultaneously).

[†] Contains an estimate of a single missing observation according to procedure described by Steel and Torrie (1960) p. 139.

fish at site 1D (Table 25). Results were complicated by diminished response with time, which became obvious when the results were placed in chronological order. There is some evidence from these data that recovery from long-term diminished response was occurring after 13 days (9 Oct. 75 to 22 Oct. 75).

Reintroduction of the 69-mm SL conspecific intruder at site 1D, position "0," 3 months after the disappearance of the adult female fish, failed to elicit any attacks from the resident adult male fish on either of two occasions. Furthermore, there was no territorial aggression observed in the resident adult male toward either of two small juveniles (approximately 25 and 40 mm SL) present at the time. At the same time, site 1D could be considered under-inhabited because the total standard length of resident fishes was only 145 mm (see Table 3 and Figure 6).

Subadult and juvenile fish were also shown to defend territory (Table 26). Their subterritories were, however, much smaller than those of the adult breeding pair, and were located entirely within the area defended by the adult pair. Considerable agonistic behavior between adult members and non-adult members was observed as a result. Successful defense of subterritory (subadult or juvenile threat, for example, resulting in adult escape or failure to enter subterritory) appeared to be related to the size of the defender. The small juvenile was rarely successful in excluding adults, but the subadult fish was often successful. Border conflicts between subadult and adult territorial centers were observed frequently in the form of threats, tail jerking, and escape. On occasion the subadult fish was

Table 25. The effect of size of intruder on both the maximum distance of attack and the number of attacks per 5 minutes by the resident adult pair of <u>Amphiprion</u> <u>melanopus</u> at site 1D.*

Date of Experiment	Size of Intruder (mm SL)	Maximum Distance of Attack (cm)	No. Attacks Per 5 Min.
15 Sep. 75	69	237	78
24 Sep. 75	69	237	54
26 Sep. 75†	36	173	2
1 Oct. 75	36	79	2
5 Oct. 75	36	79	7
6 Oct. 75†	69	237	3
9 Oct. 75	56	79	6
22 Oct. 75	56	173	1
24 Oct. 75†	56	79	1

*Data are arranged chronologically so that diminished response with continued exposure, in addition to the effect of size of intruder, can be evaluated.

†Experimental dates preceded by less than a 3-day "rest period."

Table 26. The number of attacks per 5 minutes by subadult (1J3) and juvenile (1J4) subterritorial fish on a conspecific intruder (38 mm SL) at site 1J.*

Test Position†	8 Dec. 75			12 Dec. 75			16 Dec. 75			18 Dec. 75ψ			Total		
	1J3	1J4	Adult	1J3	1J4	Adult	1J3	1J4	Adult	1J3	1J4	Adult	1J3	1J4	Adult
JA/JB	1	0	H	2	0	L	2	0	H	0	0	H	5	0	H
JB	27	0	L	57	0	1	62	0	L	55	0	N	201	0	L
JB/JC	0	0	L	2	2	N	13	2	L	0	16	L	15	20	L
JC	0	7	H	0	79	N	0	58	N	0	76	N	0	220	L
JA/JC	0	0	H	0	4	L	0	1	H	0	0	H	0	5	H

*Concurrent adult attack levels indicated as heavy (H), light (L), or none (N).

†JA represents adult center of activity, JB represents 1J3 center of activity, and JC represents 1J4 center of activity (see Figure 5). Combinations of these (such as JA/JB) represent positions half-way between the two centers.

ψExperiment preceded by less than a 3-day "rest period."

even observed to attack a conspecific intruder as far from the nest as did the adults.

Removal of a subterritorial individual from a population of A. melanopus resulted in subterritorial instability for the remaining non-adult fish (Table 27). Fish 1J3 alternately defended its original territory and the newly vacated site before strengthening a hold on its original territory. The vacated site was successfully reoccupied by an immigrant fish some 3 weeks after removal of the original resident. No diminished response to continued exposure to a conspecific intruder occurred in subadult or juvenile fish.

There were essentially no attacks by resident adult A. melanopus on a non-conspecific intruder (Table 28). Only one species (Dascyllus aruanus) was introduced, however.

Laboratory and field experiments with models of A. melanopus failed to produce any conclusive results in terms of visual stimuli important in eliciting territorial behavior. Laboratory-held fish responded initially to a natural model (by attacking the plastic bag holding it) but not long enough for a series of controlled experiments. In the field, members of population 1J failed to respond to the model. Lack of response was probably due to either the color or absence of movement in the model.

Four species of fish were observed to attack A. melanopus individuals: Dascyllus aruanus, D. trimaculatus, Chromis caerulea, and Eupomacentrus lividus. Attacks by the first three species were rare and probably related to the proximity of A. melanopus to their spawns. E. lividus attack rates, however, were quite numerous at times and may have been related to common food resources (benthic algae)

Table 27. The number of attacks per 5 minutes by a subterritorial, subadult fish (1J3) on a conspecific intruder (38 mm SL) after removal (on 22 Dec. 75) of a subterritorial juvenile (1J4) from the population.*

Test Position[†]	27 Dec. 75		30 Dec. 75		4 Jan. 76		6 Jan. 76[ψ]		Total	
	1J3	Adult	1J3	Adult	1J3	Adult	1J3	Adult	1J3	Adult
JA/JB	0	H	0	H	2	H	0	H	2	H
JB	37	L	0	H	39	L	89	N	165	L
JB/JC	6	L	0	H	0	L	0	N	6	L
JC	8	L	75	L	0	H	0	H	83	L/H
JA/JC	0	H	0	H	0	H	0	H	0	H

*Concurrent adult attack levels indicated as heavy (H), light (L), or none (N). Test position JC was successfully reoccupied by an immigrant fish on 16 Jan. 76 (see Table 9 for more information).

[†] Test positions shown in Figure 5. Combinations (such as JA/JB) represent positions half-way between the two centers.

[ψ] Experiment preceded by less than a 3-day "rest period."

Table 28. The number of attacks per 5 minutes on an adult <u>Dascyllus aruanus</u> (46 mm SL) by resident adult <u>Amphiprion melanopus</u> at site 1J.

Distance From Territorial Center (cm)	Date of Experiment 22 Dec. 75		24 Dec. 75		8 Jan. 76		12 Jan. 76		Total	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
+139	0	0	0	0	0	0	0	0	0	0
+46	0	0	0	0	0	0	0	0	0	0
0	1	0	3	0	1	0	0	0	5	0
-61	0	0	0	0	0	0	0	0	0	0
-138	0	0	0	0	0	0	0	0	0	0
-259	0	0	0	0	0	0	0	0	0	0

aggressively defended by this fish. The territories of *E. lividus* and *A. melanopus* often overlapped. *A. melanopus*, in turn, was observed to attack all the above species of fish except *E. lividus*. In addition, *Acanthurus triostegus*, *Chaetodon lunula*, and *Mulloidichthys samoensis* were attacked by *Amphiprion melanopus* adults at times.

Intraspecific rates of aggression were far greater than interspecific rates (Table 29). A comparison of observed rates in the present study with those reported for other *Amphiprion* species indicated that *A. melanopus* is probably more aggressive than *A. chrysopterus* but less so than *A. perideraion*.

Table 29. A comparison of observed aggression rates (number of agonistic encounters per 15 minutes) in the present study with those reported for <u>Amphiprion</u> species elsewhere.

Individual Observed	$\bar{X}$ No. Per 15 Minutes Intraspecific	Interspecific	No. Min. Observed
1B1	1.2	0.3	165
1B2	1.0	0	60
1B3	0.5	0	165
1B4	0.5	0	60
1D1	0.5	0	85
1D2	1.7	0	115
Allen's (1975) <u>A. perideraion</u> <u>(4 individuals)</u>	8	2	?
Allen's (1975) <u>A. chrysopterus</u> <u>(2 individuals)</u>	0.5	0.5	?
Allen's (1975) <u>A. tricinctus</u> <u>(2 individuals)</u>	0	0	?
Okuno's (1963) Aquarium-held <u>A. frenatus</u>	7*	15*	50
Okuno's (1963) Aquarium-held <u>A. chrysogaster</u>	0*	18*	100

*Highest values observed.

DISCUSSION

Population Ecology

Observations on the colonization of sea anemones by the anemonefish Amphiprion melanopus show that this species exploits the Physobrachia sp. microhabitat extensively. The fish is capable of exploiting other actiniarian microhabitats, but it may be outcompeted there by other species of anemonefish. Alternatively, colonization may be affected by water depth or reef zonation. The anemone Radianthus sp., for example, was successfully colonized by A. melanopus in shallow reef-flat waters but only by A. chrysopterus in deeper water or on slopes. Fricke (1974) showed a similar zonation effect on Radianthus colonization by the anemonefish A. bicinctus. More than 80% of the Radianthus (n = 27) occurring in shallow reef-flat waters were uninhabited by A. bicinctus, whereas only 21% or fewer of the Radianthus (n = 95) occurring at the reef margin or in deeper water were uninhabited by A. bicinctus.

Physobrachia sp. density obviously determines the density of A. melanopus populations over the reef habitat. Within anemone aggregations, the areal coverage of anemones, rather than their numbers, determines the number and size of fish sharing the aggregation. For a given area of anemones there appears to be an upper limit (carrying capacity) on the total standard length of inhabiting anemonefish. The data (Tables 3 and 4 and Figure 6) support Allen's (1975) general observation that the carrying capacity of an anemone is influenced by the size of the anemone and the number and size of Amphiprion occupants. The adaptive significance of this close relationship is uncertain. The anemones apparently provide some resource, perhaps protection or food, that is required by the fish. The observation that breeding populations require proportionally more anemone area suggests that food is the critical resource, since proportionally more food would be required to raise a brood. However, no studies have shown food to be a limiting factor in plankton-feeding pomacentrids, nor has interspecific territoriality (discussed below) indicated that food is critical. If protection afforded by the anemones is critical, increased anemone requirements in breeding populations may reflect egg requirements for anemone contact mediated through adult egg-mouthing activity.

The even size frequency distribution suggests much higher turnover rates for smaller size classes than for larger ones, as it is unlikely that 100% survival occurs from size class to size class. Fricke (1974) observed that population size frequency distributions in A. bicinctus varied over reef-zone types. Overall, somewhat fewer numbers were observed in the intermediate size classes of that species.

Observed variability in the occurrence of multiple white bars on young juvenile fish raises the question of whether this phenomenon is adaptive from a behavioral standpoint or simply ontogenetic and non-adaptive. If it is adaptive from a behavioral standpoint, retention of multiple bars may indicate sex. Alternatively, multi-barred individuals may draw less agonistic behavior from other resident fish or, perhaps, less predation.

A calculated turnover period of 4 years per fish agrees well with Allen's (1975) longevity determination of at least 5 years for some

Amphiprion including A. melanopus. This calculation is based on the most stable populations with considerable adult protection, however, and should not be taken as a population sample mean. Though a relatively high number of adults were lost in one year (Table 8), all "replacements" were small juveniles as one would expect.

Immigration is another phenomenon contributing to optimum population size. The relatively short period in which "vacated" territories were refilled by migrating fish suggests that migratory input may be just as important as larval recruitment at large stable populations. Non-breeding populations, furthermore, may function as a reserve of fish from which, periodically, some individuals successfully migrate to larger populations.

Display Behavior

The relatively high percentage (75%) of observed behavioral events determined to be directly related to defense of territory (largely from conspecifics) is some index of the importance of territory in A. melanopus. Another 20% of observed behavioral events (head shaking) apparently function as appeasement, since they greatly reduced the chance of continued aggressive behavior by another fish. The same function was ascribed to head shaking behavior by Moyer and Sawyers (1973) and Moyer and Bell (in press), all of whom referred to the behavior as "convulsive body-jerking." Allen (1975) ascribed the same function to this form of behavior though he called it a "submissive posture." Another likely appeasement display observed was head standing (3%). Described also as a "submissive posture" by Allen (1975), this display may be typical of some behavior patterns which appear to have evolved as ritual forms of behavior (communicating some message) from other forms of behavior (with no message content) (Manning, 1972). In this case substrate biting probably functions to clean the nest, whereas the very similar head-standing behavior may serve to communicate appeasement or submission.

Dorsal leaning (1%) appears also to function as an appeasement or submissive display in A. melanopus as it did for those Amphiprion studied by Allen (1975). This behavior was often observed as the initial response of resident fish toward a conspecific intruder during field experiments. Though heavy attacks on the intruder invariably followed dorsal leaning, the intruder was a potentially "dangerous" fish to the defender. It is believed that dorsal leaning was utilized initially, when the defender was "dangerously" close to the intruder for the first time, to prevent attack by the intruder. Subsequently, the intruder was attacked heavily and dorsal leaning was never observed again in the defender. The frequent use of dorsal leaning by small juveniles during similar experiments with laboratory-held defenders strengthens this interpretation. These findings contrast with those of Moyer and Bell (in press) in studies of A. clarkii. Their study indicated that dorsal leaning functions as a "low intensity threat posture" in A. clarkii.

Tail jerking (Figure 8) was utilized frequently, along with threat, escape, and raised dorsal, during border confrontations, apparently to prevent further aggression when a fish had gone too far into another's territory. Clicking was not observed sufficiently to assess its function. Anemone biting has no apparent function and may be a displacement activity. A similar form of behavior, tentacle nibbling, was observed during spawning and may be related in some way to anemone biting.

In addition to outright attack, then, most of the behavior patterns discussed above appear to communicate threat or appeasement at various levels of intensity and are either related to defense of territory or, perhaps, to dominance (in the case of appeasement displays, discussed more fully below).

Reproductive Behavior and Ecology

Nest preparation in *A. melanopus* may be nearly identical to that reported by Moyer and Bell (in press) for *A. clarkii*. They observed both substrate-biting behavior and anemone-biting behavior by the adult pair prior to spawning. Though I did not actually observe anemone-biting behavior prior to spawning, it seems likely anemone biting as well as substrate biting (observed prior to spawning) are the elements of nest-preparation behavior. Substrate biting was reported to be the major form of courtship behavior in *A. clarkii* (Moyer and Bell, in press). It may function similarly in *A. melanopus*, though I did not observe the activity in a situation where it could not have functioned simply to clean the nest area of algae. Nest longevity is related to changes in breeding partnership, to changes in the physical features of the territory, and to unknown events, based on observed changes in nest location immediately following such events.

Spawning behavior is similar to that reported for *A. clarkii* by Moyer and Bell (in press) except for the time of occurrence and the occurrence of substrate biting. Substrate biting was not observed during A. melanopus spawning. Variations in observed incubation periods of eggs are probably due to temperature fluctuation, as was reported by Bell (1976) for A. clarkii eggs.

Though quantified in a different way than that of Allen (1975) on A. chrysopterus and Moyer and Bell (in press) on A. clarkii, egg-fanning behavior in A. melanopus does not drop during intermediate stages of incubation, but rather levels off until the final stages. Whether the function of egg fanning is to provide water movement alone or increased oxygen concentration near the eggs is not known. Eggs that do not receive vigorous agitation do not hatch (Allen, 1975). Lack of observed nocturnal egg care suggests that egg metabolism slows down at night and that egg-eating predators are not nocturnal.

The lunar cyclic nature of reproduction in the anemonefish A. melanopus is likely an adaptive response to tidal rhythm rather than to varying light intensity due to moon phase (as suggested by Allen, 1975), though it may be keyed by the latter. There are several reasons for this. Spawning occurs during the daytime when moonlight confers no particular advantage. In addition, there appears to be no nocturnal egg care, an observation supported by studies of the anemonefish A. clarkii (Moyer and Bell, in press). Care of eggs does occur on the night of hatching, as reported for A. clarkii (Moyer and Bell, in press), but even so, the second clutch of a lunar cycle typically hatches when there is essentially no light from the moon (13 days after full moon). Hence, parental care does not appear to be facilitated by the light of the moon. Nor would the photopositive response of newly hatched larvae (Allen, 1975 and Moyer and Bell, in press) be optimally facilitated by the observed hatching synchrony. However, assuming that hatching regularly occurs approximately an hour after sunset (as was observed once in the present study and demonstrated in the anemonefish A. clarkii by Moyer and Bell, in press), observed hatching periodicity is synchronized very closely to high tides (Table 30). Analysis of variance shows that combined water heights (C1 plus C2: Table 30) on peak hatching days (+2 and +13 days from full moon) are significantly greater, at the 0.001 level ($F_{1, 34} = 18.5$), than water heights of days 90° out of phase (±7 days) in the lunar cycle.

The functional significance of such an adaptive response is probably related to dispersal. Greater water velocity and stronger currents are present, at least on reef-flat areas, during high tides. These stronger currents would aid in the immediate dispersal of newly hatched larvae from the area of the nest, where predators might otherwise concentrate and take a large percentage of the larvae. Long-distance dispersal is not implied, because the advantageous effect of the observed correlation lasts only for the duration of the high tide. On the basis of the above hypothesis, reproductive cycles of anemonefish at other localities could be predicted and tested with a knowledge of moon phase and tidal cycles.

The lack of seasonal breeding activity in observed populations of A. melanopus is consistent with the findings of Allen (1975) for several Amphiprion species in the tropical waters of Enewetak Atoll. A. clarkii at Miyake Island, Japan were highly seasonal, spawning only six to eight times between May and October (Bell, 1976). Fricke (1974) reported an annual fecundity of 13.7 clutches in Red Sea A. bicinctus. My observed annual fecundity of 24 clutches in the most stable pairs

Table 30. A comparison of predicted water heights 1 hour after sunset on observed peak hatching days with water heights of days 90° out of phase (±7 days) in the lunar cycle.*

	Predicted Water Height One Hour After Sunset							
	-7 Days		Observed Peaks		+7 Days			
Lunar Month	C1	C2	C1	C2	C1	C2	Lunar Monthly Range	Displacement From Peak Water Ht. (Days)†
Jan. 75	0.7	0.4	2.1	1.9	1.0	1.5	-0.4 to 2.7	
Feb.	0.7	0.1	1.5	2.0	1.0	1.5	-0.4 to 2.7	+2
Mar.	0.6	0.2	1.4	2.0	0.9	1.5	-0.2 to 2.6	
Apr.	0.6	0.4	1.5	1.9	0.7	1.3	-0.4 to 2.5	+1
May	1.1	0.6	1.2	2.1	0.9	1.5	-0.4 to 2.5	
Jun.	1.2	1.2	1.4	2.0	1.0	1.4	-0.6 to 2.5	+1
Jul.	1.7	1.[illegible]	1.3	2.2	1.4	1.6	-0.6 to 2.6	
Aug.	1.9	1.5	1.7	2.2	1.5	1.8	-0.5 to 2.6	-1
Sep.	2.0	1.7	1.8	2.1	1.7	1.9	-0.1 to 2.6	
Oct.	1.9	1.7	1.9	2.3	1.7	2.0	-0.4 to 2.6	-1
Nov.	1.7	1.6	2.1	2.0	1.4	1.8	-0.6 to 2.6	
Dec.	1.5	1.0	2.1	2.0	1.1	1.6	-0.7 to 2.6	-1
$\bar{x}$	1.1		1.9		1.4			0

*Based on tide tables published by U. S. Department of Commerce (1975 and 1976). All values were obtained by linear interpolation and are expressed in feet above mean lower low water. C1 and C2 represent the water heights corresponding to Clutch 1 (first observed hatching peak, +2 days from full moon) and Clutch 2 (second observed hatching peak, +13 days), respectively. Because there are two peak hatching days nearly two weeks apart, a 180° phase shift (in a lunar cycle) would result in peak hatching days that nearly coincide with those observed.

†This analysis of water height shows the number of days from the observed peaks that the actual, predicted, highest water heights occurred, one hour after sunset, for every other lunar month of 1975.

of A. melanopus probably reflects year-long optimal temperature and food conditions at Guam.

Territorial Behavior

The results show that both juveniles and adults defend territory. Juveniles as small as 20 mm SL apparently begin to restrict themselves to a small area within the anemone cluster and defend, or attempt to defend, the small subterritory. Success in excluding other individuals from a subterritory appears to be related to both the size of the defender and the intruder. Though, for the most part, juvenile and subadult subterritories are mutually exclusive, adults often successfully enter the subterritories of co-resident juveniles and subadults. Larger juveniles or subadults are more successful at excluding adults from their subterritories than are smaller individuals. The territories of juveniles and subadults are termed subterritories because they are mutually exclusive units of the anemone cluster located entirely within the area actively defended by the adult breeding pair (only a slightly different interpretation than that of Allen, 1975). Subadult fish may also aid, to some extent, in the defense of adult territories from conspecific intruders.

The occurrence of subterritories within adult territory implies conflict between adult and juvenile residents. Obviously these cannot be absolute territories, and hence a dominance hierarchy must also be operating within individual populations. These dominance hierarchies are probably related to the success with which subterritorial residents are able to exclude adults from their respective subterritories. The degree of success, in turn, is probably related to the size of the defender. Breeding adults, however, are always dominant over all other co-residents. There was no observed aggression between members of the adult pair; therefore, neither the female nor the male is considered dominant over the other.

The observed equality in the size of mated female and male territories is in contrast to the observations of Moyer and Sawyers (1973) in the anemonefish A. clarkii. A. clarkii female territories were much larger than male territories, and in some cases overlapped several males' territories. I did not, however, observe multi-adult territories. In addition, Moyer and Sawyers (1973) observed an inward female territorial emphasis, whereas male territorial energy focused outward in defense of the periphery. An opposite emphasis, though subtle, was observed in A. melanopus. Moyer (personal communication) believes there are considerable differences between the behavior of members of the Clarkii Complex (Allen, 1975) and members of the Ephippium Complex (which includes A. melanopus).

A. melanopus territories are not, for the most part, stable, rigid, and well defined entities. Observations have shown that territories fluctuate in size, emphasis (location of peak attack behavior within the subterritory), and even location within the anemone cluster from time to time (Tables 19, 21, and 27). Loss of individuals, changes in nest location, and immigration all contribute to territorial instability. Dominance relationships, however, are apparently maintained at all times.

Despite high levels of intraspecific aggression against intruders, some immigrant fish are successful in gaining territory. Furthermore, reduction in intraspecific aggression at under-inhabited sites (as was observed at site 1D) may facilitate increased immigration and growth of resident fish. This suggests a feedback mechanism whose effect would be the optimum colonization of all anemone sites.

There is little defense of territory against other species of fish, though, in some cases, this may be due to the rarity of incursion of certain species. Some species, in fact, regularly occupy space completely within _A. melanopus_ territory, and, presumably, have similar food requirements to those of _A. melanopus_. Most interspecific attacks, furthermore, appear to be directly related to defense of the nest or eggs rather than feeding areas. Allen (1975) suggested that interspecific territoriality functions to a certain extent in the protection of anemones from coelenterate-feeding fishes.

In light of the above observations, then, territorial behavior in _A. melanopus_ appears to function as a means of protecting resources necessary for survival (food and shelter), and, in addition, as a means of protecting the adult pair bond as a successful reproductive unit. Optimum population size may also be facilitated by territoriality, but this effect, ultimately, can be equated to reproductive success.

SUMMARY

1. The anemonefish Amphiprion melanopus colonizes aggregations of the anemone Physobrachia sp. extensively and nearly exclusively, even though capable of inhabiting other anemone species.

2. The total standard length of anemonefish at each anemone aggregation is a function of the total areal coverage of resident anemones. This relationship suggests that some critical anemonefish resource (such as food, shelter, or protection) is directly related to the quantity of anemone present. Breeding populations require proportionally more anemone area than non-breeding populations.

3. Individuals of stable breeding populations have a mean turnover period of approximately 4 years. Both larval recruitment and inter-population migration may contribute to the optimum population size. The mean population size is 3.51 individuals per anemone aggregation.

4. The display repertoire consists of some 11 behavior patterns (excluding reproductive behavior), many of which are related directly to defense of territory. Other displays, functioning as appeasement or submissive postures, may be related to dominance within populations.

5. Nest preparation probably consists of anemone biting and substrate biting. Spawning occurs 2-2.5 hours after sunrise and lasts for approximately 1.5 hours. Egg fanning occurs only during daylight hours and increases in frequency as eggs mature. Hatching occurs 1-2 hours after sunset on the seventh or eighth day of incubation.

6. Spawning is related to moon phase with peak activity at -5 and +6 days from the full moon. Hatching peaks correlate strongly with high water heights (high tides) and currents, suggesting that hatchling predation may have been the selective force resulting in the observed rhythmicity. There is no seasonal periodicity in spawning activity.

7. Both juveniles (as small as 20 mm SL) and adults defend territory. Mated adult females and males defend essentially the same territory, which is considerably larger than the area covered by resident anemones. Juveniles and subadults, however, defend mutually exclusive areas (subterritories) within the confines of the anemone aggregation. Consequently, adult-juvenile agonistic encounters are frequent. The adult female fish defends territorial peripheries to a significantly greater extent than does the male. Large conspecific intruders are attacked more heavily and at greater distances than are small ones.

8. Territorial fluctuations in size, emphasis, and location are related to loss of individuals, changes in nest location, and immigration.

9. There is reduced agonistic behavior, resulting in increased immigration and growth of juveniles, in adult fish whose mates are lost. This suggests a feedback mechanism whose effect is to stabilize populations at their optimum size.

10. Interspecific territorial behavior is sporadic and appears to be directly related to defense of the nest or eggs rather than defense of feeding areas.

11. Territorial behavior in _A. melanopus_ probably functions to protect some vital resource related to the actiniarian host as well as to increase reproductive success

LITERATURE CITED

Albrecht, H. 1969. Behavior of four species of Atlantic damselfishes from Columbia, S. America, (Abudefduf saxatilis, A. taurus, Chromis multilineata, C. cyanea; Pisces Pomacentridae). Z. Tierpsychol. 26:662-686.

Allen, G. R. 1973. Amphiprion leucokranos, a new species of pomacentrid fish, with notes on other anemonefishes of New Guinea. Pac. Sci. 27(4):319-326.

_________. 1975. The anemonefishes: their classification and biology. 2nd ed. T. F. H. Publ., Neptune City, N. J.

Baerends, G. P. 1957. The ethological analysis of fish behavior. In M. E. Brown (Ed.), The physiology of fishes, Vol. 2. Academic Press, N. Y.

Baerends, G. P., and J. M. Baerends-van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. Behaviour Supplement 1, 1-242.

Bell, L. J. 1976. Notes on the nesting success and fecundity of the anemonefish Amphiprion clarkii at Miyake-Jima, Japan. Japan. J. Ichthyol. 22(4):207-211.

Breder, C. M., and D. E. Rosen. 1966. Modes of reproduction in fish. Amer. Mus. Nat. Hist., N. Y.

Clarke, T. A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the Garibaldi, Hypsypops rubicunda. Ecol. Mono. 40(2):189-212.

___________. 1971. Territorial boundaries, courtship, and social behavior in the Garibaldi, Hypsypops rubicunda (Pomacentridae). Copeia 2:295-299.

Erlich, P. R. 1975. The population biology of coral reef fishes. Ann. Rev. Ecol. Syst. 6:211-247.

Fishelson, L. 1965. Observations and experiments on the Red Sea anemones and their symbiotic fish A. bicinctus. Bull. Sea Fish. Res. Stat. Haifa 39:1-14.

___________. 1970. Behavior and ecology of a population of Abudefduf saxatilis (Pomacentridae, Teleostei) at Eilat (Red Sea). Animal Behaviour 18:225-237.

Fricke, H. W. 1974. Oko-Ethologie des monogomen Anemonenfisches Amphiprion bicinctus (Freiwasser untersuchung aus dem Roten Meer). Z. Tierpsychol. 36:429-512.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.

Korringa, P. 1947. The moon and periodicity in the breeding of marine animals. Ecol. Mono. 17(3):349-381.

Low, R. M. 1971. Interspecific territoriality in the pomacentrid reef fish Pomacentrus flavicada Whitely. Ecology 52:648-654.

Manning, A. 1972. An introduction to animal behavior. 2nd ed. Addison-Wesley Publ. Co., London.

Mariscal, R. N. 1966. The symbiosis between tropical sea anemones and fishes: a review. In R. I. Bowman (Ed.), The Galapagos. Univ. Calif. Press, Berkeley.

_____________. 1970a. A field and laboratory study of the symbiotic behavior of fishes and sea anemones from the tropical Indo-Pacific. Univ. Calif. Publ. in Zoology 91:1-33.

_____________. 1970b. The nature of the symbiosis between Indo-Pacific anemonefishes and sea anemones. Mar. Biol. 6(1):58-65.

Moyer, J. T., and L. J. Bell. In Press. Geographic variation, dominance, and reproductive behavior in Japanese populations of Amphiprion clarkii. Japan. J. Ichthyol.

Moyer, J. T., and C. E. Sawyers. 1973. Territorial behavior of the anemonefish Amphiprion xanthurus with notes on the life history. Japan. J. Ichthyol. 20(2):85-93.

Myerberg, A. A. 1972. Social dominance and territoriality in the bicolor damselfish Eupomacentrus partitus (Poey). Behaviour 41:207-231.

Myerberg, A. A., B. D. Brahy, and A. R. Emery. 1967. Field observations on reproduction of the damselfish Chromis multilineata (Pomacentridae), with additional notes on general behavior. Copeia 4:819-827.

Myerberg, A. A., and R. E. Thresher 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Amer. Zool. 14(1):81-96.

Okuno, R. 1963. Observations and discussions on the social behavior of marine fishes. Publ. Seto Mar. Biol. Lab. 11(2):281-336.

Qasim, S. Z. 1956. Time and duration of the spawning season in some marine teleosts in relation to their distribution. J. Cons. Perm. Int. Explor. Mer. 21(2):144-155.

Randall, J. E. 1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, Acanthurus triostegus sandvicensis. Pac. Sci. 25(2):215-272.

Rasa, O. A. 1969. Territoriality and the establishment of dominance by means of visual cues in Pomacentrus jenkinsi. Z. Tierpsychol. 26:825-845.

Reese, E. S. 1964. Ethology and marine zoology. Oceanogr. Mar. Biol. Annu. Res. 2:455-488.

Sale, P. F. 1972. Effect of cover on agonistic behavior of a reef fish: a possible spacing mechanism. Ecology 53:753-758.

_________. 1974. Mechanisms of coexistence in a guild of territorial fishes at Heron Island. Proceed. 2nd Intl. Symp. Coral Reefs 1:193-206.

Steel, R. C., and J. H. Torrie. 1960. Principles and procedures in statistics. McGraw-Hill, New York, N. Y.

Stevenson, R. A. 1963. Life history and behavior of Dascyllus albisella Gill, a pomacentrid reef fish. Ph.D. Dissertation, Univ. Hawaii. 221 pp.

U. S. Department of Commerce. 1975. Tide tables: high and low water predictions 1975: Central and Western Pacific Ocean and Indian Ocean. U. S. Government Printing Office, Washington, D. C.

____________________________. 1976. Tide tables: high and low water predictions 1976: Central and Western Pacific Ocean and Indian Ocean. U. S. Government Printing Office, Washington, D. C.

Verwey, J. 1930. Coral reef studies. I. The symbiosis between damselfishes and sea anemones in Batavia Bay. Treubia 12(3-4): 305-366.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Belknap Press, Cambridge, Mass.