REPRODUCTION AND RECRUITMENT IN THE BLUEHEAD WRASSE *THALASSOMA BIFASCIATUM* IN BARBADOS

By

Ione Hunt von Herbing

Institute of Oceanography,
McGill University, Montreal
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ABSTRACT

Spawning and recruitment in the bluehead wrasse Thalassoma bifasciatum was studied on seven fringing reefs on the west coast of Barbados. Spawning occurred throughout the year but was highest between January and June with a peak in March/April. Seasonal variation in spawning resulted primarily from variation in group spawning, only secondarily from variation in pair spawning. Within a month, group spawning occurred most frequently around new and full moons, but there was no lunar periodicity to pair spawning. Nearshore currents have their maximum offshore velocity during these periods on the study reefs. Recruitment occurred throughout the year with a peak between July and August. Peak recruitment therefore followed peak spawning by a time period that approximated the duration of the larval life. This suggests that the timing of recruitment is primarily controlled by the timing of spawning. Post-recruitment mortality on most reefs was density-dependent, suggesting that the bluehead wrasse in Barbados is space-limited. Previous studies have suggested that bluehead wrasse in Panama are recruitment-limited. This difference between Barbados and Panama is consistent with the observation that the average population density of bluehead wrasse in Barbados is three times that of Panama. Barbados populations appear to be in a cycle of high density and resource/space limitation. Panama populations are in a cycle of low density and recruitment-limitation. The perspective that coral reef fish are either recruitment-limited or space-limited may be too extreme. A given species may be recruitment-limited in one location and space-limited in another.

Per capita mating success of terminal phase males in the bluehead wrasse populations in Barbados was significantly higher than either initial phase males or females. This is consistent with the size advantage hypothesis for sex reversal and phase transition. Pair spawning becomes less common on higher density reefs, the proportion of terminal phase males in the population decreasing with increasing reef density. This suggests that the competitive advantage of terminal phase males decreases on high density reefs. Lower proportions of terminal phase fish on high density reefs results from larger size at phase change on these reefs rather than from slower growth. Sex ratio in the initial phase populations was biased towards females (hermaphrodites) and as a consequence, per capita mating success of hermaphrodites and gonochores did not differ during initial phase. However, there was a higher proportion of gonochores (primary males) than hermaphrodites (secondary males) in the terminal phase population. This appears to result from a higher mortality of hermaphrodites than gonochores, and indicates that the probability of becoming terminal phase is greater for gonochores. The higher mortality of hermaphrodites may be a consequence of sex change. Gonochores and hermaphrodites did not differ in growth rates on the study reefs in Barbados. Given that per capita mating success of gonochores and hermaphrodites do not differ during initial phase, but that gonochores have a higher probability of becoming terminal phase, the question of why hermaphrodites are retained at present levels in bluehead wrasse populations was discussed.

RESUME

Le frai et le recrutement du Thalassoma bifasciatum ont été étudiés sur 7 récifs de corail en bordure de la côte ouest de la Barbade. Le frai est un phénomène qui s'étend sur toute l'année. On peut cependant noter une hausse entre janvier et juin avec un maximum en mars et avril. Cette variation saisonnière est le résultat d'un changement au niveau du frai de groupe dans un premier temps, et d'un changement du frai de couple dans un deuxième temps. Dans l'espace d'un mois, la fréquence du frai de groupe augmente durant la nouvelle et la pleine lune, tandis que le cycle lunaire n'affecte pas le frai de couple. De plus , les courants côtiers diriges au large atteignent une vitesse maximale sur les récifs étudiés lors de la nouvelle et de la pleine lune. Pour sa part, le recrutement s'étend sur toute l'année avec un maximum en juillet et en août. Une periode à peu près équivalente à la durée du stade larvaire sépare donc la période durant laquelle le frai atteint un maximum de la période optimale pour le recrutement. Ce fait suggère que la période de recrutement est majoritairement controlée par la période d'occurrence du frai. La mortalité suivant la période de recrutement est dépendante de la densité pour la majorité des récifs étudiés. On peut donc conclure que le T. bifasciatum de la Barbade est restreint par l'espace disponible. Des études antérieures sur le T. bifasciatum au Panama suggèrent qu'il est limité au niveau du recrutement. Cette différence entre la Barbade et le Panama est conforme au fait que la population de la Barbade a une densite trois fois plus élevée que celle du Panama. Les populations de la Barbade semblent être dans un cycle de haute densité ou elles sont limitées par les ressources et l'espace disponible. Les populations du Panama sont

dans un cycle de faibles densités et limitées par le recrutement. L'idée que les populations des récifs de corail soient limitées au niveau du recrutement ou au niveau de l'espace est peut-être extrême. En effet, une espèce pourrait être limitée au niveau du recrutement à un endroit donné et limitée par l'espace disponible ailleurs.

A la Barbade l'index représentant le nombre d'accouplements par individu chez mâles <u>T. bifasciatum</u> en phase terminale est significativement plus élevé que celui des mâles ou femelles en phase initiale. Ceci est conforme à l'hypothese du 'size advantage' pour le changement de sexe et de phase. Le frai de couple devient moins important sur les récifs à plus haute densité. En effet, la proportion de mâles en phase terminale dans l'ensemble de la population, diminue avec une augmentation au niveau de la densité des récifs. Ceci suggère que l'avantage compétitif des mâles en phase terminale diminue sur les récifs à haute densité. De plus,, la faible proportion d'individus en phase terminale sur ces récifs est causée par le fait qu'ils sont de plus grandes tailles au moment du changement de phase et non par le fait que leur croissance est plus lente. La proportion de mâles/femelles dans la population de phase initiale favorisait les femelles (hermaphrodites) et, en conséquence, durant cette phase , l'index représentant le nombre d'accouplements par individu chez les hermaphrodites n'était pas différent de celui des gonochores. Par contre, dans la population en phase initiale, on a observé une plus grande proportion de gonochores (males primaires) que d'hermaphrodites (mâles secondaires). Ceci semble être causé par un taux de mortalité plus éléve chez les hermaphrodites que chez gonochores et indique que la probabilité d'atteindre la phase terminale est plus éléve chez les gonochores. Le haut taux de mortalité des hermaphrodites est possiblement causé par un changemnent de sexe. Sur les récifs étudiés à la Barbade, les taux de croissance des gonochores et des hermaphrodites était semblables. Sachant que le nombre d'accouplements par individu des gonochores et des hermaphrodites n'est pas différent durant la phase initiale, et que la probabilité que les gonochores d'atteingnent la phase terminale est plus élévee, on a discuté de la présence et du maintient des hermaphrodites aux niveaux actuels chez les populations du _T. bifasciatum_.

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STATEMENT OF ORIGINALITY

This study is the first investigation of the population dynamics and reproductive ecology of the bluehead wrasse Thalassoma bifasciatum in Barbados, W.I. It is the first study to investigate seasonality of spawning in the bluehead wrasse and attempt to correlate this with seasonality of recruitment. It therefore allowed the question of whether recruitment pulses of the bluehead wrasse result from differential spawning or from differential survival in the plankton to be addressed. The study showed evidence for space-limitation in the population dynamics of T. bifasciatum in Barbados. By comparison with studies in Panama, this demonstrated for the first time that populations of the same species can be space-limited in certain locations but recruitment-limited in others. By investigating per capita mating success and proportions of hermaphrodites and gonochores in the initial phase and terminal phase populations of T. bifasciatum in Barbados, the study has contributed substantially to our understanding of the evolution and maintenance of sex change in the bluehead wrasse. By comparison with Panama, the study provides circumstantial evidence suggesting for the first time that island populations of the bluehead wrasse are genetically distinct.

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1 INTRODUCTION

The bluehead wrasse, Thalassoma bifasciatum (family, Labridae) is a common and conspicuous member of the coral reef fish communities of the Caribbean and tropical Western Atlantic. It feeds mainly on small benthic animals, on zooplankton and on ectoparasites of other reef fish. The mating system of this diandrous protogynous hermaphrodite and its mating behavior have been studied extensively (Randall and Randall 1963; Warner et al 1975; Robertson and Hoffman 1978; Warner and Robertson 1978 ; Warner and Hoffman 1980a,b; Warner 1984, 1985 ; Hoffman et al 1985). Populations consist of two sexual types and two color phases. The sexual types are primary males, which are male throughout their lifetime; and female hermaphrodites, which are born female and either remain female or become male (secondary males) at larger sizes. The two colour phases are called Initial Phase (IP) and Terminal Phase (TP). The less common brightly coloured blue-headed terminal phase individuals are either primary or secondary males and tend to be the largest (possibly oldest) in any local population (Rienboth 1970, 1973; Roede 1972; Warner and Robertson 1978). The more common individuals are the smaller less brightly coloured yellow and white initial phases, which can be either female or primary male.

Spawning in the bluehead wrasse occurs everyday around noon on fringing reefs in most areas of the Caribbean (Rienboth 1973; Warner et al 1975) and consists of a rapid ascent toward the surface with a release of gametes. Terminal phase individuals maintain temporary territories during the daily spawning period and pair spawn singly with individual females (Warner et al 1975). Initial phase males form groups of a few to several dozen individuals and group spawn with one or more females at a time (Warner et al 1975). Initial phase males can also obtain surreptitious matings by rushing in to join a pair spawn (streaking) or spawning singly with a female on the edge of a terminal phase male territory (sneaking) (Warner et al 1975). Individual terminal phase males may obtain a large number of matings per day while initial phase males are believed to have considerably lower mating success (Warner et al 1975).

Recent studies have noted that, while coral reef fish are relatively sedentary (most do not move between reefs and may not move more than a few metres during juvenile and adult life), most species, including the bluehead wrasse, have a pelagic larval phase lasting between a week and three months depending on the species (Brothers et al 1976; Pannella 1980; Brothers and McFarland 1981; Victor 1982, 1983b; Brothers et al 1983; Brothers and Thresher 1985; Thresher and Brothers 1985). After this period in the plankton, larvae settle to the reef surface or adjacent sand and/or Thalassia beds, (e.g. bluehead wrasse; Victor 1982), to metamorphose, gain pigmentation and recruit to the community of reef residents . It has been argued that the small seasonal changes in tropical latitudes produce an environment in which reproduction and hence recruitment can take place throughout, or at any time of, the year (Luckhurst and Luckhurst 1977). However, predation is thought to be high on reefs and in the plankton (Johannes 1978; McFarland 1982; Doherty 1983b; Williams et al 1986). Perhaps partly because of this, coral reef fish have high fecundities. For example, a female bluehead wrasse may produce approximately 2000 eggs per day of spawning (Rienboth 1973; Warner et al 1975).

Temporal variation in reproduction has been studied for some species of reef fish in the Caribbean (Randall 1961; Munro et al 1973; Powles 1975; Johannes 1978; Jones 1980). Reproductive peaks have been found to occur in the spring and sometimes in the autumn (Munro et al 1973; Powles 1975). Seasonal variation in spawning is now believed to be caused by seasonal changes in environmental conditions such as, temperature (Qasim 1955; Munro et al 1973; Russell et al 1974), oceanic currents and eddy formation (Watson and Leis 1974; Powles 1975; Lobel and Robinson 1983), rainfall (Lowe-McConnell 1975) and possibly food availability (Qasim 1955; Nikolsky 1963; Cushing 1972; Sissenwine 1984). In addition, reef fish show both lunar and diel variation in spawning (Johannes 1978). The fish of 24 tropical families, including Labrids, are known to have spawning peaks which are synchronized with full and/or new moon. Many of these species, including the bluehead wrasse, dash toward the surface to spawn, and do so at specific times of the day (Hobson and Chess 1978; Johannes 1978; Lobel 1978). This behavior is probably to ensure that eggs are released high above the reef surface into ebbing currents that carry them offshore and away from reef predators. Once offshore they may be retained near their natal areas by current gyres and eddies until they are conveyed back onto reefs (Lobel and Robinson 1983). One objective of the first section of the thesis is to investigate seasonal, lunar and diel patterns of spawning in Thalassoma bifasciatum and thereby comment on the relationship between spawning variation and variation in environmental conditions, including nearshore current systems.

Recent developments in the use of daily otolith increments have allowed determination of the temporal variation in settlement/recruitment in some tropical fish (Thalassoma bifasciatum, Victor 1983a, 1986a; Haemulom flavolineatum, McFarland et al 1985). From this technique and from juvenile fish censusing, settlement in a number of reef fish has been found to be high during the austral summer on the Great Barrier Reef (Russell et al 1977 ; Talbot et al 1978; Williams and Sale 1981; Williams 1983) and in spring and autumn in the Caribbean (Luckhurst and Luckhurst 1977; Shulman 1984; McFarland et al 1985). Peak settlement of the bluehead wrasse in Panama occurs in late summer and fall (Victor 1986a). The second objective of the first section of the thesis is to use otolith dating to investigate the temporal patterns of recruitment of Thalassoma bifasciatum in Barbados.

Many studies of coral reef fish have been carried out with the implicit assumption that reef fish populations are limited by two types of resource, space and food (Smith and Tyler 1972, 1975; Smith 1978; Clarke 1977; Itzkowitz 1977; Lassig 1977; Dale 1978; Anderson et al 1981). Of these, space has been thought to be the more limiting resource (Smith and Tyler 1972, 1975: Sale and Dybdahl 1975; Sale 1977, 1978) and heavy predation on the reef to be partly the consequence of limited availability of space/cover. Fish populations on the reef are therefore often considered to be 'space-limited' and competition for space, interacting with predation, is believed to maintain populations near numerical equilibrium. Competition for resources may in turn act as an agent of selection for evolution of narrower niches thereby allowing the high diversity of fish species characteristic of reefs (Anderson et al 1981). An alternative hypothesis, termed the 'lottery hypothesis', was developed by Sale (1977, 1978, 1982). He suggested that, if reefs were 'space-limited',recruitment can only occurr when space became available on the reef due to mortality. He argued that recruitment was random in the sense that what species recruited at any time depended only on what larvae were near to the reef and ready to settle when space became available on the reef. The implication is that periods of recruitment may be preceded by declines in the population density of fish on the reef. Victor (1983a, 1986a) suggested that reefs are 'recruitment-limited', i.e population size is governed mainly by the numbers of larvae surviving the planktonic phase. Recent studies in Australia have shown that mortality in the plankton is phenomenally high (one recruit is returned for every 100,000 to 1,000,000 eggs produced (Doherty 1983b; Williams et al 1986). Victor (1983a,1986a) assumed that spawning of Thalassoma bifasciatum was continuous throughout the year and therefore that temporal variation in recruitment resulted from temporal variation in survival in the plankton, not from temporal variation in either spawning or mortality on the reef. A third objective of the first section in the present thesis is to use the information gathered on temporal variation in reproduction, recruitment and population density of Thalassoma bifasciatum in Barbados to comment on whether populations of Thalassoma bifasciatum on Barbados reefs tend to be 'space-limited' or 'recruitment-limited'.

Bluehead wrasse populations consist of two sexual types (primary males and sequential hermaphrodites) and two colour phases (initial phase (IP) and terminal phase (TP)). However, the proportion of types within bluehead wrasse populations apparently varies with population abundance and reef size (Warner et al 1975; Warner and Robertson 1978; Warner and Hoffman 1980 a,b). Small populations of bluehead wrasse in Panama contained smaller proportions of IP males and larger proportions of both TP males and females (Warner and Robertson 1978; Warner and Hoffman 1980 a,b). In larger populations, IP males contributed up to 50% of the population while TP males and females decreased proportionately (Warner and Hoffman 1980 a,b). However, in all populations, TP males obtained the highest individual mating success of all sex types. The latter observation presumably explains why, under appropriate conditions, both IP males (i.e. primary males) and IP females (i.e. female hermaphrodites) become TP males i.e. it presumably explains why TP males are maintained in the bluehead wrasse populations. An interesting question is why IP males are maintained in bluehead wrasse populations (see Charnov 1982). If breeding sex ratios approximate 1:1, IP males will have lower per capita mating success than female hermaphrodites, since some portion of females mate with TP males. Hence, individuals would maximize life-time mating success by mating first as females and later as TP males.

It was first suggested that IP males could be maintained in bluehead wrasse populations by frequency dependent selection i.e. that the per capita mating success of IP males would increase and exceed that of females, the more rare IP males became (Warner et al 1975). The rationale was that females would become proportionately more common as IP males became more rare, that TP males would increasingly be unable to fertilize the available females, and hence that per capita IP male mating success would rise to exceed that of females. Note the assumption that the proportion of TP males would remain constant. However, if females became proportionately more common, they could respond to the proposed reduction in mating opportunities by transforming to TP males with increasing frequency. Hence the per capita mating success of IP males need not increase with increasing rarity. Warner and Hoffman (1980a) have subsequently acknowledged that frequency-dependent selection on its own may not maintain IP males in bluehead wrasse populations. Instead they suggested that IP males are maintained by differential selection in different habitats, since they observed that IP males have higher per capita mating success on large reefs than on small reefs (Warner and Hoffman 1980 a,b). Note that this observation does not specifically address the central question of whether the per capita mating success of IP males rises high enough to exceed that of females on large reefs.

Charnov (1982), and later Warner (1984), adopted an alternative approach. Charnov suggested that IP males could be maintained in bluehead wrasse populations if they had a higher probability of becoming TP males than did IP females; either through faster growth or lower mortality. The principal objective of the second section of the thesis is to investigate the effects of population density and reef size on per capita mating success, population composition, individual growth rate and mortality of <u>Thalassoma bifasciatum</u> in Barbados.

2 STUDY SITES

The island of Barbados lies between the latitude 13°04' and 13°20' north and longitudes 59°26' and 59°39' west in the Caribbean Sea. It is 140 km east of the Lesser Antilles island chain and 250 km north-northeast of Trinidad (Figure 1a). Currents around Barbados originate from the North Equatorial current during the winter months (November to April) and from the South Equatorial Current during the rest of the year (Parr (1938) in Powles 1975; Lewis et al 1962; Froelich et al 1978). Both currents flow to the west and flow around Barbados and are thought to create an unstable eddy system in the lee of the island (Emery 1972; Powles 1975; Peck 1978; Barbados Coastal Conservation Project 1984; Figure 1b).

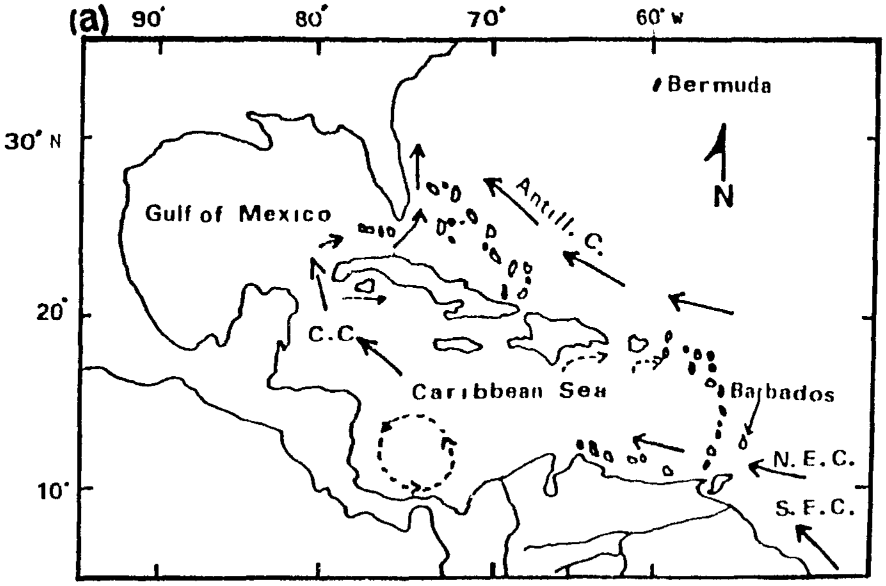
Populations of the bluehead wrasse were studied on seven large fringing reefs differing in size along the west coast of Barbados. They are located, from the north to the south of the island, as follows : Sandridge, Greensleeves, Glitter Bay, Heron Bay, North Bellairs, Golden Palms and Paynes Bay (Fig. 1b). All observations and censuses were carried out between September, 1984 and October, 1985.

The coral reefs of Barbados have been described in detail by Lewis (1960) and Stearn et al (1977). Inshore fringing reefs and outer bank reefs occur off the west and south coasts of the island. No typical fringing reefs are found on the windward (east) side of the island. A typical fringing reef of Barbados is composed of four major zones. From the shore seaward they are : the swash or breaker zone, the reef crest zone, the coalesced spur zone and the spur and groove zone (Fig. 2). These will be described sequentially.

Figure 1a. Geographic location of Barbados showing major Caribbean water current systems (after Froelich _et al_ 1978; Peck 1978).

Figure 1b. Map of Barbados showing location of study sites and probable nearshore currents (Murray _et al_ 1977; Peck 1978; Coastal Conservation Project 1984).

(a)


90°
80°
70°
60° W
30° N
20°
10°
Bermuda
N
Gulf of Mexico
Antill. C.
C.C.
Caribbean Sea
Barbados
N.E.C.
S.E.C.

(b)

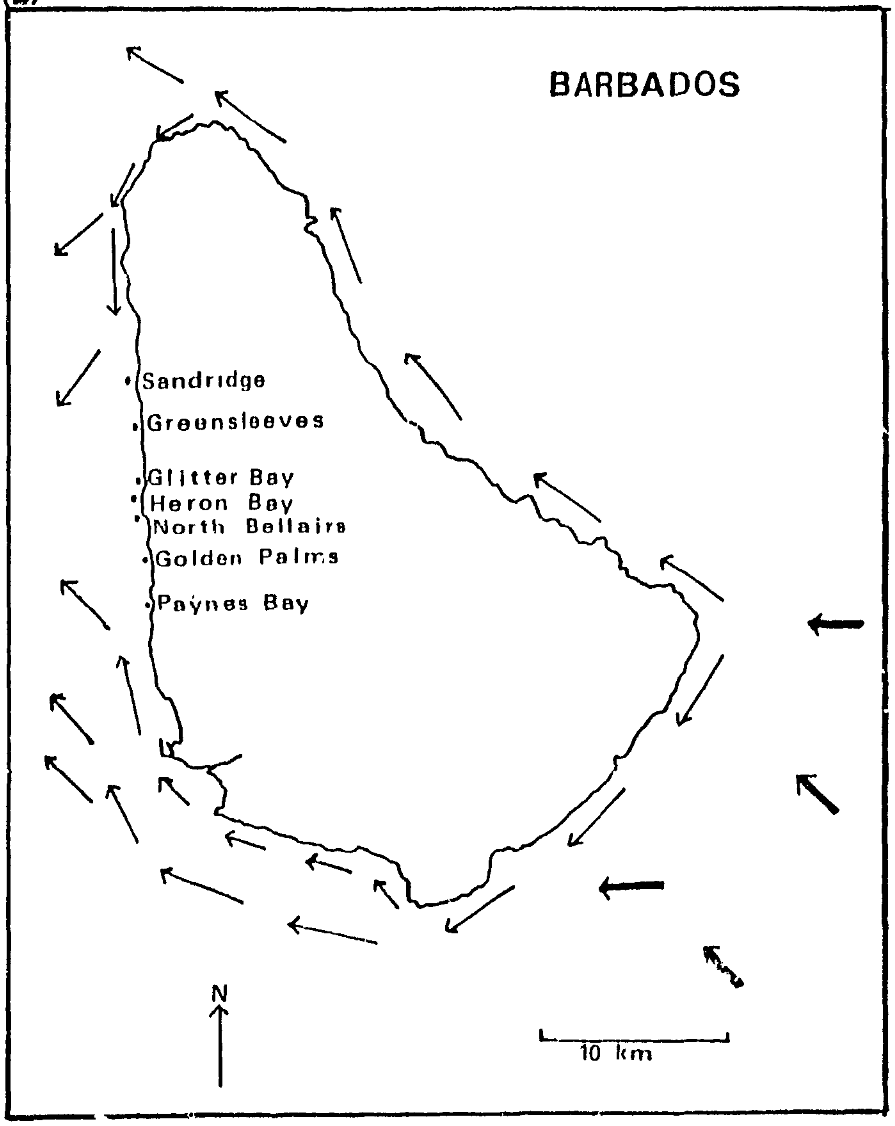

BARBADOS
Sandridge
Greensleeves
Glitter Bay
Heron Bay
North Bellairs
Golden Palms
Paynes Bay
N
10 km

Figure 2. Ecological zonation of North Bellairs reef, a typical fringing reef from the west coast of Barbados (after Stearn _et al_ 1977).

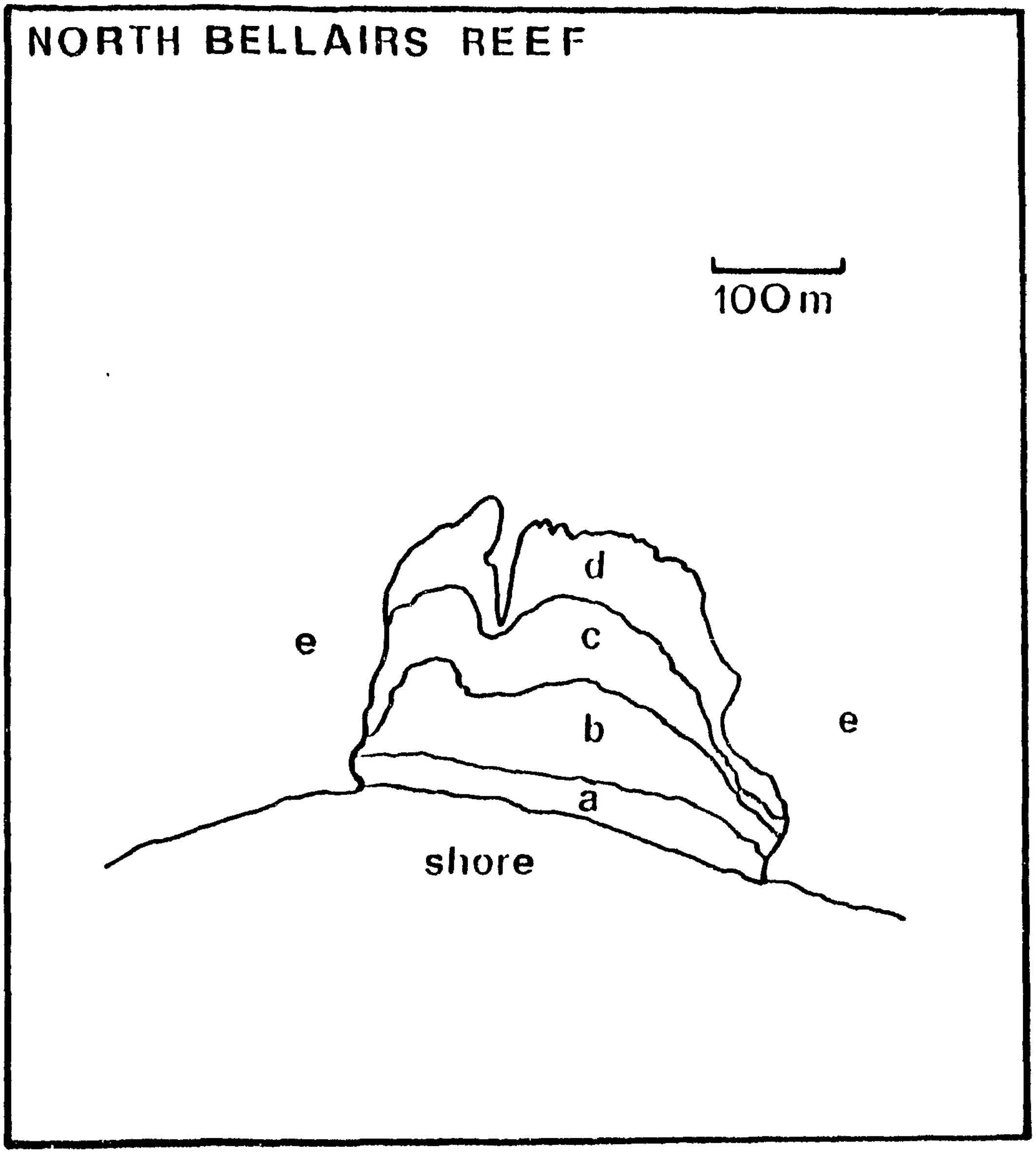
a = swash zone

b = crest zone

c = coalesced spur zone

d = spur and groove zone

e = sand


NORTH BELLAIRS REEF
100 m
d
e
c
b
e
a
shore

The narrow swash or breaker zone, where small waves break, runs parallel to the shore and is composed of sand and dead coral rock covered by filamentous algae. Bluehead wrasse are not abundant here, but young juveniles can often be found hiding within the coral rubble or among spines of the black sea urchin Diadema antillarum. The crest zone of the fringing reef is seaward of the swash zone. Parts of this zone can become emergent during very low spring tides and waves often break here during winter storms. It is composed of irregular patches of dead coral covered by coralline algae. Bluehead wrasse are often found feeding here during the non-spawning period. The coalesced spur zone is seaward of the swash zone and is composed of a variety of corals. Coral coverage was more uniform here before Hurricane Allen damaged the reef in 1980 (Mah and Stearn 1986). It now consists of mostly dead coral rock covered by coralline algae. Bluehead wrasse are numerous here and are often found defending territories over elevated parts of the zone close to the edge of irregular sand channels between the spurs. The spur and groove zone occurs at the seaward edge of the reef. Spurs are perpendicular to the shore and narrow toward the edge of the reef. This zone is composed of mixed coral species dominated by Porites porites and Porites rubble and are separated by deep (~5m) sand channels. Coral projections occur on the seaward tips of some of the spurs, e.g. a one and half metre projection of Dendrogyra cylindrus on the most southern tip of the North Bellairs reef. Bluehead wrasse are abundant in this zone especially during the daily spawning period and often use downcurrent promontories as mating sites.

3 SPAWNING AND RECRUITMENT

3.1 INTRODUCTION

This section is a study of spawning and recruitment in the bluehead wrasse Thalassoma bifasciatum on the fringing reefs off the west coast of Barbados, West Indies.

Studies of coral reef fish ecology began in earnest in the 1950's (Sale 1984). Since then, the prevailing paradigm has been that reef fish communities show little fluctuation either in terms of abundance of individual species populations or in terms of species composition, i.e. they are at equilibrium (sensu MacArthur 1972). The assumption was that the relatively constant environmental conditions characteristic of tropical marine environments would ensure that populations remain relatively close to carrying capacity of the environment as set by availability of resources (Hiatt and Strassburg 1960; MacArthur 1972). The consequent competition for resources would maintain populations near numerical equilibrium, and would simultaneously act as an agent of selection for the evolution of narrower niches i.e. greater specialization. This in turn would result in the high species diversity characteristic of coral reef fish communities.

Tropical marine environments differ substantially from those in the temperate latitudes. Two tradewind seasons, with sharp differences in rainfall, generally replace the four seasons of the temperate zones. Consequently, Caribbean fish often have longer reproductive seasons than do temperate fish, but can also show seasonal (Munro et al 1973) and even lunar spawning peaks (Lobel 1978; Johannes 1978; Robertson et al 1988). Evidence for such temporal variation consists of changes in gonadal indices, ova diameters (Munro et al 1973; Fishelson 1976; Taylor et al 1979; Ralston 1981) and observable spawning behavior (Colin 1978; Ross 1978; Pressley 1980; Tribble 1982). In many of these studies observations of spawning frequency and gonad analyses have been undertaken too infrequently and over too short a time period to determine temporal patterns in spawning. In particular, small scale (e.g. daily) variation in spawning activity in many species, as well as changes in such variation through time, may have been missed (Johannes 1978). One objective of the present study is to use spawning observations and gonad analyses to investigate spawning patterns in T. bifasciatum on both a lunar and seasonal time-scale.

Coral reef fish produce either demersal or pelagic eggs. Except for one known species (Acanthochromis polycanthus, Robertson 1973) all reef fish produce pelagic larvae (e.g. Breder and Rosen 1966; Leis and Miller 1976; Sale 1980 ; Thresher 1984). There are two major explanations for the high incidence of pelagic larvae; the dispersal hypothesis (Barlow 1981) and the antipredator hypothesis (Dale 1978; Johannes 1978; Sale 1978; Smith 1978). The former suggests that advantages associated with dispersal (e.g. reduced intraspecific competition, reduced probability of inbreeding, reduced probability of local extinction of sub-populations) have been the major selective force in the evolution of pelagic larvae. The latter hypothesis depends on the assertion that predation is heavier on reefs than in waters offshore (Sale 1971, 1978; Smith 1978; Johannes

1978; but see Shapiro et al 1988), and suggests that this is the major force for the evolution of pelagic larvae. However, the advantages of escaping higher predation may be offset by larvae being swept away in oceanic currents and never successfully recruiting to reefs (Hjort (1914) in Powles 1975). Johannes (1978) has suggested that such oceanic losses are a major selective force favouring seasonal reproduction in the tropics; reproduction occurring when current systems are most likely to return pelagic larvae to reefs. A second objective of the present section is to investigate the effects of tide and of current speed and direction on lunar variation in spawning activity of T. bifasciatum.

Whatever the selective forces that produced the pelagic larval stage, it seems likely that this life history stage may have important implications for the dynamics of reef fish populations and for the structure of coral reef fish assemblages. The orthodox view is that reef fish populations are space/resource limited (Anderson et al, 1981; Shulman et al 1983, 1985a,b). The rationale is that since most coral reef fish spawn over extended periods within each year, there will be a reservoir of planktonic larvae above the reefs. Consequently populations will be regulated by competition for resources on the reef, and reef fish will tend to be specialists. A variation of this is the lottery hypothesis of Sale (1977, 1978, 1982). He suggested that colonisation/recruitment patterns will reflect the chance openings of settlement sites on the reef; the implication being that reef fish are generalists. Such chance openings can be caused by mortality due to predation or by disturbances (Lassig 1983). An alternative hypothesis, supported by some recent studies, is that a shortage of larvae can keep larval reef fish populations below the carrying capacity of the reef i.e. the populations are recruitment-limited (Williams 1980; Doherty 1982a, 1983b; Victor 1983a, 1986a).

To investigate recruitment processes, it is necessary to obtain information on the early life history stages (recruitment phase) of the fish. Until recently much of what is known about coral reef fish was gleaned from studies of the relatively sedentary adults, but this has changed with development of the otolith increment aging technique. This technique is particularly useful for aging early life stages and therefore can be used to assess growth rates of larval, juvenile and adult fish (Panella 1971, 1980; Brothers et al 1976, 1983; Brothers and McFarland 1981; Victor 1982, 1983b, 1986a). In addition, the date of settlement of a fish from the plankton to the reef can be determined using this technique.

Victor (1983a, 1986a) used the otolith dating technique to study recruitment of T. bifasciatum on the San Blas Islands, Panama. He suggested that spawning was constant throughout the year, but that recruitment occurred in brief sporadic episodes which therefore did not reflect any variation in spawning of the species at that location (Victor 1983a). He concluded that variation in recruitment reflected variation in survival in the plankton. He further found that periods of high mortality of residents on the reef were not followed by increased recruitment (Victor 1983a, 1986a); results which do not support the lottery hypothesis of Sale (1977, 1978, 1982). Finally temporal patterns of recruitment were subsequently reflected in changes in the population size of adults Victor (1983a, 1986a).

Victor therefore concluded that the populations of T. bifasciatum in Panama were primarily recruitment limited, and that adult population dynamics was primarily driven by recruitment processes.

The final objective of the present section is to use otolith aging to investigate recruitment patterns in T. bifasciatum in Barbados. This has two main purposes. First, by investigating a possible correlation between peak spawning and peak recruitment, the question of whether recruitment pulses result from differential spawning activity or from differential survival in the plankton can be addressed. Second, by investigating effects of changes in resident population density on recruitment and effects of recruitment strength on subsequent juvenile mortality, the question of whether populations of T. bifasciatum in Barbados are recruitment-limited or space-limited can be addressed.

3.2 METHODS AND MATERIALS

3.2.1 Temporal variation in spawning

Spawning events in the bluehead wrasse are readily observed as upward rushes of spawning fish towards the surface. Spawning frequency can therefore be investigated by visual observation of spawning events. Bluehead wrasse populations on two fringing reefs (North Bellairs and Heron Bay) in Barbados were monitored for 14 months to investigate whether lunar and/or seasonal variation existed in spawning frequency. Spawning frequency was quantified by surface snorkeling along five transects parallel to shore, (a 50 minute swim), and counting the number of spawning events separately for group spawning and pair spawning (see Section 1). Each transect was 150m long and all spawning events that were observed in a 2m radius around the transect line were recorded. The data were recorded on small waterproof slates. The transect surveys were conducted twice a week on each reef throughout the 14 month sampling period. Spawning in the bluehead wrasse is known to take place for a few hours around midday each day (Warner et al 1975). To characterise diel spawning patterns in the Barbados population, and therefore control for this when comparing spawning between weeks and months, I initially conducted transect surveys from 0700hrs to 1700hrs every hour for 30 minutes, for three consecutive days. Most spawning activity (98%) occurred between 1100hrs and 1500hrs Consequently, on each sampling day used to investigate monthly and seasonal variation in spawning, I randomly picked one of those four hours to conduct the 50 minute snorkeling transect. Periodic checks conducted over the study period indicated that spawning occurred within the identified 4-hour period throughout the year.

To further investigate seasonal variation in spawning, monthly samples of approximately 50 fish were taken, from Heron Bay, between October, 1984 and October, 1985. Fish were captured by using a 2 litre glass jar filled with a crushed sea urchin (Diadema antillarum) placed at high points on the reef surface. Five sites across the reef were each sampled twice for each monthly sample. The jar was left for a maximum of 5 minutes during each sample. This was enough time for fish to be attracted to the jar and consequently captured. The same sites were used for each monthly sample. This sampling technique was size selective for larger fish, over 98% of the fish caught being either at or over the size at sexual maturity (about 30mms SL and 3 months of age; Victor 1986a). Gonads from the fifty fish sampled monthly were removed and weighed (to the nearest 10^{-2} gm). These data were used to calculate monthly variation in gonadosomatic indices (GSI's), where GSI is the proportion of total fish wet weight contributed by the gonads.

To investigate possible effects of local currents on spawning frequency, the direction and speed of nearshore surface currents (i.e. 10m to 500m from shore) were measured on alternate weeks over the two study reefs throughout the entire study period. Measurements were taken twice a day, or once a day on consecutive days, close to the turn of high and low tides. This was done by using a Perspex drogue suspended at 1.0 metre from the sea surface. Each drogue was dropped from a small rowboat near to the central onshore point of the reef, and sitings with a compass were taken from the boat to points on shore, every five minutes for an hour. Through a series of triangulations, using the compass readings, the path followed by each drogue over the reef was plotted to determine direction and speed of surface currents.

Finally, to investigate possible effects of tidal stage (i.e. ebb and flood tide) on daily bluehead wrasse spawning frequency, a two week experiment was conducted in May, 1985 on North Bellairs reef. Bluehead wrasse spawning frequency was monitored each day at selected and marked spawning sites across the reef, between 1100hrs and 1500hrs. for thirty minutes each hour. Continuous observations of spawning frequency throughout the daily spawning period were used to determine if the timing of peak spawning per day, within the 4-hour spawning period, is influenced by tidal stage. Times of low and high tides were obtained from tables supplied by the Barbados Port Authority, Bridgetown, Barbados.

3.2.2 Temporal variation in recruitment

Temporal variation in recruitment of the bluehead wrasse in Barbados was investigated by dating the otoliths of the 50 fish sampled each month as described in Section 3.2.1. Two pairs of the larger otoliths (sagittae and lapillae) were removed from the ear canals of each fish caught (N=790). Minimal preparation is needed to view and read otoliths in T. bifasciatum (Victor 1982). The otoliths were rinsed in 90-100% ethanol and then cleared for 24hrs in xylene. Pairs of otoliths were then mounted with mounting medium on glass slides. They were then viewed with polarization under 400x magnification with a compound microscope. Victor (1982) demonstrated the presence of settlement marks on otoliths of T. bifasciatum. In addition he showed that wrasse larvae (including T.bifasciatum) spend approximately five days in the sand metamorphosing after settlement from the plankton, before recruitment to the reef population. This time spent in the sand results in a band of five faint increments, the settlement band, which occurs on the otolith after the settlement mark. The date of settlement from the plankton can be calculated by subtracting the total number of daily increments between the settlement mark and the perimeter of the otolith (including the increments within the settlement band, this gives the number of days since settlement) from the collection date. These data can then be used to investigate seasonal variation in settlement/recruitment frequency. Patterns of settlement, as indicated by settlement dates, were also used to determine if there was lunar variation in settlement frequency.

3.2.3 Temporal variation in adult density

Adult population density was censused once per month on North Bellairs reef and once per week on Heron Bay reef. Densities were measured by swimming slowly along a 50m transect line while holding a one metre expandable ruler and counting the number of adult fish (>3 cms) within half a metre on either side of the transect line. (The fast-count visual census technique; see Miller and Hunte, 1987). Counts of IP and TP adults were recorded.At each site on each sampling day, three transects were censused for density estimates. The three transects were laid parallel to the shore over the central part (coalesced spur zone) of the reef. Each transect was placed in the same position on the reef each month. Density samples were taken either early in the morning or late afternoon, i.e. outside the daily spawning period. This avoided bias that might arise from individuals moving to spawning sites. For comparisons of density between the two reefs, and between months on a given reef, a single mean monthly density value was calculated for each reef from data obtained from the three transect surveys.

3.3 RESULTS

3.3.1 Seasonal variation in population spawning frequency

The total number of spawning events observed every second week for 14 months on North Bellairs (NB) and Heron Bay (HB) reefs combined is shown in Figure 3a. Combining the data from the two reefs is justified since the seasonal variation in number of spawning events did not differ between reefs (Kolmogorov-Smirnov two-sample test (Sokal and Rohlf 1981), D=0.33, P>0.05). Spawning frequency was not uniformly distributed across months (Kolmogorov-Smirnov one-sample test (Zar 1984), D=0.19, P<0.01), occurring primarily between January and July with a peak between March and June (Fig. 3a). January to June are the drier months of the year in Barbados (Fig 4). Spawning in the bluehead wrasse can therefore be divided into a non-reproductive season (July to December) and a reproductive season (January to June), which largely coincide with the wet and dry seasons in Barbados respectively. Note that this does not imply an absence of spawning in the non-reproductive period. Spawning frequency was significantly higher in the dry season than in the wet season on both reefs (Mann-Whitney U test, for sample sizes >20 (Siegel, 1956; SAS, 1987) ; For NB, z=2.24, P<0.05; For HB , z=2.70, P<0.01) and for the reefs combined (Mann-Whitney U test, for sample sizes >20, z=3.2, P<0.005). In summary, spawning frequency of T. bifasciatum is not constant throughout the year, spawning occurring primarily in the drier months.

Seasonal variation in group and pair spawning is shown in Fig. 3b and 3c respectively. Group spawning was not uniformly distributed

Figure 3. Total number of spawning events (3a), number of group spawning events (3b), and number of pair spawning events (3c) vs. time of year for Thalassoma bifasciatum from North Bellairs and Heron Bay reefs (Barbados) combined. Data are presented at two-week intervals for the period September, 1984 to October, 1985. Total observation time per two week interval is 400mins.

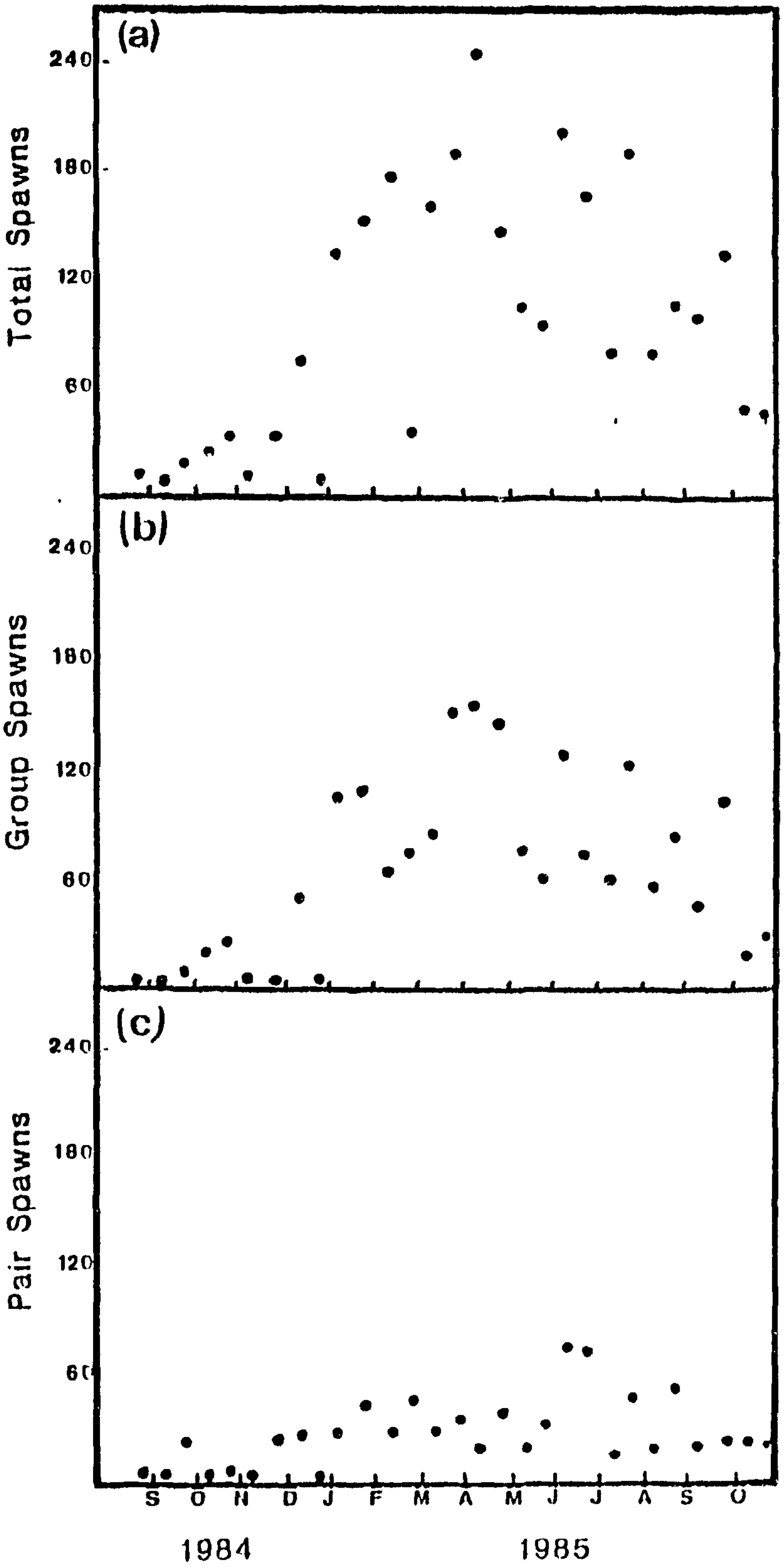
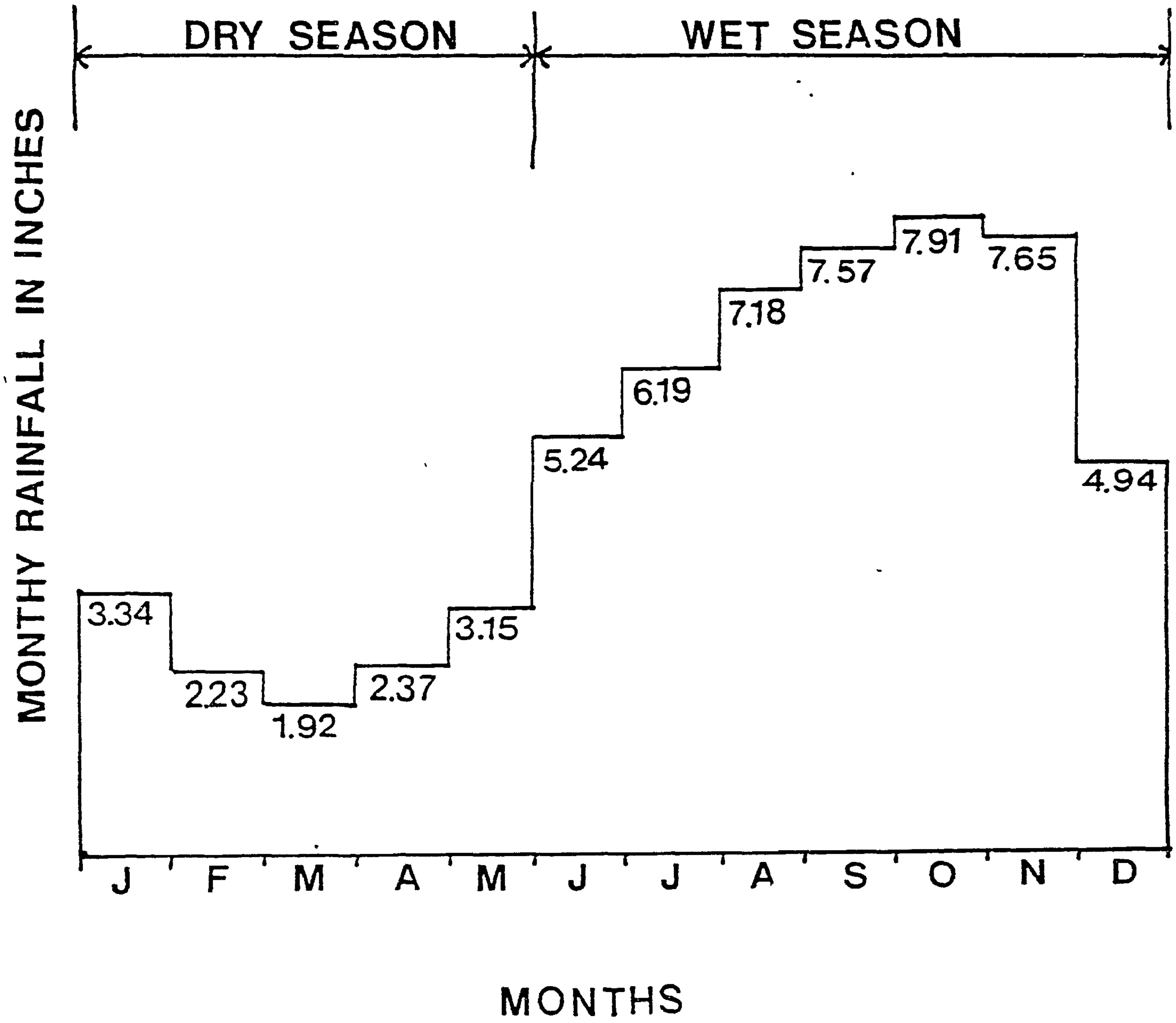

(a)
(b)
(c)
Total Spawns
Group Spawns
Pair Spawns
240
180
120
60
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1984
1985

Figure 4. Average monthly rainfall in inches Barbados for the period 1847-1976 inclusive, displaying distinct wet and dry seasons (Barbados Coastal Conservation Project 1984).


DRY SEASON
WET SEASON
MONTHY RAINFALL IN INCHES
3.34
2.23
1.92
2.37
3.15
5.24
6.19
7.18
7.57
7.91
7.65
4.94
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

throughout the year (Kolmogorov-Smirnov one-sample test, D=0.209, P<0.05) , occurring more frequently in the dry season than in the wet season (Mann-Whitney U test, for sample sizes >20, z=3.1, P<0.005; Fig. 3b). Pair spawning was not uniformly distributed throughout the year (Kolmogorov-Smirnov one-sample test, D=0.19, P<0.001). It appeared to be less common in the wetter months (September-November; Fig. 3c), but the differences between seasons were not statistically significant (Mann-Whitney U test, for sample sizes >20, z=0.87, P>0.05).

Seventy-one percent of all spawning events observed during the study were group spawns (71%>50%;X^2= 476.53, P<0.001, Table 1), suggesting that significantly more females group spawn than pair spawn. The frequency of group spawning almost doubled in the reproductive season compared to the non - reproductive season, while pair spawning only increased by a factor of 1.2 (Table 1). The results suggest that increases in group spawning are largely responsible for the greater total spawning activity observed in the drier months. This is further illustrated by a plot of the monthly ratio of pair spawning to group spawning (P / R ratio) vs the total number of spawning events in the month (Fig. 5). The greater the number of total spawning events , the lower the ratio of pair spawning to group spawning.

3.3.2. Seasonal variation in spawning frequency per fish

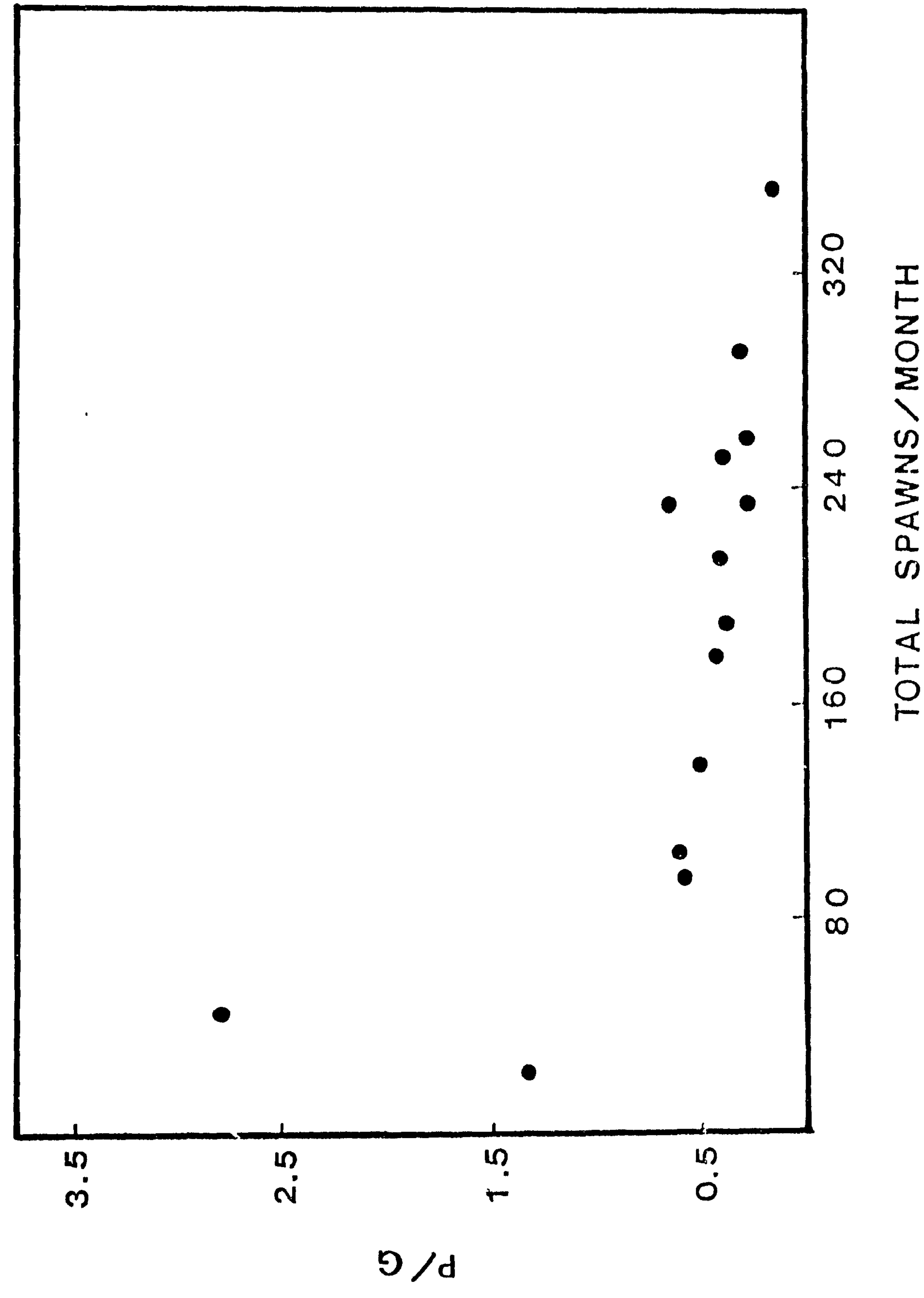
The larger number of spawning events observed during the drier months could result from there being a larger number of adult fish present on the reefs to spawn in those months and / or from an

TABLE 1

The number of spawning events by Thalassoma bifasciatum in the non-reproductive and the reproductive periods in Barbados, and the percentage of events that are group or pair spawns in each period. The data are pooled for North Bellairs and Heron Bay reefs.

	NUMBER OF SPAWNS				
PERIOD	GROUP	PAIR	TOTAL	PERCENT GROUP SPAWNS	PERCENT PAIR SPAWNS
NON-REPROD.	698	357	1055	66	34
REPROD.	1258	448	1706	74	26
TOTAL	1956	805	2761	71	29

Figure 5. The ratio of pair spawning and group spawning (P/G) vs. total number of spawns in each month for Thalassoma bifasciatum on North Bellairs and Heron Bay reefs, Barbados. The data presented are from the period September, 1984 to October, 1985.


P/G
3.5
2.5
1.5
0.5
80
160
240
320
TOTAL SPAWNS/MONTH

increase in spawning frequency per fish present. Variation in adult density did occur during the year and showed similar patterns on North Bellairs and Heron Bay reefs (Figs. 6a & 6b respectively). Mean density was significantly higher in the wet months, (x_{NB}=1.17± 0.40 N/m^2, x_{HB}=1.67± 0.20 N/m^2 than in the dry months, (x_{NB}=0.89± 0.07 N/m^2; x_{HB}=1.38± 0.50 N/m^2), (t-test for NB, t=2.29, $P<0.05$, t-test for HB, t=2.40, $P<0.05$). A plot of monthly adult density for the two reefs combined is shown in Figure 6c. The data suggest that adult density is the lowest in the drier months when the number of spawning events observed is highest. The increased spawning activity observed in the drier months must therefore result from a higher spawning frequency per fish in those months.

The total number of spawning events in a month divided by the density estimate for that month gives an index of spawning frequency per fish and is shown for each month in Figure 7a. This illustrates that the greater spawning activity in the dry season results from a greater spawning frequency per fish present. Note that the index of spawning frequency per fish for IP individuals (group spawns divided by IP density) peaks earlier (March-May) than that for TP individuals (pair spawns divided by TP density) which peaks between May and July (Figs. 7b and 7c respectively).

3.3.3 Seasonal variation in gonadosomatic indices

Seasonal variation in mean monthly gonadosomatic indices (wt of gonad/wt of fish) was not marked, but complemented the seasonal variation in spawning frequency observed. Mean GSI peaked near the middle of the dry season (Fig. 8) when the frequency of group spawning

Figure 6. Monthly adult densities (N/m^2) vs. month for <u>Thalassoma bifasciatum</u> on North Bellairs reef (6a) and Heron Bay reef (6b), and for the two reefs combined (6c). Data from the more frequent monitoring of density (once per week) on Heron Bay are shown as the dashed line in (6b). The data are presented over the period September 1984 to October 1985.

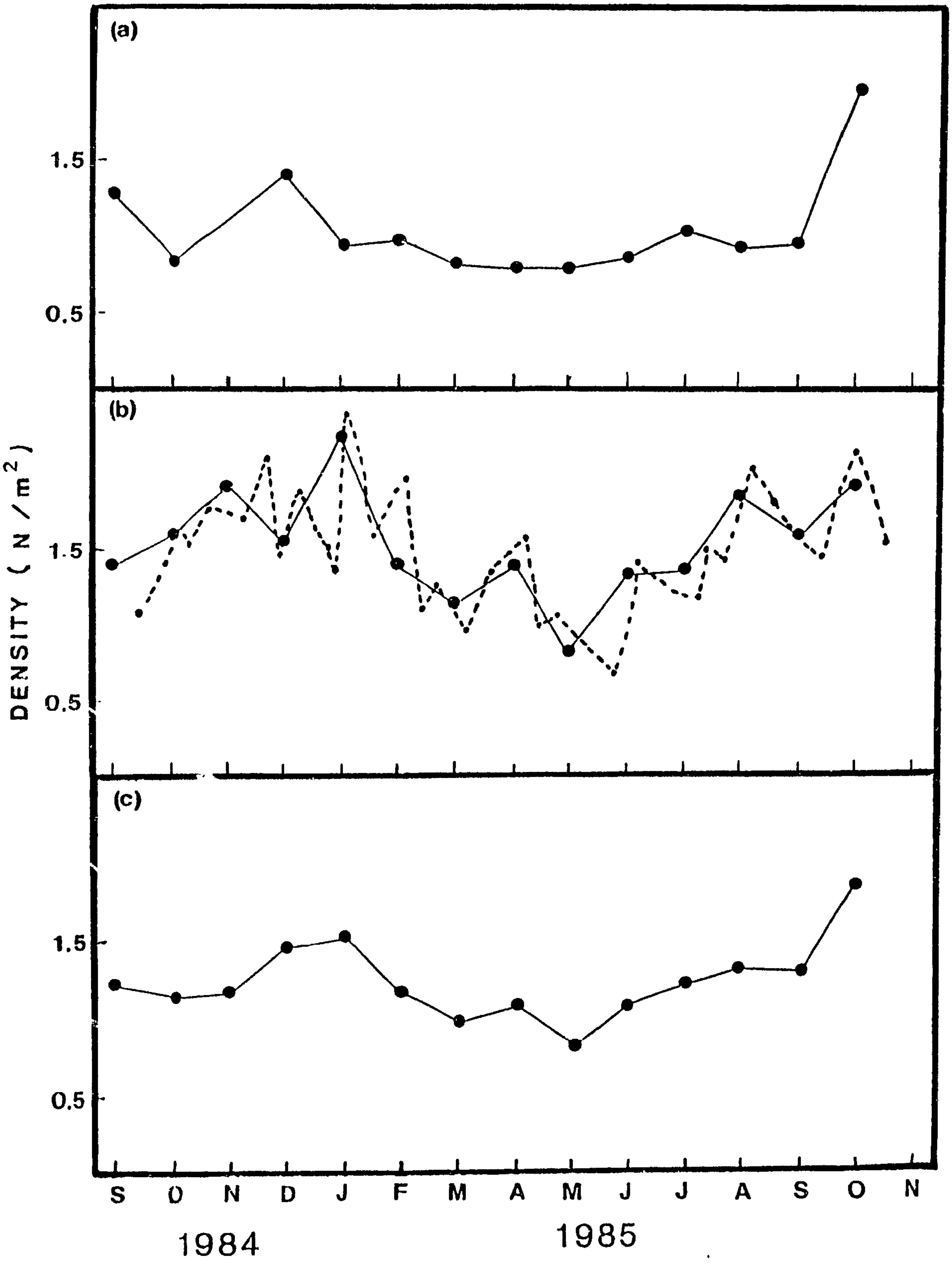

(a)
(b)
(c)
DENSITY (N / m²)
1.5
0,5
1.5
0,5
1.5
0,5
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1984
1985

Figure 7. An index of spawning frequency per fish (spawns / density) for <u>Thalassoma bifasciatum</u> on North Bellairs and Heron Bay reefs, Barbados. The data are presented separately for total spawns (7a), group spawns; (males are IP) (7b) and pair spawns; (males are TP) (7c). The data cover the period October 1984 to October 1985.

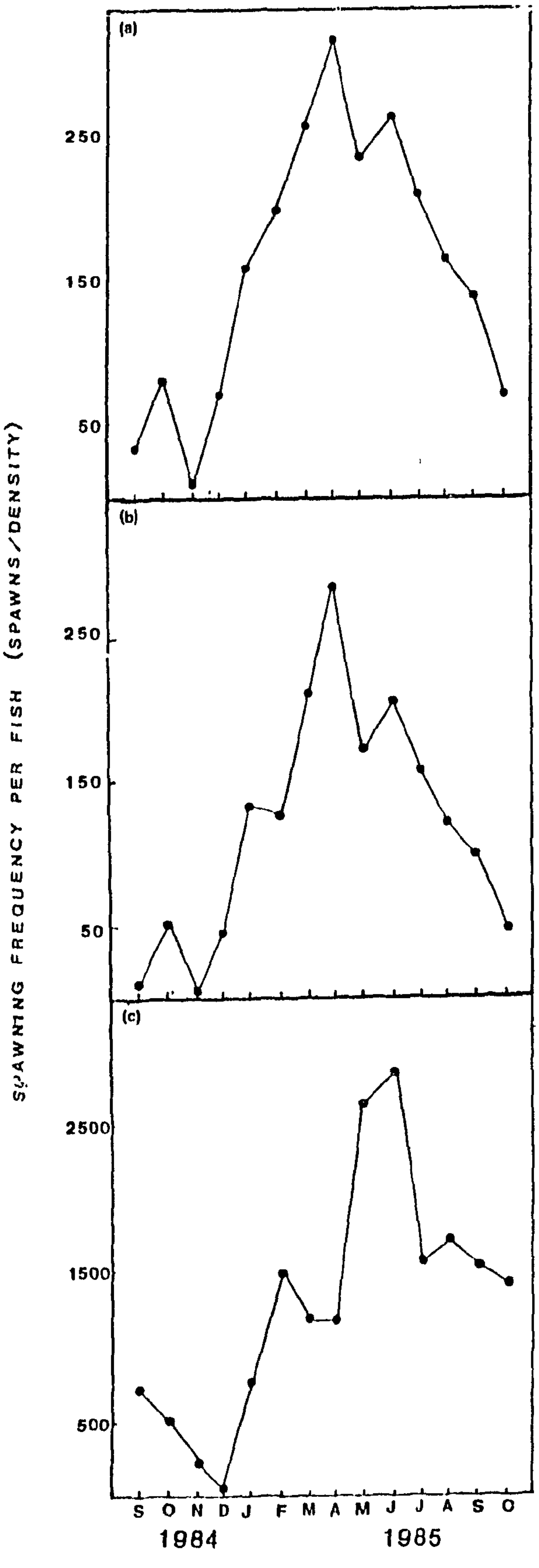
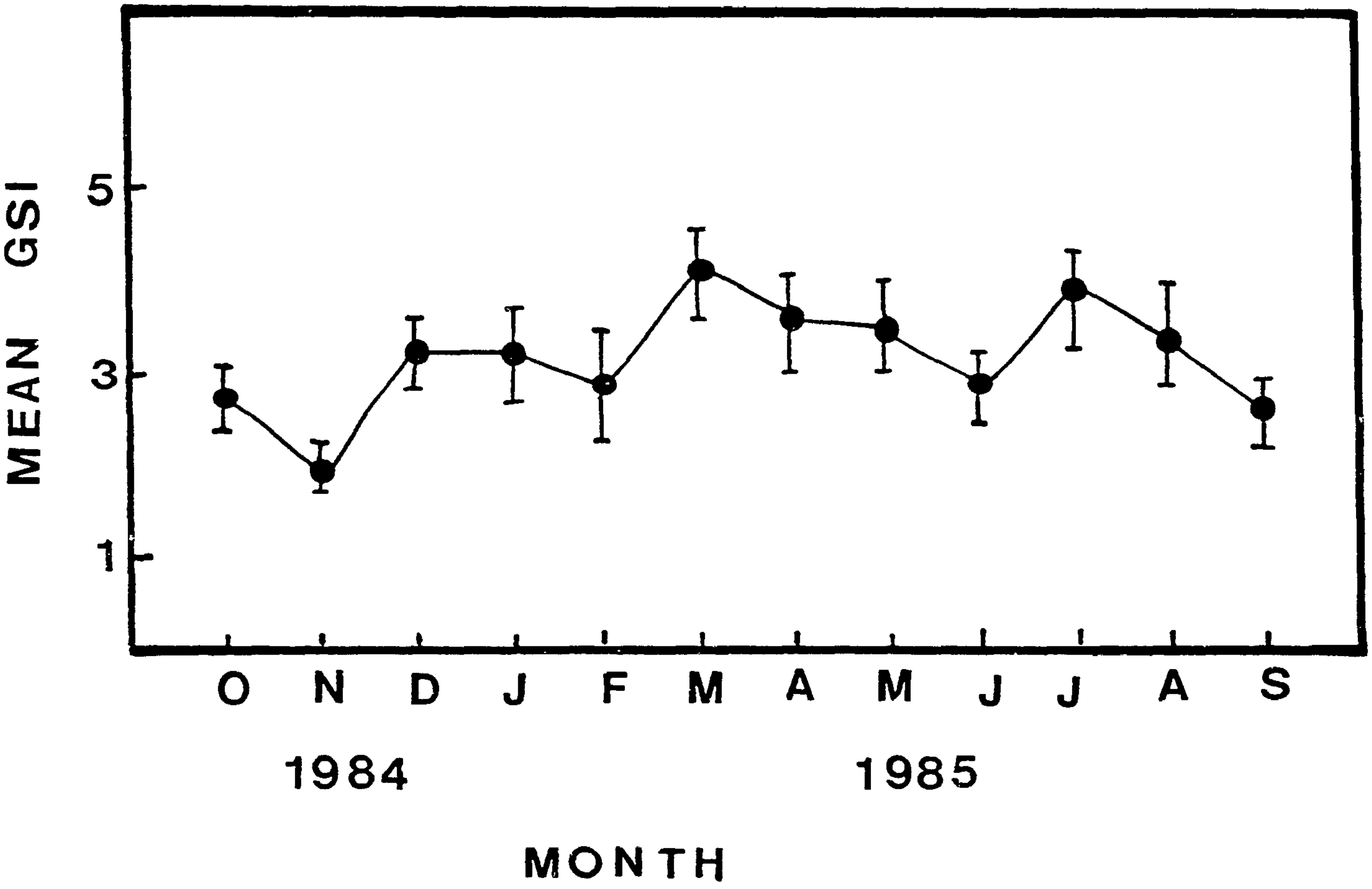

SPAWNING FREQUENCY PER FISH (SPAWNS/DENSITY)
(a)
250
150
50
(b)
250
150
50
(c)
2500
1500
500
S O N D J F M A M J J A S O
1984
1985

Figure 8. Mean monthly gonadosomatic index (GSI) vs. time of the year for *Thalassoma bifasciatum* on Heron Bay reef, Barbados.

T indicates 95% confidence limits.


MEAN GSI
5
3
1
O
N
D
J
F
M
A
M
J
J
A
S
1984
1985
MONTH

was highest (Fig. 7b) (Spearman's Rank Correlation, $r_s=0.7$, $P<0.05$). A second smaller peak in GSI occurred towards the end of the dry season when the frequency of pair spawning was highest (Fig. 7c).

3.3.4 Monthly variation in spawning frequency

Considering North Bellairs and Heron Bay reefs combined, spawning events were monitored four times per week for 14 months, making it possible to investigate lunar variation in spawning activity. Figure 9 shows the number of group and pair spawning events on a weekly basis throughout the year. Note that some data were unavailable in November and December 1984 due to rough seas and poor visibility, and some were unavailable for a two week period in May 1985 since a study on diel variation in spawning was in progress (see Section 3.3.5). Separately for group and pair spawning, data for all months in the non-reproductive season were pooled by lunar phase. Neither group nor pair spawning activity differred between lunar phases in this season (Friedman's test (Zar, 1981), (group); $P>0.05$, (pair), $P>0.05$).

Separately for group and pair spawning, data for all months of the reproductive season were pooled by lunar phase. Niether group nor pair spawning activity differred between lunar phases in this season, Fig. 10; Friedman's test, (group); $P>0.05$; (pair) $P>0.05$). However, figure 10 suggests that during the reproductive season, group spawning may be more common at spring tides (new and full moon) than at neap tides (first and last quarter). Group spawning events during the reproductive period were therefore pooled into two periods , spring tides and neap tides. The frequency of spawning events during spring

Figure 9. Weekly frequency of group and pair spawning vs lunar phase for *Thalassoma bifasciatum* on North Bellairs and Heron Bay reefs combined.

N = new moon

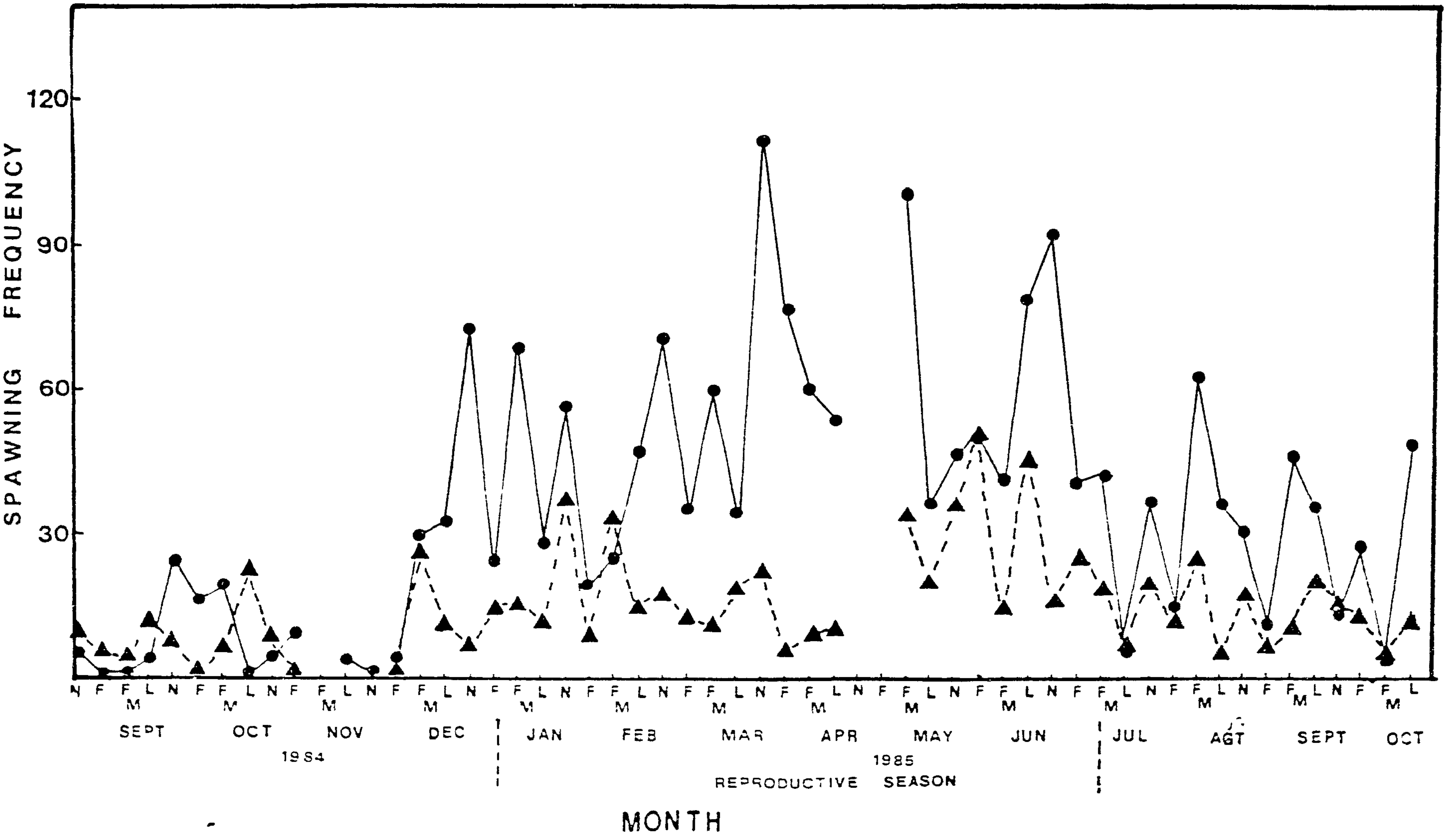
F = first quarter

F_M = full moon

L = last quarter

●—● group spawning

▲-▲ pair spawning


SPAWNING FREQUENCY
120
90
60
30
N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L N F F L
M M M M M M M M M M M M M M
SEPT
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AGT
SEPT
OCT
1984
1985
REPRODUCTIVE SEASON
MONTH

tides was significantly greater than that during neap tides (Wilcoxon signed-ranks test (Sokal and Rohlf, 1981); z=1.99, P<0.05). By contrast , niether pair spawning frequency during the reproductive period (Wilcoxon's signed-ranks test, z=0.52, P>0.05), group spawning frequency during the non-reproductive period (Wilcoxon's signed-ranks test, z=1.15, P>0.05), nor pair spawning frequency during the non-reproductive period (Wilcoxon's signed-ranks test, z=0.94, P>0.05) differred significantly between spring and neap tides.

3.3.5. Daily variation in spawning frequency

Observations of spawning activity throughout the daily spawning period (between 1100hrs. and 1500hrs. each day) were carried out each day for 2 weeks in April, 1985 to investigate if the timing of daily spawning peaks varied with tidal stage (i.e. whether wrasses timed their daily spawning to coincide with either ebb or flood tide). The daily spawning frequency at each tidal stage is expressed as the mean, for all days, of the spawning events that occurred at each tidal stage. The data are presented separately for group and pair spawning. Group and pair spawning occurred at all stages of the tidal cycle (Figs. 11a & 11b). Group spawning frequency was not uniformly distributed throughout the tidal cycle (Kolmogorov-Smirnov one-sample test, D=0.279, P<0.001 ; Fig. 11a) occurring more frequently during ebb tides than flood tides (Mann-Whitney U test, U_S=51.5, P<0.05). The frequency appeared highest near the beginning of ebb-tide (i.e. near high tide ; Fig. 11a). Pair spawning frequency was also not

Figure 10. Mean number of group (●–●) and pair spawning (▲–▲) events during the reproductive season of 1985 (Jan – June) vs. lunar phase, for *Thalassoma bifasciatum* on Heron Bay and North Bellairs reefs combined.

I indicates 95% confidence limits.

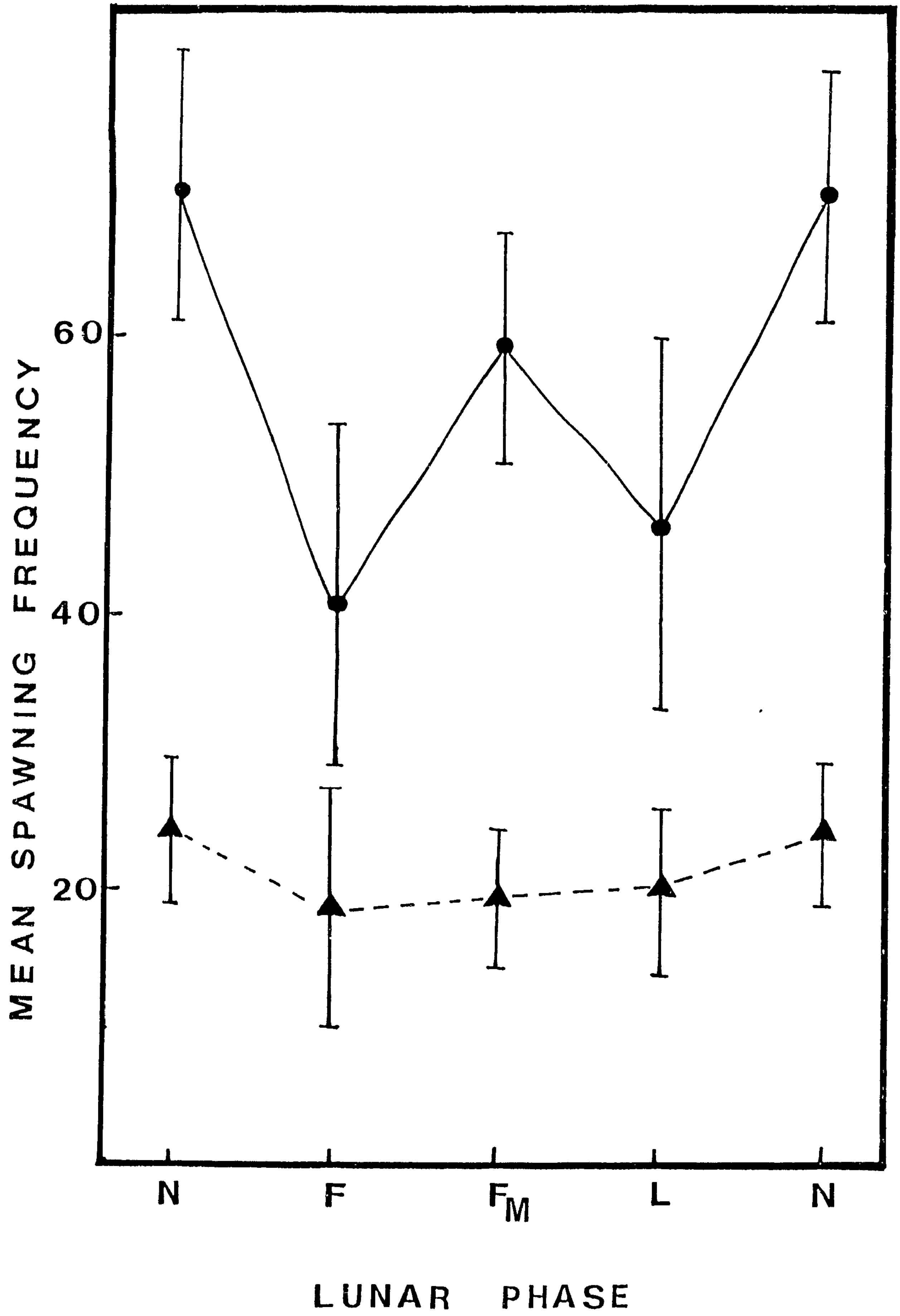
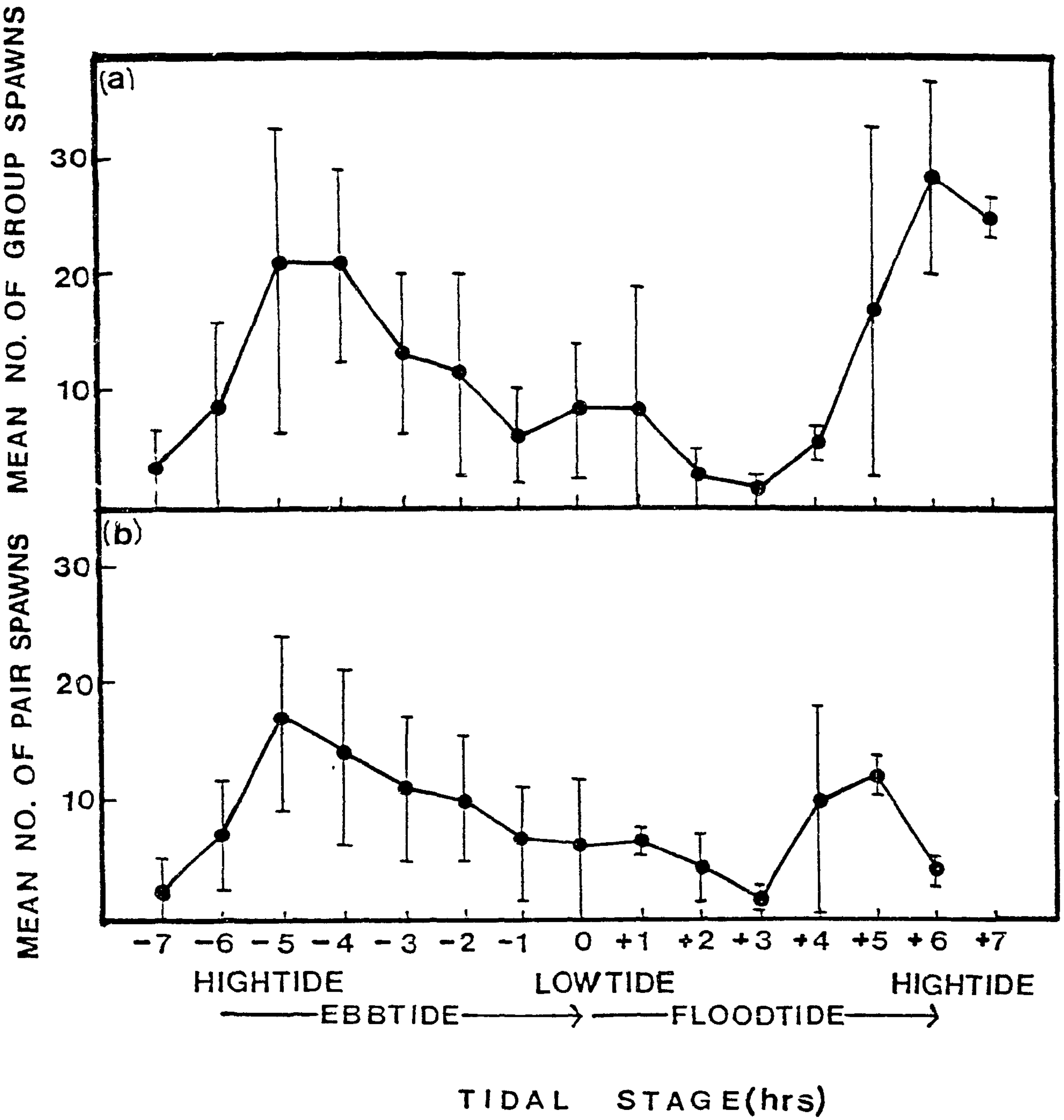

MEAN SPAWNING FREQUENCY
60
40
20
N
F
F_M
L
N
LUNAR PHASE

Figure 11. Mean number of group (11a) and pair (11b) spawns vs. tidal stage for *Thalassoma bifasciatum* on North Bellairs reef, Barbados. The data were recorded during a two week experiment in April, 1985.

T indicates 95% confidence limits


MEAN NO. OF GROUP SPAWNS
(a)
30
20
10
MEAN NO. OF PAIR SPAWNS
(b)
30
20
10
−7 −6 −5 −4 −3 −2 −1 0 +1 +2 +3 +4 +5 +6 +7
HIGHTIDE
LOWTIDE
HIGHTIDE
EBBTIDE
FLOODTIDE
TIDAL STAGE(hrs)

uniformly distributed throughout the tidal cycle (Kolmogorov-Smirnov one-sample test, D=0.289, P<0.001 ; Fig. 11b) and was significantly higher during ebb tides than flood tides (Mann-Whitney U test, $U_s=44$, $P<0.05$). As with group spawning, pair spawning frequency appeared highest near the beginning of ebb tide (i.e. near high tide ; Fig. 11b). In summary these results suggest that daily spawning in the bluehead wrasse tracks tidal stages being more frequent during ebb tides than flood tides, and being particularly frequent near the onset of ebb tides when water depth is greatest.

3.3.6 Variation in current speed and direction

Inshore surface current data recorded on Heron Bay and North Bellairs reefs are shown in Table 2. The net direction of current movement on both reefs was offshore on 96% of the occasions on which currents were sampled, regardless of tidal phase. On the remaining 4% of occasions the currents ran parallel to the shore. Similar observations have previously been made for west coast fringing reefs in Barbados by Bevan (unpubl. data), Giraldeau (unpubl. data) and Tomascik (unpubl. data). The mean current direction was west-northwest ($\bar{x}=293.0$ WNW). Occasional reversals to the south west occurred, mostly at flood tide. At ebb tide , northwest currents were more frequent than southwest currents ($X^2=11.25$, $P<0.001$). At flood tide, northwest and southwest currents occurred with equal frequency ($X^2=0.56$, $P>0.05$). These data suggest that pelagic eggs released at any phase of the tidal cycle would be carried offshore by the prevailing surface current. In spite of considerable variation in current speed, there was a non-significant tendency for surface

Table 2. Current data from drogue studies (depth 1m.) on North Bellairs and Heron Bay reefs.

NB= North Bellairs HB= Heron Bay

North= 360°/ 0° West= 270° South= 180°

	EBB TIDE				FLOOD TIDE			
REEF & DATE	CURRENT DIRECTION (DEGREES)	SPEED (M/S)	TIME OF HIGH TIDE	TIME OF SAMPLING	CURRENT DIRECTION (DEGREES)	SPEED (M/S)	TIME OF LOW TIDE	TIME OF SAMPLING
1984								
NB 27/08	337	0.041	1640	1639-1743	280	0.013	1020	1020-1109
NB 05/09	252	0.029	1453	1451-1603				
NB 06/09					150	0.007	0828	0824-0935
NB 11/09	352	0.052	0355	0926-1016	317	0.013	1013	1550-1616
NB 21/09	267	0.037	1320	1352-1459	333	0.059	0704	0750-0853
NB 01/10					312	0.044	0913	0919-1015
NB 08/10	346	0.122	0858	0953-1016	334	0.018	1446	1444-1544
NB 15/10	29	0.020	0713	0806-0909				
NB 24/10	318	0.030	1517	1514-1615	252	0.031	0917	0920-0916
NB 07/11	328	0.179	1428	1415-1445				
HB 08/11	321	0.097	1500	1516-1531	313	0.082	0913	0915-0945
NB 15/11	227	0.083	0935	0916-1016	275	0.051	1439	1427-1507
NB 21/11	215	0.015	1404	1414-1506	241	0.024	0810	0818-0915
HB 23/11	312	0.047	1527	1524-1628	352	0.036	0928	0936-1034
HB 06/12	198	0.041	1351	1400-1456	334	0.049	0808	0811-0907
NB 13/12	289	0.029	0816	0814-0910	201	0.015	1336	1332-1453
HB 14/12	333	0.117	0904	0901-0949	322	0.040	1449	1655-1750
HB 20/12	209	0.070	1340	1335-1428	181	0.051	0747	0800-0857
1985								
NB 07/01					254	0.028	0954	1002-1052
HB 08/01	261	0.069	1639	1635-1731	235	0.044	1042	1039-1144
HB 14/01	303	0.026	1005	1007-1059	203	0.081	1643	1643-1730
NB 05/02	281	0.060	1537	1546-1627	227	0.130	0945	0950-1024
HB 06/02	333	0.168	1631	1639-1722	208	0.052	1032	1044-1131
HB 27/02	299	0.053	0920	0918-1018	288	0.049	1459	1442-1543
NB 01/03	298	0.025	1048	1041-1125	288	0.039	1805	1742-1822
NB 07/03					284	0.059	1013	1006-1052
HB 08/03	294	0.090	1709	1656-1733	246	0.034	1058	1044-1127
NB 13/03	195	0.050	0850	1429-1523	286	0.014	0231	0751-0844
NB 21/03	271	0.048	1544	1547-1634	259	0.072	0944	0937-1023
HB 03/04	326	0.056	1416	1412-1458	335	0.011	0828	0845-0940

TABLE 2 continued

	EBB TIDE				FLOOD TIDE			
REEF & DATE	CURRENT DIRECTION (DEGREES)	SPEED (M/S)	TIME OF HIGH TIDE	TIME OF SAMPLING	CURRENT DIRECTION (DEGREES)	SPEED (M/S)	TIME OF LOW TIDE	TIME OF SAMPLING
NB 04/04	234	0.073	1504	1510-1557	319	0.049	0909	0900-0945
HB 11/04	338	0.089	0819	0830-0915	200	0.051	1513	1443-1540
NB 12/04					296	0.054	1707	1704-1750
HB 17/04	288	0.114	1432	1424-1512	153	0.041	0845	0832-0919
NB 18/04	232	0.086	0900	0940-1026	354	0.103	1454	1451-1537
NB 09/05					246	0.071	1349	1343-1435
NB 10/05	334	0.089	0754	0814-0906				
HB 27/05	325	0.218	0920	0919-0955	272	0.045	1605	1603-1646
HB 10/06					228	0.080	1559	1559-1650
HB 11/06	281	0.059	1054	1130-1215				
HB 18/06	308	0.106	1619	1613-1700	187	0.046	0955	1012-1058
HB 25/06	326	0.151	0904	0840-0910	310	0.070	1523	1730-1831
HB 09/07					345	0.324	1428	1442-1529
HB 10/07	345	0.316	0927	0953-1030				
NB 18/07	185	0.024	1751	1721-1808				
NB 19/07					311	0.071	1113	1123-1208
HB 26/07	300	0.086	1118	1343-1435	198	0.055	1644	1634-1719
NB 08/08					348	0.074	1358	1356-1431
NB 09/08	350	0.043	0924	0927-1015				
HB 18/08					326	0.119	1128	1257-1339
HB 19/08	312	0.084	0559	0722-0808				
NB 23/08					208	0.033	1507	1505-1530
NB 25/08	281	0.023	1255	1323-1408				
HB 01/09	329	0.138	0400	0629-0648	270	0.028	1023	1320-1356
NB 14/09	8	0.023	1545	1545-1615				
NB 16/09					168	0.122	1056	1113-1143
HB 09/10	320	0.050	1249	1347-1412				
HB 10/10					301	0.013	0707	0751-0856
NB 21/10					294	0.029	1654	1641-1726
NB 23/10	292	0.037	1329	1440-1525				
HB 31/10	303	1.994	0450	0630-0705	337	0.047	1023	1212-1232

currents at ebb tide to be faster than those at flood tide (ebb tide $\bar{x}$ = 0.12 m/sec , flood tide $\bar{x}$ = 0.06 m/sec ; t-test, t= 1.491, P=0.068). Hence, pelagic eggs released primarily during ebb tide, as is apparently the case with bluehead wrasse, would be carried offshore faster during flood tides than ebb tides.

At spring tides (daily tides around full and new moon) ebb tide currents were five times faster than flood tide currents (ebb tide $\bar{x}$ = 0.21 m/sec , flood tide $\bar{x}$ = 0.04; t-test, t=1.427, P<0.01). At neap tides (daily tides around first and last quarters) ebb tide currents were only twice as fast as flood tide currents (ebb tide $\bar{x}$= 0.08 m/sec , flood tide $\bar{x}$ = 0.04 m/sec ; t-test, t=2.363, P<0.05). In the bluehead wrasse in Barbados, group spawning is the most common mode of reproduction (Section 3.3.1). It occurs primarily during ebb tides (Section 3.3.5) and is more frequent near new and full moon (spring tides) than near first and last quarters (neap tides ; Section 3.3.4). Hence, most eggs in the bluehead wrasse are released when offshore currents are at their fastest.

The seasonal reproductive and non-reproductive periods of the bluehead wrasse did not differ in terms of mean current speed at flood tides (reproductive, $\bar{x}$=0.07 m/sec ; non-reproductive, $\bar{x}$=0.08 m/sec ; t-test, t=0.41, P>0.05) or at ebb tides (reproductive, $\bar{x}$=0.09 m/sec ; non-reproductive, $\bar{x}$=0.14 m/sec; t-test, t=0.64, P>0.05) nor in terms of mean current direction at flood tides (reproductive,$\bar{x}$=281° WSW non-reproductive, $\bar{x}$=289° WNW ; Watson-Williams test (Zar, 1981), F=0.22,P>0.05) or at ebb tides (reproductive, $\bar{x}$=290° WNW; non-reproductive, $\bar{x}$=272° WNW; Watson- Williams test, F=0.81, P>0.05). Hence, seasonal variation in spawning is not apparently influenced by seasonal variation in nearshore current speed and direction.

3.3.7 Seasonal variation in recruitment

As determined by settlement marks on otoliths, recruitment of juveniles of T.bifasciatum to the population on Heron Bay reef occurred throughout the year (Fig. 12). However, recruitment was not uniformly distributed across months (Kolmogorov-Smirnov one-sample test, D=0.098, P<0.01); occurring primarily between June and December in 1984, with a sharp peak in July and August. January to June were periods of relatively low recruitment in both 1984 and 1985 (Fig. 12).

An index of seasonal variation in recruitment for the latter part of 1985 was generated by lagging the mean adult density for North Bellairs and Heron Bay reefs by two months (Table 3). Two months is the approximate time that it takes for a newly recruited bluehead wrasse (10mm) to become large enough to be censused as part of the adult population (>30mm; Victor, 1986a; Section 3.3.10). Note that this approach assumed that the seasonality of recruitment is strong enough to cause a correlated seasonal rise in adult density (see Section 3.3.10). For both reefs, densities are low in April and May, and begin to rise between June and August. The recruitment profiles generated are therefore similar on the two reefs, and similar to the recruitment profile of 1984 on Heron Bay reef obtained from otolith settlement marks. In both 1984 and 1985 recruitment was lower in the earlier part of the year, began to increase in June and reached a peak in July and August (Fig. 12 ; Table 3). Spawning in the bluehead wrasse in Barbados also varied seasonally with peak spawning

Figure 12. Number of recruits vs. time of the year for *Thalassoma bifasciatum* on Heron Bay reef, Barbados. Data presented separately by month from January 1984 to June, 1985.

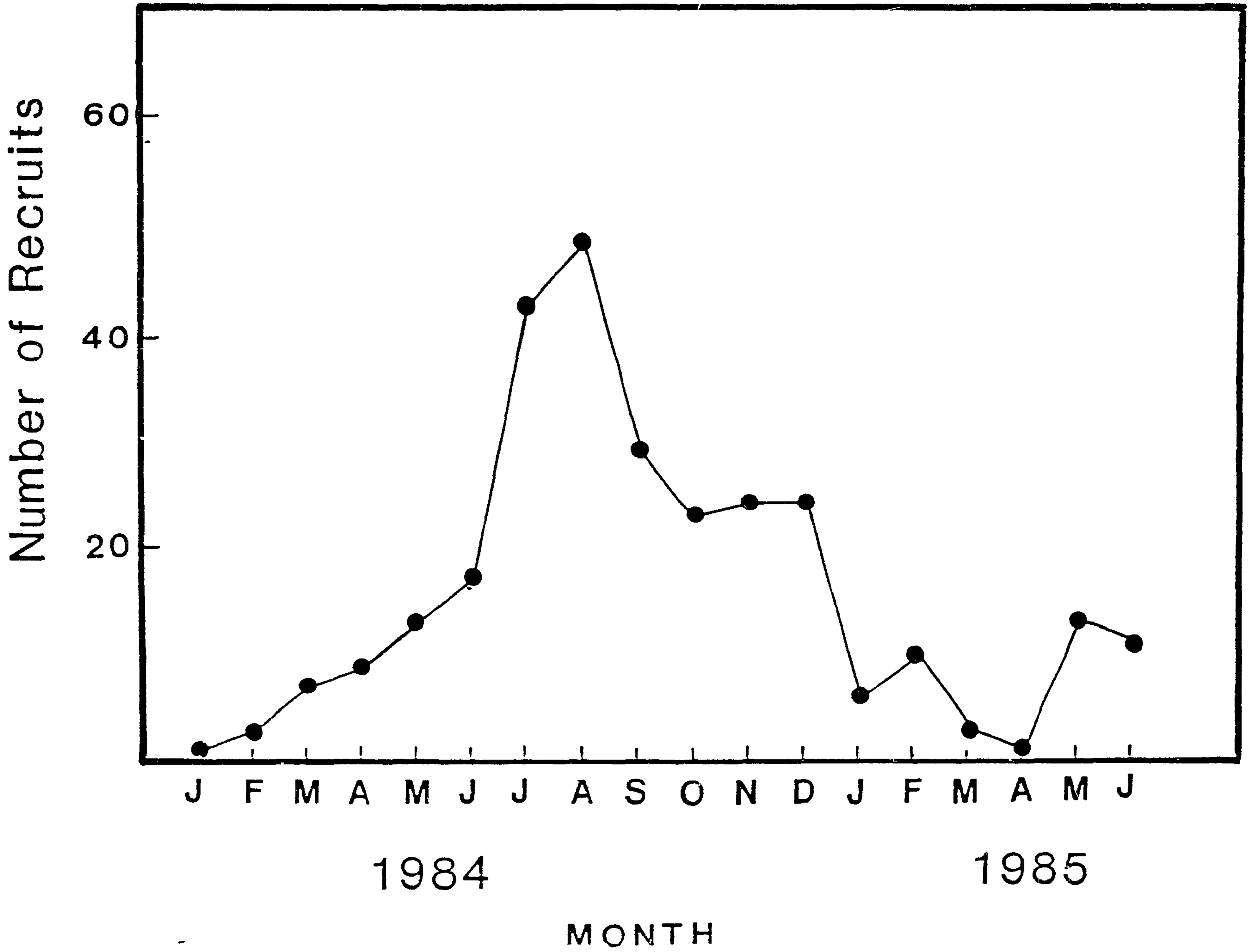

Number of Recruits
60
40
20
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1984
1985
MONTH

Table 3

Recruitment profile for the latter part of 1985 for Thalassoma bifasciatum on two fringing reefs, North Bellairs and Heron Bay, in Barbados. The profile is generated by time-lagging adult density by 2 months.

RECRUITMENT
(Adult density in N/m^2
time lagged by two months)

MONTH	NORTH BELLAIRS	HERON BAY
APRIL	0.89	1.31
MAY	1.05	1.31
JUNE	0.95	1.82
JULY	0.97	1.56
AUGUST	1.97	1.88

preceding peak recruitment (Fig. 3a; Fig. 12). This is circumstantial evidence suggesting that the principal factor influencing seasonal variation in recruitment is seasonal variation in spawning. The similar recruitment profiles in 1984 and 1985 also suggest that between-year variation in the timing of seasonal recruitment and seasonal spawning may not be substantial.

Assuming seasonal variation in spawning to be similar in 1984 and 1985, Spearman's Rank correlation coefficients between the number of spawning events in a month and the number of recruits in a month (1984 data) can be generated (Table 4). Correlations between spawning and recruitment were high and significant when recruitment was lagged on spawning by two and three months, but were insignificant with time lags of 0,1,4, and 5 months (Table 4). Using otolith dating, larval life of bluehead wrasse in Barbados is estimated at between 33 and 69 days, that in Panama is slightly longer at about 38 to 78 days (Victor 1986b). Hence a time lag of 2-3 months between peak spawning and peak recruitment, particularly given the assumption of identical spawning profiles in 1984 and 1985, is largely consistent with the suggestion that the timing of seasonal recruitment is primarily controlled by the the timing of seasonal spawning.

3.3.8 Lunar variation in recruitment

Otolith dating was used to investigate variation in recruitment by combining individuals from all months that settled on each lunar day. Settlement of bluehead wrasse seemed to be higher on the days around the new moon than in the other days of the lunar month (Table 5).

Table 4

Spearman's correlation coefficients (r_s) for different time lags between the number of spawning events in a month and the number of recruits per month in (1984) for *Thalassoma bifasciatum* on Heron Bay reef in Barbados.

+ denotes significance at the 0.10 probability level

* denotes significance at the 0.05 probability level

TIME LAG (MONTHS)	CALCULATED (r)	p
0	-0.33	0.32
1	0.18	0.56
2	0.56	0.06 +
3	0.85	0.003*
4	-0.18	0.52
5	0.11	0.69

Table 5

Total number of newly settled *Thalassoma bifasciatum* occurring on each day of the lunar month on North Heron Bay reef, Barbados.

0=FULL MOON 7=LAST QUARTER 14=NEW MOON 21=FIRST QUARTER

LUNAR DAY	NUMBER OF SETTLERS
0	5
1	8
2	10
3	14
4	13
5	8
6	7
7	12
8	5
9	12
10	8
11	13
12	7
13	11
14	21
15	15
16	10
17	7
18	5
19	9
20	9
21	10
22	9
23	10
24	11
25	15
26	9
27	7

The pattern of settlement was different from a uniform distribution (X^2 =11.2, $P<0.05$). Victor (1986a) found settlement to be strongest around the new moon for bluehead wrasse in Panama.

3.3.9 Effects of density on recruitment

The effects of resident-adult density on recruitment were investigated to comment on whether space availability on a reef appears to influence the timing and strength of recruitment. The overall mean densities of *T. bifasciatum* on the study reefs were: Greensleeves, 1.72 N/m^2; Heron Bay, 1.51 N/m^2 ; Paynes Bay, 1.49 N/m^2; Sandridge, 1.31 N/m^2; Golden Palms, 1.21 N/m^2; Glitter Bay, 1.04 N/m^2; North Bellairs, 1.01 N/m^2. The study reefs showed similar seasonal variation in density; density declining from around December to May/June, and then increasing as the year's recruits became large enough (>30mm) to be censused as adults (Fig. 13).

An estimate of the rate of recruitment on any reef can therefore be obtained from the slope of the density line between May and October (when the study was terminated). Note that this is strictly recruitment to the adult population, rather than recruitment to the reef, and that it is a conservative estimate of recruitment since it does not discount for mortality of resident adults following recruitment. The recruitment rates to each reef, estimated as above, are presented in Table 6. The effects of adult density prior to recruitment on subsequent recruitment rate can then be investigated by plotting the lowest pre-recruitment density on a given reef against subsequent recruitment rate on that reef (Fig. 14a). The variables are not correlated (Spearman's Rank Correlation (STSC, 1985) r_s=0.19,

Figure 13. Monthly densities (N/m^2) vs time of year for *Thalassoma bifasciatum* on each of seven fringing reefs in Barbados. Data presented separately by month for the period from September 1984 to October 1985.

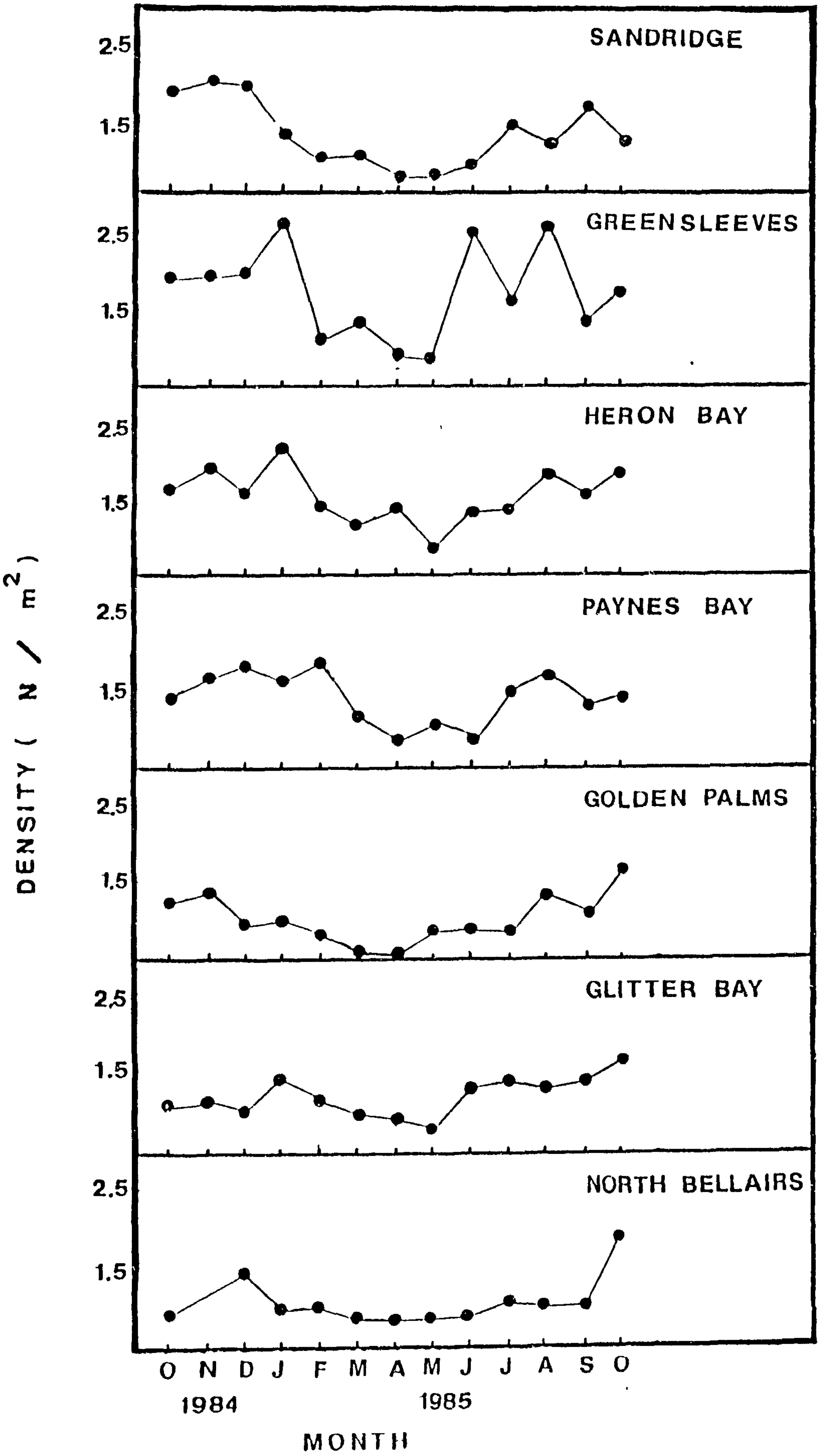

SANDRIDGE
GREENSLEEVES
HERON BAY
PAYNES BAY
GOLDEN PALMS
GLITTER BAY
NORTH BELLAIRS
2.5
1.5
DENSITY (N / m^2)
O N D J F M A M J J A S O
1984
1985
MONTH

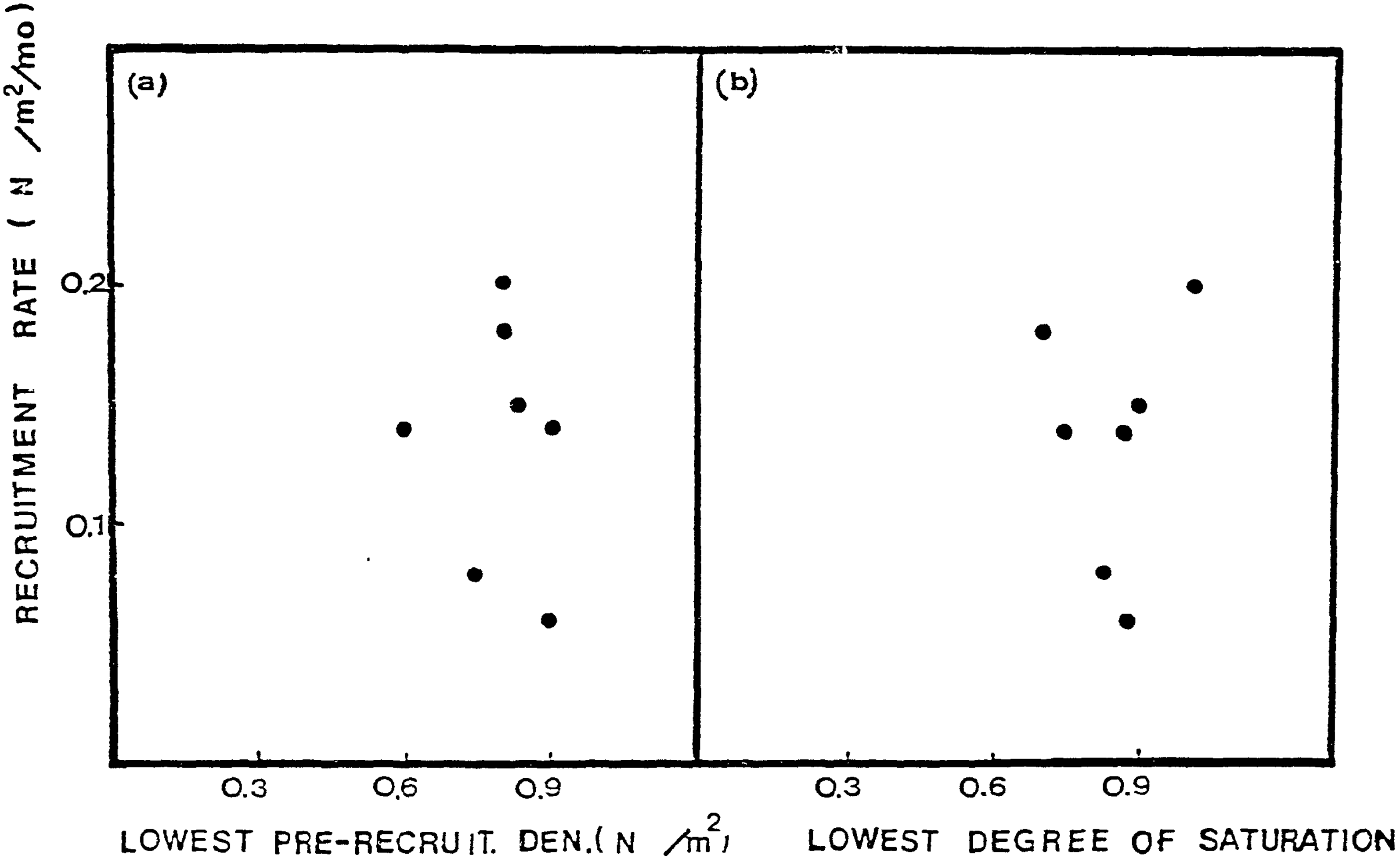
TABLE 6

Estimated recruitment rates for *Thalassoma bifasciatum* on seven fringing reefs in Barbados between May and October 1985. The recruitment rates are generated as the slopes of the increase in density following recruitment on each reef (Figure 13).

REEF	ESTIMATED RECRUITMENT RATE (increase in density (N/m^2 per month)
North Bellairs	0.20
Heron Bay	0.18
Glitter Bay	0.15
Golden Palms	0.14
Greensleeves	0.14
Sandridge	0.08
Paynes Bay	0.06

Figure 14a. Recruitment rate (N/m^2 / month) to a reef vs the lowest pre-recruitment density on the reef for each of seven fringing reefs in Barbados. Data span the period May to October, 1985.

Figure 14b. Recruitment rate (N/m^2 / month) to a reef vs lowest pre-recruitment degree of saturation (density/carrying capacity) on the reef, for each of seven fringing reefs in Barbados. Data span the period May to October, 1985.


(a)
(b)
RECRUITMENT RATE (N /m²/mo)
0.2
0.1
0.3
0.6
0.9
0.3
0.6
0.9
LOWEST PRE-RECRUIT. DEN.(N /m²)
LOWEST DEGREE OF SATURATION

$p>0.05$), tentatively suggesting that resident adult density on a reef does not influence subsequent recruitment rate to the reef.

The problem with the above approach is that the carrying capacity of the reefs for the bluehead wrasse may differ. Consequently, density on a reef may not be a good indicator of space availability on the reef. I will define carrying capacity of each reef as the mean density around which density values stabilize following the recruitment pulse in any given year. Recruitment of juveniles primarily occurs between June and December (Fig. 12), and the resulting peak density of individuals of census size occurs by December or January on each reef (Fig. 13). Following recruitment, densities fall sharply, stabilizing on the different reefs by either February or March (Fig. 13). The values used as estimates of carrying capacity are therefore the mean density between February and May for Greensleeves, between March and June for Heron Bay, between March and June for Paynes Bay, between February and June for Sandridge, between March and May for Glitter Bay, between February and July for Golden Palms and between March and June for North Bellairs. The resulting estimates of carrying capacity are presented in Table 7. The degree of saturation on any reef in any given month can therefore be estimated as the ratio of density / carrying capacity.

Effects of degree of saturation prior to recruitment on subsequent recruitment rate could then be investigated by plotting the lowest degree of saturation on any reef in the pre - recruitment period against the subsequent recruitment rate to the reef generated as in Table 6 (Fig. 14b). The variables are not correlated (Spearman's Rank Correlation, $r_s = -0.126$, $p>0.05$), tentatively suggesting that

TABLE 7

Estimates of carrying capacity for Thalassoma bifasciatum on seven fringing reefs in Barbados and months over which reefs are relatively stable in density (see Fig. 13).

REEF	MONTHS OF STABLE DENSITY	ESTIMATES OF CARRYING CAPACITY (N/m^2)
Heron Bay	March - June	1.17
Greensleeves	Feb. - May	1.06
Paynes Bay	March - June	1.04
Glitter Bay	March - May	0.93
Sandridge	Feb. - June	0.90
North Bellairs	March - June	0.84
Golden Palms	Feb. - July	0.79

degree of saturation of a reef does not influence subsequent recruitment rate to the reef.

3.3.10 Effects of recruitment on density

Recruitment of juveniles to Heron Bay reef in 1984 occurred primarily between June and December (Fig. 12). This was reflected in the adult population density, which rose in the latter part of 1984 to reach a peak by January 1985 (Fig. 13). Adult density on Heron Bay was significantly correlated with number of recruits on Heron Bay when it was lagged behind the latter by two months (Spearman's Rank Correlation, r_s-0.76,P<0.01; Table 8). The lag time of two months corresponds to the time estimated by Victor (1986a) for new recruits (10mm SL) to grow to adult size (30mms SL) and therefore become detectable during density surveys. Prior to this size,juveniles are hidden and difficult to detect during censuses.These data support the use of a two month lag to generate recruitment profiles from adult density profiles in Section 3.3.7. Note that the new adult density produced by the recruitment pulse on Heron Bay (i.e. density in January 1985) is not maintained at that level but falls sharply (eg. January to February), again approaching pre-recruitment levels within about three months (Fig. 13). The adult density profiles on all study reefs were similar (Fig. 13), suggesting that the seasonality of recruitment is similar across all reefs.

The post-recruitment period is considered to be January to May for Greensleeves, January to May for Heron Bay, February to June for Paynes Bay, December to May for Sandridge, January to May for Glitter Bay, November to April for Golden Palms and December to May for North

TABLE 8

Spearman's rank correlation coefficients (r_s) for different time lags between recruitment and adult density in *Thalassoma bifasciatum* on Heron Bay reef in Barbados. Recruitment was determined from otolith dating monthly subsamples from Heron Bay reef and the correlations were generated by time-lagging adult density by 1 to 5 months.

* denotes significice at the 0.05 probability level.

TIME LAG (MONTHS)	CALCULATED r	p
0	-0.100	>0.77
1	0.447	>0.17
2	0.760	<0.01*
3	0.474	>0.14
4	0.236	>0.49
5	0.009	>0.98

Bellairs (Fig. 13). The decline in density following recruitment can be used to calculate post-recruitment mortality, and thereby comment on whether post-recruitment mortality is density-dependent. For each reef during the post-recruitment period, the monthly mortality rate (% dying each month) can be calculated and plotted against the density at the start of that month (Fig. 15), and against the degree of saturation of the reef (Section 3.3.9) at the start of that month (Fig. 16). For most reefs, the highest mortality rate occurred when reef density was highest (Fig. 15) and when the extent to which the reef was above its estimated carrying capacity was at its highest (Fig. 16). These results suggest that post-recruitment mortality is density-dependent, and hence imply that competition for resources on the reef (space-limitation) is an important factor influencing population size and population dynamics of the bluehead wrasse on fringing reefs in Barbados.

It is possible to look at effects of density on mortality by between-reef comparisons. An estimate of mortality rate on any given reef following the recruitment pulse can be obtained from the slope of the density line during the post-recruitment period for that reef. Mortality rate estimates obtained as above are presented for each reef in Table 9. Note that these are conservative estimates of mortality since loss due to mortality may be buffered by continuing low levels of recruitment in the post-recruitment period. The effects of recruitment strength on subsequent mortality can be investigated by plotting the peak density following recruitment on any reef against the subsequent mortality on that reef as estimated in Table 9. The variables are positively correlated (Spearman's Rank Correlation,

Figure 15. Monthly mortality rate (% dying) vs density at the start of the month (N/m^2), during the post-recruitment period of 1985, for *Thalassoma bifasciatum* on seven fringing reefs in Barbados. Data are presented separately for each reef.

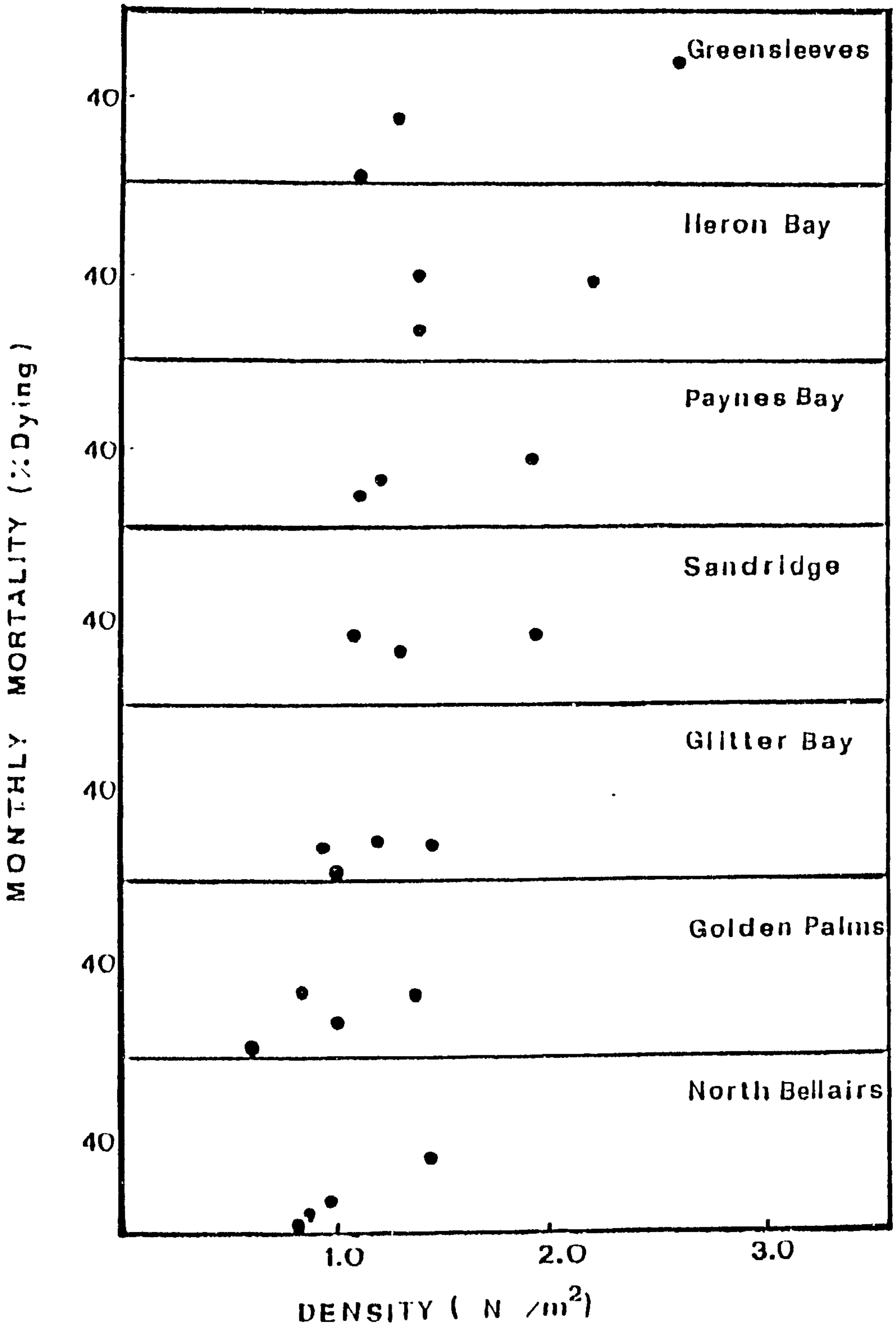

Greensleeves
Heron Bay
Paynes Bay
Sandridge
Glitter Bay
Golden Palms
North Bellairs
40
40
40
40
40
40
40
MONTHLY MORTALITY (% Dying)
1.0
2.0
3.0
DENSITY (N /m²)

Figure 16. Monthly mortality rate (% dying) vs degree of saturation (density/carrying capacity) at the start of the month during the post-recruitment period of 1985 for Thalassoma bifasciatum on seven fringing reefs in Barbados. Data are presented separately for each reef.

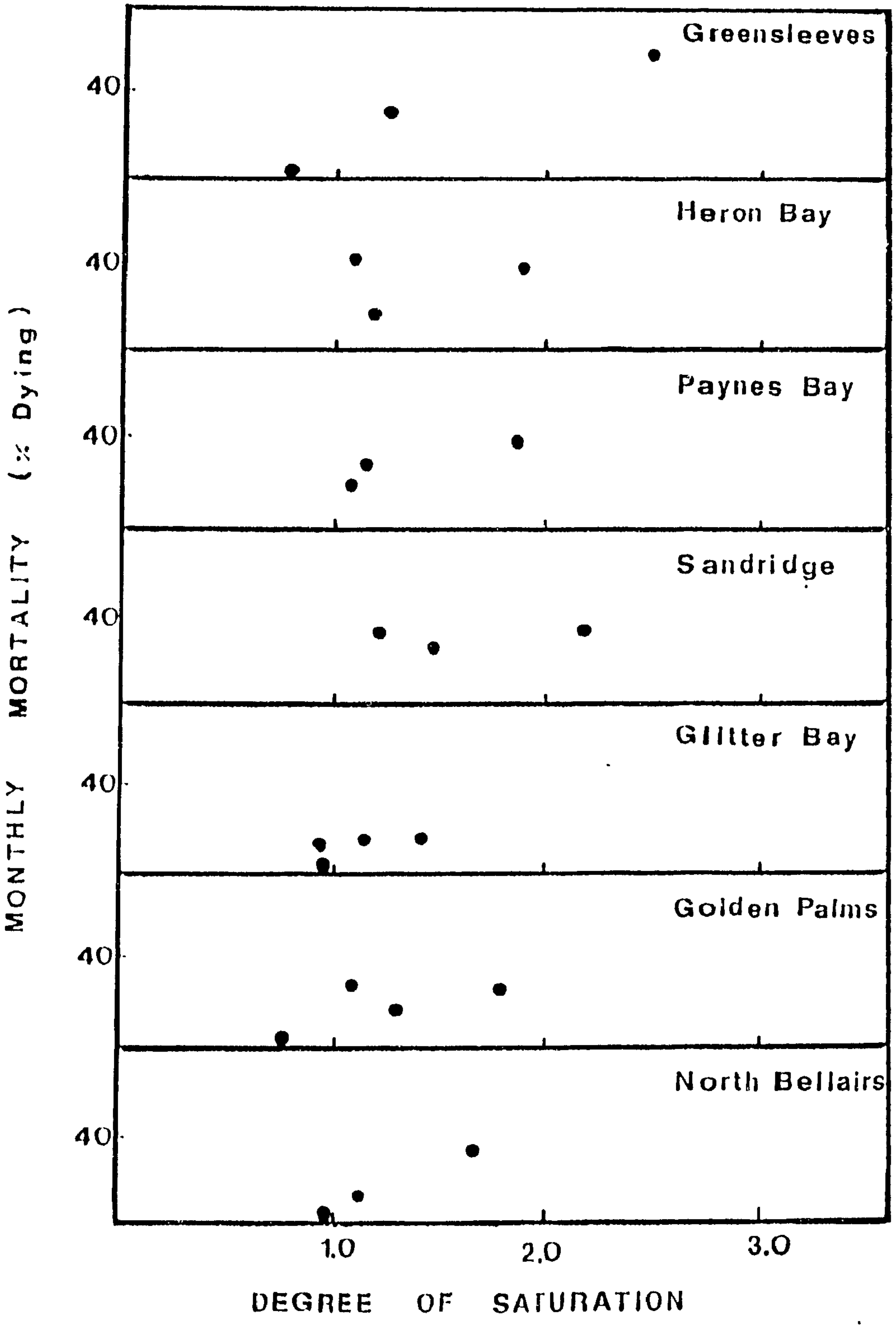

Greensleeves
Heron Bay
Paynes Bay
Sandridge
Glitter Bay
Golden Palms
North Bellairs
40
MONTHLY MORTALITY (% Dying)
1.0
2.0
3.0
DEGREE OF SATURATION

TABLE 9

Estimates of mortality rate following the recruitment pulse for <u>Thalassoma bifasciatum</u> on seven reefs in Barbados. The estimates are obtained from the slopes of the density lines in the post-recruitment period (see Fig. 13).

REEF	ESTIMATE OF MORTALITY RATE (No dying $/m^2/$ month)
Greensleeves	1.49
Heron Bay	0.53
Paynes Bay	0.52
Sandridge	0.49
North Bellairs	0.48
Golden Palms	0.38
Glitter Bay	0.23

$r_s=0.86$, $p<0.05$; Fig. 17). The procedure was repeated using the maximum extent to which a reef was driven above carrying capacity by the recruitment pulse (highest density / carrying capacity) against the subsequent mortality on that reef. The variables are again positively correlated (Spearman's Rank Correlation, $r_s=0.82$, $p<0.05$; Fig. 18). These analyses suggest that mortality following recruitment is a function of recruitment strength, as indicated either by peak reef density following recruitment or by the extent to which the reef was driven above carrying capacity by recruitment.

Figure 17. Post-recruitment mortality on a reef (No dying/ m^2 / month) vs peak density following recruitment on that reef (N/m^2) for seven fringing reefs in Barbados.

Greensleeves = GS
Heron Bay = HB
Sandridge = SD
Paynes Bay = PB
Glitter Bay = GB
Golden Palms = GP
North Bellairs = NB

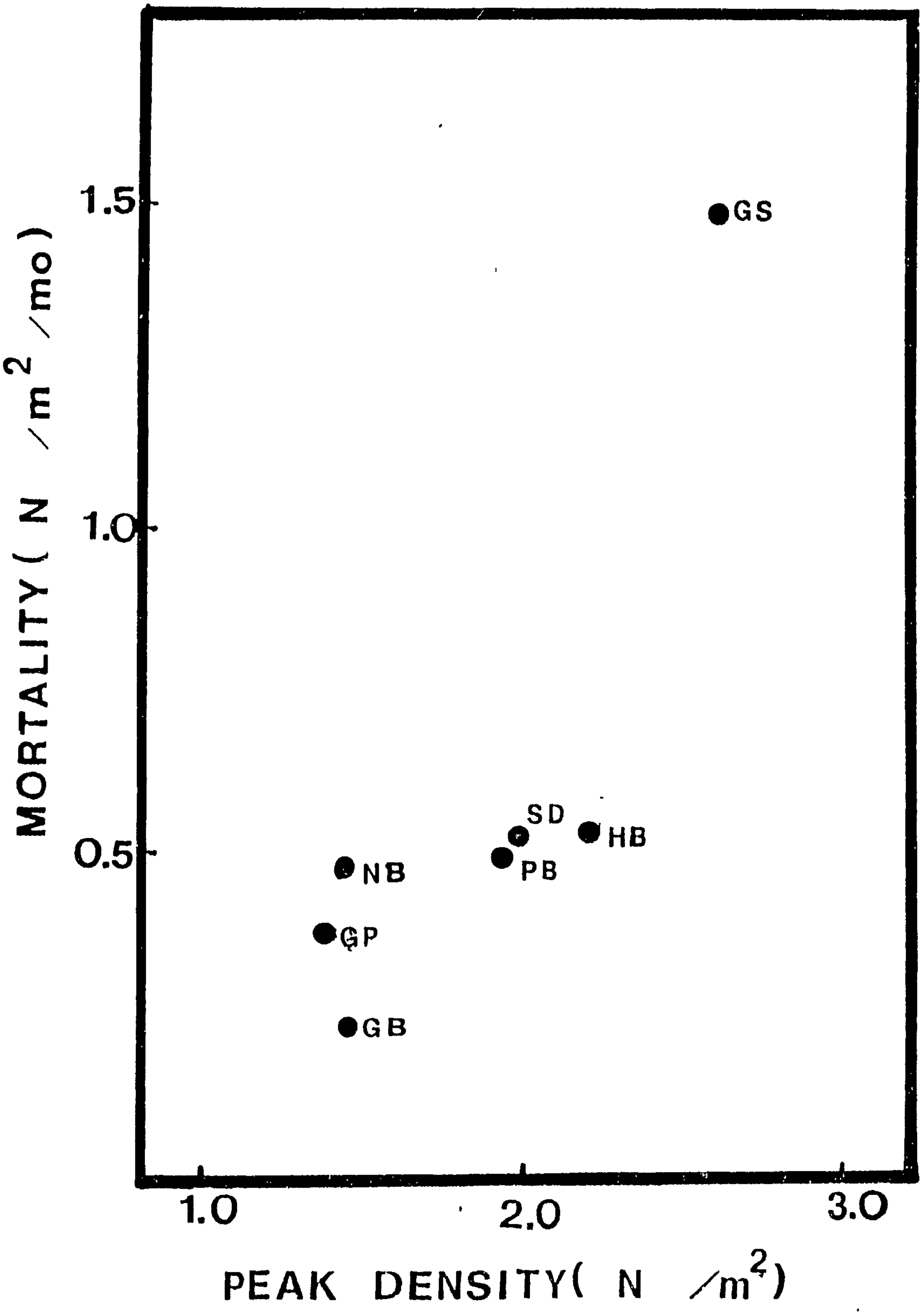
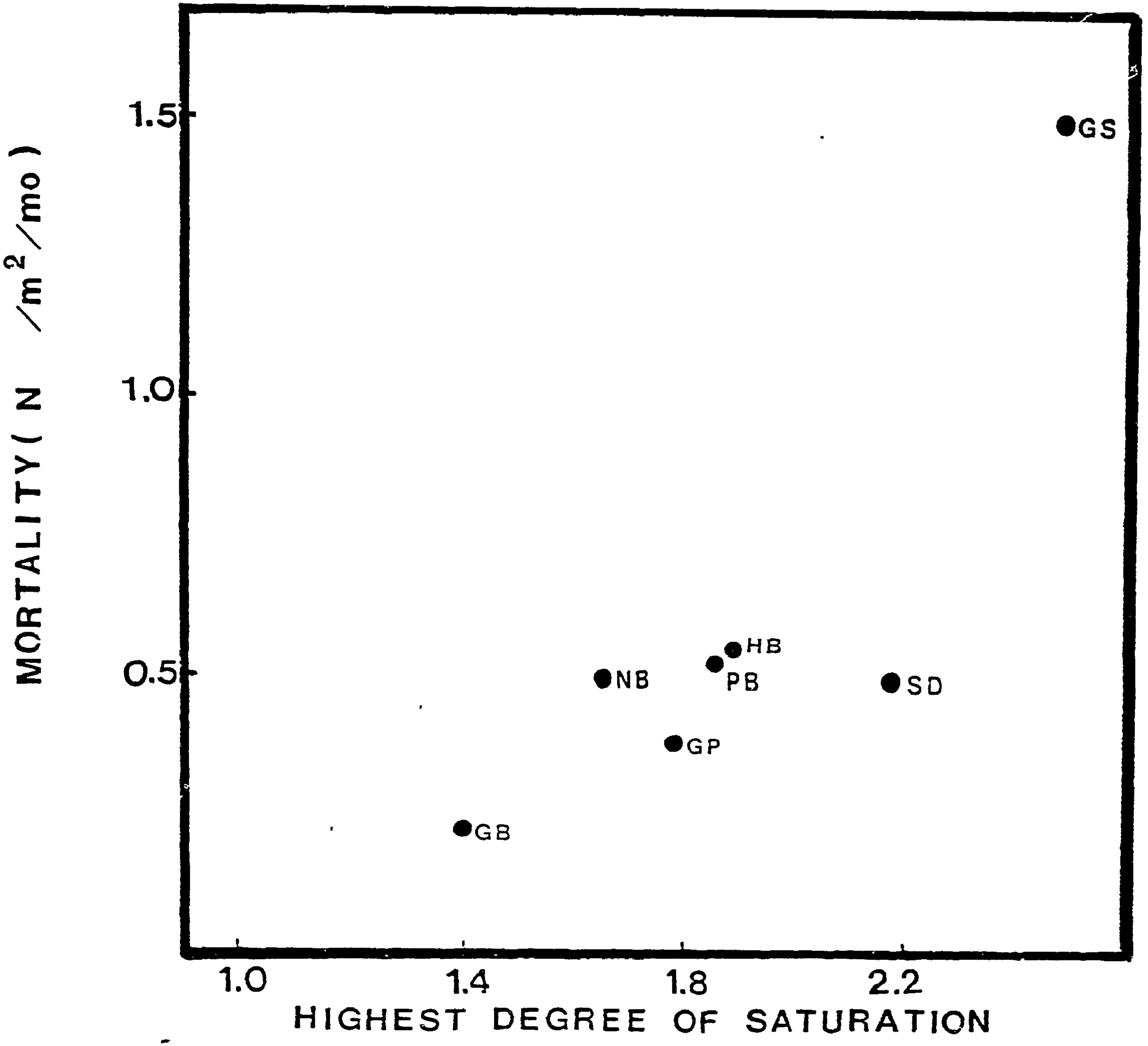

MORTALITY(N /m^2 /mo)
1.5
1.0
0.5
GS
SD
HB
PB
NB
GP
GB
1.0
2.0
3.0
PEAK DENSITY(N /m^2)

Figure 18. Post-recruitment mortality on a reef (N/m^2 / month) vs. the highest degree of saturation (highest density/carrying capacity) following recruitment on that reef for *Thalassoma bifasciatum* on seven fringing reefs in Barbados.

Greensleeves = GS
Heron Bay = HB
Sandridge = SD
Paynes Bay = PB
Glitter Bay = GB
Golden Palms = GP
North Bellairs = NB


MORTALITY (N /m^2/mo)
1.5
1.0
0.5
1.0
1.4
1.8
2.2
HIGHEST DEGREE OF SATURATION
GS
HB
NB
PB
SD
GP
GB

3.4 DISCUSSION

3.4.1 Seasonal variation in spawning

The direct enumeration of spawning events conducted in the present study suggests that spawning in the bluehead wrasse T. bifasciatum occurred throughout the year in Barbados. However, spawning was markedly seasonal, with most spawning occurring between January and July, the drier months of the year (Fig. 3a). This increased spawning activity did not simply result from more fish being present to spawn, but was caused by increased spawning activity per fish present (Fig. 7a). Seasonal variation in gonadosomatic indices supported the suggestion that spawning activity was greatest during the dry season (Fig. 8). Interestingly, the increased spawning activity resulted primarily from a higher frequency of group spawning, only secondarily from an increase in pair spawning (Table 1 ; Figs 3b & 3c). Seasonal changes in the proportion of pair to group spawning in the bluehead wrasse (Fig. 5) have not previously been studied.

Feddern (1965) was the first to study reproductive activity in the bluehead wrasse, and found it to occur throughout the year in Florida. However, Roede (1972) suggested that there might be some seasonality in reproductive activity. She found a higher percentage of functional gonads during November and December and from April until June in both Puerto Rico and Curacao. Victor (1983a, 1986a) conducted recruitment studies of the bluehead wrasse in the San Blas Islands in Panama. As the species is known to spawn every day (Robertson and Hoffman 1977; Warner et al 1975, Warner & Robertson 1978), Victor (1983a, 1986a) assumed a uniform spawning frequency throughout the year. It was this assumption which led him to suggest that the temporal variation in recruitment he observed was due to variation in larval survival in the plankton rather than to variation in reproductive activity of adults. In turn, this was a factor leading to his assertion that the population dynamics of the bluehead wrasse in Panama was controlled primarily by processes in the plankton, rather than by processes on the reefs (Victor 1986a).

It is becoming increasingly clear that the original paradigm that tropical reef fish spawn throughout the year with no seasonal variation (eg. Qasim 1955; Hiatt and Strassburg 1960) is untrue for most species. Coral reef fish in Jamaica (Munro et al 1973), in the eastern Caribbean (Powles 1975; Luckhurst and Luckhurst 1977) and in Hawaii (Watson and Leis 1974; Lobel 1978) show seasonal spawning; most spawning occurring in spring, with occasionally a secondary peak in fall. On both the north (tropical, Lizard Island) and the south (subtropical, One Tree Island) of the Great Barrier Reef, seasonal spawning peaks also occur, although primarily in the austral summer (Russel et al 1974, 1977; Johannes 1978; Doherty 1983a).

Seasonal variation in reproduction of coral reef fish is presumably controlled by both proximate (environmental cues) and ultimate (adaptive value) factors. Waters around Barbados originate from the North Equatorial Current during the winter months and are of high salinity and relatively low temperature. Summer water driven by the South Equatorial Current is more strongly influenced by the major river discharges of the South American mainland, and is low in salinity and higher in temperature (Lewis and Fish 1969; Ryther et al 1967; Parr 1937, 1938 (in Powles 1975); Tomascik 1986). In

Barbados (present study), peak spawning of the bluehead wrasse takes place in the dry season between February and May, beginning when water temperatures are lowest and salinities are highest and continuing as temperatures increase and salinities decrease (Tomascik 1986). In Jamaica maximum spawning of reef fish also occurs during months of lowest water temperatures (Feb-April) (Munro et al 1973) and this may be a common occurrence in the Caribbean (Johannes 1978). This may imply that the temperature and salinity are proximate factors influencing seasonality of reproduction. Note , however that on the Great Barrier Reef (north and south), peak spawning occurs during months of the highest water temperatures (Russell et al 1974, 1977; Doherty 1983a).

If spawning of most reef fish in the Caribbean occurs primarily in the spring, larval abundance will be highest in early summer (Munro et al 1973; Powles 1975). There is some indication that zooplankton abundance in Barbados is higher during the summer months (Lewis and Fish 1969). This implies that the abundance of food for fish larvae may be highest in these months (Watson and Leis 1974; Powles 1975; Luckhurst and Luckhurst 1977), and hence that larval food abundance may be an ultimate factor influencing seasonal variation in spawning of reef fish. However, other studies have found no correlation between plankton abundance and fish larval abundance in the Caribbean (Miller 1973; Munro et al 1973).

Like most other coral reef fish, the larvae of bluehead wrasse are positively buoyant (pers. obs.; Powles 1975; Thresher 1984), and spend most of their larval life near the surface of deeper offshore waters (Powles 1975). More predators are believed to be associated with inshore reefs than with offshore waters (Breder and Rosen 1966; Johannes 1978; Shulman 1985b), partly because larvae may be susceptible to both benthic and planktonic predators when inshore. This difference in offshore and nearshore predation may have been a strong selective factor in the evolution of the pelagic larval phase in reef fish (Johannes 1978, but see Shapiro et al 1988). However, there has been little work on seasonal variation in predator abundance in offshore waters, consequently, whether this is a causal factor in the evolution of seasonal reproduction in coral reef fish remains unknown.

Johannes (1978) suggested that many tropical reef fish spawn at the time of year when wind and / or oceanic offshore current strength is reduced, and hence when larval loss to oceanic waters is low. Nearshore currents on the west coast of Barbados are generally offshore (see 3.3.6 (present study), Bevan (unpublished)). Consequently, larvae are carried off from inshore reefs irrespective of tidal state or time of year. However, the larvae may then either be retained offshore in a slow current region or in eddies and gyres which exist around Barbados (Emery 1972; Powles 1975; Peck 1978) or be swept into the westward flowing Equatorial Current. Slower currents in offshore waters usually occur when there are shifts in major current systems (Lobel and Robinson 1983). Off Barbados, this occurs when the North Equatorial Current switches to the South Equatorial current in April and reverses again in October (Parr (1938) in Powles 1975). Interestingly, the first switch coincides with peak spawning and the second with peak recruitment of the bluehead wrasse in Barbados.

3.4.2 Lunar variation in spawning

In a study of 50 species of tropical fish encompassing 24 families, including T.bifasciatum, most were found to spawn with some lunar periodicity (Johannes 1978). Of these, 23 species spawned near or at the full moon, 35 at the full moon and 14 at both full and new moon (Table 4 in Johannes 1978). The widespread nature of the phenomenon suggests some selective advantage in lunar cycle spawning periodicity. An analysis of over 2000 spawning events of the bluehead wrasse in the present study suggested that group spawning occurred most frequently around new and full moons (Fig. 10a); but there was no apparent lunar periodicity to pair spawning (Fig. 10b). Randall, who had been observing scarids for many years, opportunistically noticed and recorded spawning labrids. His notes suggest that peak spawning occurs twice in a lunar month, on the full and new moons, in labrids (Randall and Randall 1963). The present results and those of Randall and Randall (1963), both of which suggest a tendency towards new and full moon spawning, are further supported by gonad analyses of T.bifasciatum conducted by Roede (1972).

Many suggestions have been advanced for the semi-lunar spawning peaks observed in the bluehead wrasse and other reef fish (Allen 1972; Fricke 1974; Johannes 1978; Lobel 1978; Pressley 1980; McFarland 1982; Doherty 1983a). First, spring tides occur only around new and full moons, and are typically characterised by fast ebb and flood currents. Spawning peaks at new and full moon therefore coincide with the fastest currents. If the spawning occurred during ebb tides, and ebb tide surface currents were offshore, spawning at new and full moon would maximize transport of eggs and larvae off of reefs, and thereby minimize their mortality due to predation. However, lunar variation in the direction and speed of nearshore surface currents has seldom been studied at the same time and place as lunar variation in spawning frequency. In the present study of the west coast fringing reefs in Barbados, both ebb and flood tide surface currents were offshore, but ebb tide currents were five times faster than flood tide currents. However during neap tides, ebb tide currents were only twice as fast as flood tide currents (Section 3.3.6). Since daily spawning, although restricted to a four hour period around midday, occurs more frequently during ebb tides than flood tides (Figs. 11a & 11b), bluehead wrasse in Barbados are spawning when nearshore surface currents have their maximum offshore velocity.

Secondly, reef fish may be synchronizing their spawning peaks with the extremes of tidal height that occur during spring tides. High water levels may help to keep eggs and larvae away from benthic predators. It is of interest in this context that daily spawning of both pairs and groups occurred most frequently at the onset of ebb tides i.e. at high tide when water depth is at its greatest (Figs. 11a & 11b). Moreover, by spawning primarily at spring tides, as is true for group-spawners, the wrasses are spawning when high tide water depth is at its monthly maximum. These data all suggest that minimizing predation on eggs and larvae by reef-based predators is an important factor in the evolution of lunar variation in spawning in the bluehead wrasse in Barbados.

Finally most coral reef fish eggs, including those of T.bifasciatum, are positively buoyant and hatch into photopositive larvae (pers. obs. ; Thresher 1984). If most larvae are released near full moon, their tendency to swim towards the well illuminated surface may help minimize benthic predation (Thresher 1984). However, this can not explain a second spawning peak near new moon, when illumination is at its lowest (Thresher 1984); and new moon spawning was more common than full moon spawning in the present study. Note that none of the above hypothesis for lunar spawning in reef fish are mutually exclusive and any combination of them may result in the lunar patterns observed (Lobel 1978).

Bluehead wrasse in the present study and those in Panama (Warner et al, 1975) move to downcurrent projections on the reef to spawn. This apparently does not occur in Puerto Rico (Shapiro et al 1988). The results from Barbados and Panama suggest that there are advantages to getting eggs and larvae rapidly off of reefs, a process that may be facilitated by spawning primarily at ebb and spring tides. Note that the fact that the fish migrate to downcurrent positions to spawn may decrease the intensity of selection for tight synchronization of spawning with ebb and spring tides. Selection may be stronger on more sedentary non-migrating reef organisms to synchronize spawning with rapid offshore currents (eg. Diadema antillarum; Younglao 1987). Warner and Robertson (1980a) found no synchronization of bluehead wrasse spawning peaks with ebb tide in the San Blas Islands in Panama, where current systems are weak. However, numerous studies on other labrids have shown a strong association between spawning activity and ebbing tides (Robertson and Choat 1974; Choat and Robertson 1975; Robertson and Hoffman 1977; Kuwamura 1981; Ross 1983).

3.4.3 Seasonal variation in recruitment

Studies of reef fish in Curacao (Luckhurst and Luckhurst 1977) and St. Croix (McFarland et al 1985 (Haemulon flavolineatum)) indicated seasonality in recruitment, with peaks in late summer and occasionally secondary peaks in spring. On both the south (subtropical, One Tree Island) and the north (tropical, Lizard Island) of the Great Barrier Reef, recruitment is now known to be seasonal for some species of reef fish, occurring between September to May with ε peak in January - February (Russell et al 1977; Talbot et al 1978; Williams and Sale 1981 (pomacentrids); Williams 1983; for further studies see Doherty and Williams, in press). A question of interest is whether seasonal recruitment reflects seasonality of spawning, or seasonal variation in larval survival in the plankton (Sale 1980; McFarland et al 1985; Victor 1986a). Otolith dating of bluehead wrasse in Barbados revealed that recruitment occurred all year, but was strongest between June and December with a peak in July / August (for 1984; Fig. 12). This recruitment pulse in Barbados was presumably responsible for the increasing density that was occurring on all reefs at the start of the study in October 1984 (Fig. 13). The recruitment pulse apparently occurs at about the same time each year, since density was again rising on all the reefs during the summer / fall of 1985. A seasonal peak in recruitment of Thalassoma bifasciatum was also found in Panama (Victor 1986a). It occurred at approximately the same time each year for the four years studied, but was later in the year (Sept - Nov) than was the case in Barbados.

Spawning activity of the bluehead wrasse in Barbados is also seasonal. Spawning occurs primarily between January and July, with a peak between March and June (Figure 3a). Peak recruitment appears to follow peak spawning with a time lag of 2 to 3 months. Otolith dating in the present study indicated that larval life of the bluehead wrasse ranged from 33 to 72 days, with a mean of 45 days. In Panama, mean larval life was estimated at 49 days (Victor 1986b). The time lag observed in Barbados between spawning and recruitment is therefore largely consistent with the known duration of the larval life of the bluehead wrasse, particularly since Victor (1986c) has more recently shown that the bluehead wrasse can vary its larval life by varying its growth rate, thereby delaying settlement until appropriate habitats are located.

The observation that peak recruitment follows peak spawning by a time lag similar to the estimated duration of the larval life has two implications. First, it suggests that seasonal variation in recruitment may be a function of variation in spawning rather than of variation in larval survival in the plankton. Victor (1983a, 1986a) assumed that in areas close to the equator where environmental seasonality is less marked, the bluehead wrasse would show little seasonal variation in spawning frequency. Since he found marked seasonality in recruitment, he attributed this to seasonal variation in larval survival. (For similar suggestions, see Luckhurst and Luckhurst 1977). Tropical reef fish are highly fecund (Sale 1980), and mortality in the plankton is undoubtedly high (Doherty 1983b; Williams <u>et al</u> 1986). However, the extent tc which there is seasonal variation in larval survival in the plankton, and the degree of inter-annual variability in larval survival, remain largely unknown for reef fish. The results of the present study suggest that any seasonal variation in larval survival of bluehead wrasse that might occur is insufficient, in the Barbados context, to obliterate the correlation between peak spawning and peak recruitment observed.

The second implication is that the correlation between peak recruitment and peak spawning of the bluehead wrasse in Barbados is circumstantial evidence suggesting that recruits to the reefs in Barbados are primarily products of the spawning stock in Barbados, i.e. that the island population is largely discrete. The belief that planktonic larvae are passive and largely at the mercy of oceanic currents has been accepted with little evidence (Hjort (1914) in Powles 1975; Walsh et al 1981). However, the presence of eddies and gyres can trap larvae and thereby restrict larval dispersal (Sale 1970; Emery 1972; Powles 1975; Leis and Miller 1976; Johannes 1978; Lobel and Robinson 1983), and a number of recent studies suggest that larvae have some control over their vertical position in the water column and hence over their horizontal distribution (Victor 1981; Leis 1982; Leis and Goldman 1984, Leis 1986).

The alternative to the hypothesis of discrete island stocks is that peak spawning, and therefore recruitment, occurs at similar times in all neighbouring countries in the region. Hence, peak recruitment could follow peak spawning in Barbados by a time lag which corresponds to the length of the larval life even though recruits to Barbados were primarily from islands/land masses farther upcurrent. The Antillean islands are all downcurrent of Barbados (Fig. 1a). However, in the summer, water from the continental shelf of South America drifts to Barbados (Lewis and Fish 1969; Mazieka 1973; Powles 1975; Tomascik 1986; Hunte et al 1986), and this is when recruitment of the bluehead wrasse primarily occurs. Powles (1975) estimates that larval travel time from the mouth of the Amazon to Barbados would be approximately 80 days, and would of course be shorter if larvae originated from Trinidad or Tobago. It may therefore be possible for some bluehead wrasse larvae originating in South America and/or Trinidad and Tobago to reach Barbados, particularly given their apparent flexibility in duration of larval life (Victor 1986c). It is of interest in this context that bluehead wrasse have been found in deep offshore waters (Miller 1973; Richards 1984) and Williams et. al (1984) suggests that reef fish larvae on the Great Barrier Reef may be carried hundreds of kilometres from their natal reefs before settling. It therefore remains conceivable that some portion of recruits of the bluehead wrasse to Barbados reefs could have originated elsewhere. To be consistent with the correlation between peak spawning and peak recruitment in Barbados, this would require that spawning and recruitment occur at similar times in those countries of the region experiencing larval exchange. Whether this occurs could not be assessed, since seasonality of spawning in the bluehead wrasse has not previously been studied in the Caribbean. However, seasonality of recruitment has been studied in Panama (Victor 1986a). Peak recruitment occurred in September/November; some three months out of phase with peak recruitment in Barbados (July / August).

3.4.4 Recruitment limitation or space limitation?

There are three competing hypotheses about the population dynamics and community structure of coral reef fish. The first, and traditional view, is that reef fish populations are space / food limited, are typically near carrying capacity and are therefore structured by competitive and predatory process on the reef (eg. Smith and Tyler 1973, 1975 ; Clarke 1977; Itzkowitz 1977; Lassig 1977; Dale 1978). An extension of this is that reef fish species are specialists, selection having favoured narrower niches in the competitive reef environment (Sale 1975, 1977, 1979; Sale and Dybdahl 1975). The second hypothesis, a variation of the first, is the 'lottery hypothesis' of Sale (1977, 1978, 1982). This again suggests that reef fish populations are at or near carrying capacity. It envisages an ample supply of recruits in the vicinity of the reef, and suggests that recruitment reflects chance openings of settlement sites on reefs occurring through the death of residents. The typical interpretation of this is that recruits are capable of utilizing any settlement site that becomes available; which implies that reef fish, at least whilst juveniles, are generalists. The implication is that mortality following recruitment will not be compensatory (i.e. density dependent) since recruitment only occurs to the extent that space is available. The third hypothesis, the 'recruitment - limitation' hypothesis, suggests that reef fish populations are typically kept below the carrying capacity of the reef by an inadequate supply of larvae and are therefore not limited by resources such as space or food on the reef (Williams 1980; Doherty 1982a, 1983a,b; Victor 1983a, 1986a; Wellington and Victor 1985). Victor (1986a) further developed the recruitment - limitation hypothesis. He defined two types of recruitment limitation, primary and secondary. Primary recruitment limitation occurs when the input of settling larvae is less than the number of adults the available resources can support. Secondary recruitment limitation occurs when the number of larvae settling is sufficient for adult carrying capacity to be reached, if there were no juvenile mortality. However, juvenile mortality reduces the numbers to below carrying capacity. Note that even with secondary recruitment limitation, the implication is that mortality following recruitment is not compensatory (i.e. density dependent), and 'the absolute size of populations is determined by settlement rates and is not a product of competitive interactions on the reef.' (Victor 1986a).

Recent studies on damselfish populations support the recruitment - limitation hypothesis. Doherty (1982a) found no compensatory mortality in these populations manipulated to 50 times their average year class strength. Doherty (1983b) further demonstrated that the removal of resident damselfishes from patch reefs in the Great Barrier Reef did not increase the survival of new juveniles. Moreover two years of recruitment to these reefs was not sufficient to bring the damselfish populations, which had been severely reduced, back to their original levels (Doherty 1982a). In addition Jones (1987) found no change in mortality rate of juveniles of <u>Pomacentrus amboinensis</u> when transplanted to reefs with older juveniles, even though densities were thereby raised to three times the normal level. Further support for recruitment-limitation was provided by Victor (1983a, 1986a) for bluehead wrasses in Panama. He assumed constant spawning, observed that recruitment occurred in sporadic episodes, and suggested that this resulted from differential larval survival in the plankton. He observed that recruitment rates were highest when plankton concentrations over the reef were highest. He further found that the recruitment strength of one year directly affected the size of the population in the next year (Victor 1983a) . He therefore suggested that mortality following recruitment was constant and density independent, and concluded that the populations were kept below carrying capacity by recruitment limitation.

In the bluehead wrasse in Barbados, spawning is markedly seasonal. Moreover, peak recruitment follows peak spawning by a time period largely consistent with the duration of the larval life of the fish. This suggests that recruitment pulses are not products of differential survival in the plankton (as suggested by Victor (1986a) for the bluehead wrasse in Panama) but are products of adult spawning activity (see also Robertson et al 1988). In short, mortality in the plankton is not sufficiently strong and variable to eliminate the correlation between peak spawning and peak recruitment. More importantly, the present data suggest that more individuals are recruited to the reefs than can be supported by the resources available there. On most reefs, mortality following recruitment was density-dependent, i.e. the proportion of the population dying per month is highest at highest densities (Fig. 15). However, as pointed out by Victor (1986a), density and average age of individuals on the reef are auto-correlated; i.e. individuals are youngest (immediately after recruitment) when population densities are highest (immediately after recruitment). Since young individuals may have higher mortality, this could in principle explain the proportionately higher mortality observed following recruitment. Note, however, that in the present study the post-recruitment mortality was assessed for individuals larger than 30mm, and hence is unlikely to be a product of higher mortality in younger individuals. Moreover, a comparison between reefs, for individuals of similar age-class, suggests that overall mortality rate following recruitment is highest on reefs with heaviest recruitment (Fig. 17). On all reefs, numbers returned and leveled off at pre-recruitment values within three months following peak recruitment. The results of the present study therefore suggest that the bluehead wrasse population in Barbados was not recruitment - limited, at least during the period of the present study. Density-mediated juvenile mortality been recently been documented for other reef fish by Shulman (1984, 1985a,b).

It is of interest that two populations of the bluehead wrasse in the Caribbean (i.e. Barbados and Panama) appear to differ markedly in terms of the processes influencing their population dynamics. Note that the difference is consistent with the observation that average population density of the bluehead wrasse in Barbados is two to three times the average density of wrasses in the San Blas Islands, Panama (Warner and Hoffman 1980a ; Victor 1986a). This is consistent with the suggestion that Barbados populations may be space-limited; and that that the large population (per reef area) produces enough larvae to survive the plankton and cause recruitment pulses which drive density above carrying capacity. This in turn results in compensatory mortality dropping density back to carrying capacity. By contrast, the lower density on Panama reefs suggests that the populations may typically be below carrying capacity. The small population (per reef area) may not produce enough larvae, given mortality in the plankton, to saturate the reefs on recruitment. Hence the populations may typically remain below carrying capacity. Interestingly, the studies of damselfish populations which support the recruitment-limitation hypothesis (Doherty 1982 a,b, 1983b) were conducted on reefs of One Tree Island (Great Barrier Reef). These reefs have the lowest damselfish density in the region and are typical of the reefs of the South Great Barrier Reef which have lower recruitment rates than the reefs of the North Great Barrier Reef (Thresher 1984; Sweatman 1985; Doherty and Williams in press). What has driven the bluehead wrasse on Barbados reefs into a cycle of high density and space / resource limitation, and on Panama reefs into a cycle of low density and recruitment limitation remains unresolved. More generally, the present results, when compared with those of Victor (1986a), imply that hypotheses that coral reef fish, and indeed reef organisms in general, are either recruitment - limited or space - limited may be too rigid, even though they are valuable as organizing perspectives from which to investigate the population dynamics of reef organisms. It seems likely that different species in the same place, the same species in different places, and perhaps the same species in the same place at different times, may differ in the extent to which they are recruitment-limited or space-limited (see also Sale 1984; Shulman 1985b).

4.0 POPULATION COMPOSITION AND MATING SUCCESS

4.1 INTRODUCTION

The mating system of the bluehead wrasse Thalassoma bifasciatum has been studied extensively for the last ten years (Warner et al 1975; Robertson and Hoffman 1977; Warner and Robertson 1978; Warner 1980a,b; Warner 1984; Hoffman et al 1985; Warner 1985), and has been briefly reviewed in Section 1. The species is a protogynous hermaphrodite occurring as two sexual types and in two colour phases. The sexual types are primary males, which are born males and remain males throughout their life (gonochores); and female hermaphrodites, which are born females and either remain females or become males (secondary males) at larger sizes. The two colour phases are called Initial Phase (IP) and Terminal Phase (TP). Terminal phase fish are blue-headed and brightly coloured. They are less common than initial phase fish and are typically the largest individuals in the population. They can either be primary males or secondary males. Initial phase fish are smaller with a more subdued yellow and white colouration. They are typically younger than terminal phase fish and are either females or primary males. The size of transition from initial phase to terminal phase varies with social/ecological conditions on the reef, but the precise physiological/behavioral mechanisms causing transition remain unclear (Warner et al 1975; Shapiro 1988; Warner 1988 a,b).

Daily spawning is common among coral reef fishes, particularly in the wrasses (Labridae), parrotfishes (Scaridae), and the basses (Serranidae) (Robertson and Hoffman 1977; Robertson and Warner 1978;

Warner and Robertson 1978). In T. bifasciatum in Barbados, spawning takes place each day around mid-day with most activity occurring between 1100 hrs. and 1500 hrs. (Section 3.2.1). Terminal phase males pair spawn individually with females. Initial phase males group spawn, each group consisting of several males and typically one female (Warner and Hoffman 1980a). Initial phase males can also obtain matings by 'streaking' and 'sneaking' i.e. strategies which attempt to exploit pair spawning by terminal phase males (Warner and Robertson 1978). Large terminal phase males hold and defend temporary spawning territories during the spawning period while group spawners are non-territorial (Warner et al 1975). It is believed that terminal phase males may spawn more than forty times per day and females once per day (Warner et al 1975).

According to the size-advantage hypothesis for sex reversal (Ghiselin 1969; Warner 1988 a,b), sequential hermaphroditism evolves in a population when selection favours individuals that produce as one sex when small and as a second sex when large. For example, if females have higher reproductive success than males at smaller body sizes, but males have higher reproductive success than females at larger body sizes, selection will favour individuals who reproduce first as females and later as males. In T. bifasciatum in Panama, terminal phase males have considerably higher daily mating success than either initial phase males or females (Warner et al 1975, 1980a). Consequently, selection should favour the observed sex-reversal of females to terminal phase males at larger sizes. One objective of the present section is to compare the daily mating success of terminal phase males and females for bluehead wrasse in Barbados. An aspect of the mating system of the bluehead wrasse which is less clear is whether initial phase females have higher mating success than initial phase males. If they do, one may wonder why initial phase males exist in bluehead wrasse populations; i.e. why have hermaphrodites not replaced gonochores in bluehead wrasse populations (e.g. Charnov 1982)? Individuals (genotypes) who reproduce first as females and later as terminal phase males (hermaphrodites) should have higher life-time reproductive success, and therefore should ultimately replace, individuals (genotypes) who reproduce first as initial phase males and later as terminal phase males (gonochores). Note that, if the initial phase sex ratio is 1 : 1, the average mating success of initial phase males must be lower than that of females since some portion of females mate with terminal phase males. A second objective of this section is to ascertain the sex ratio of bluehead wrasse populations in Barbados, to quantify the numbers of pair (TP) and group (IP) spawnings, and thereby to comment on the relative mating success of initial phase males and females.

Several suggestions have now been proposed for the maintenance of initial phase males in bluehead wrasse populations. Warner *et al* (1975) first suggested that initial phase males are maintained by frequency dependent selection, the implication being that per capita mating success of initial phase males increases and surpasses that of females, the more rare males become. They reasoned that females would become proportionately more common as initial phase males became more rare, that terminal phase males would be unable to fertilize all the females, and hence that initial phase male mating success would rise to surpass female mating success. However, selection should favour females responding to the reduced availability of males by increasing their transition rate to terminal phase. Hence, the sex ratio need not skew toward females, and the predicted per capita increase in initial phase male mating success need not occur.

Subsequently, Warner and Hoffman (1980a) stated that frequency dependent selection alone can not maintain initial phase males in bluehead wrasse populations. They suggested instead that initial phase males are maintained by differential selection in different habitats, initial phase males having higher per capita mating success on large reefs than on small reefs. Warner et al (1975), Warner and Robertson (1978) and Warner and Hoffman (1980a) found that in large populations initial phase males concentrate their spawning activities at downcurrent sites where terminal phase male territories are located. Warner and Hoffman (1980b) suggested that, as a consequence of the high local densities of initial phase males at terminal phase male territory locations in such populations, terminal phase males must spend more time defending territories from initial phase males and will therefore have less time for spawning. Moreover, they suggest that in response to pressure from initial phase males, terminal phase males move away from prime mating sites. These factors lower the per capita mating success of terminal phase males and raise that of initial phase males. Note that this observation does not strictly address the question of why hermaphrodites do not replace gonochores in bluehead wrasse populations, since both gonochores and hermaphrodites are affected by a decrease in terminal phase mating success. The key question is not whether initial phase males improve their per capita mating success relative to terminal phase males in certain habitats/populations, but whether the per capita mating success of initial phase males surpasses that of females under any conditions. It is interesting in the context of the above that both Warner et al (1975) and Warner and Hoffman (1980a,b) report that terminal phase males are rare in large populations and more common in small populations; and that sex ratios are skewed markedly towards females, and hence away from initial phase males, in small populations. Additional objectives of this section are to investigate (1) whether per capita mating success of females, initial phase males and terminal phase males varies with population size and/or population density, and (2) whether the proportion of initial phase to terminal phase males and the population sex ratio vary with population size and/or population density.

In the preceding hypotheses, it was assumed that growth and mortality of females and initial phase males were the same (Warner et al 1975; Warner and Hoffman 1980 a,b). However, Charnov (1982), and later Warner (1984), suggested that even if initial phase males had lower mating success than females, gonochores could be maintained in bluehead wrasse populations if they had a higher probability of becoming terminal phase males than did hermaphrodites, either through faster growth or lower mortality. Warner (1984) used tagging to provide preliminary data on growth and mortality, but stated that the values do not reflect normal rates since tagging is traumatic. His results indicated no differences in mortality between females and initial phase males in any study population, and no difference in growth between males and females on large reefs. However, he suggested that males grow twice as fast as females on small reefs (i.e. smaller populations), and that males grew twice as fast on small reefs than on large reefs. The final objective of the present section is to test Charnov's hypothesis by (1) investigating growth of initial phase males and females using otolith rings (Victor 1983b), (2) investigating mortality of initial phase males and females by comparing their relative abundance in different size classes, and (3) investigating the proportion of terminal phase males that are gonochores.

4.2 METHODS AND MATERIALS

4.2.1 Mating Success

Indices of the per capita mating success of the bluehead wrasse in Barbados were determined for terminal phase males, by dividing the total number of pair spawning events observed on a reef by terminal phase density on that reef; for initial phase males by dividing the total number of group spawning events on a reef by initial phase male density on a reef; and for females by dividing the total number of pair and group spawning events on a reef by female density on a reef. Since initial phase males and females could not be differentiated in density surveys, it was necessary to ascertain the proportions of initial phase individuals that were male or female in each month. This was determined by sub-sampling the populations as described in Section 4.2.3. Spawning events were monitored for 14 months on two fringing reefs, North Bellairs and Heron Bay, by surface snorkeling along five transects on each reef parallel to shore (a 50 minute swim), and counting the number of spawning events separately for group and pair spawning. Each transect was 150m long and all spawning events that were observed in a 2m radius around the transect line were recorded. The data were recorded on small waterproof slates (see Section 3.2.1). Effects of adult population density on the relative mating success of the different types of bluehead wrasse were investigated by comparison of mating success on two reefs differing in density; North Bellairs and Heron Bay.

4.2.2 Population Density

Adult population density was censused once per month on seven fringing reefs in Barbados, namely Paynes Bay (PB), Golden Palms (GP), North Bellairs (NB), Glitter Bay (GB), Greensleeves (GS), Sandridge (SD); and once per week on Heron Bay (HB) (Figure 1a). Densities were measured by swimming slowly about 1m above the reef surface along a 50m transect line, while holding a one metre expandable ruler and counting the number of adult fish (>3 cms) within half a metre either side of the transect line. Counts of initial phase and terminal phase adults were recorded separately. On each sampling day, three transects were censused for density estimates (see Section 3.2.3). For comparisons of density between reefs, mean values for the whole year were used. Adult population abundance on each reef was estimated by multiplying reef area by density of adults on that reef. For each reef, area was determined from aerial survey maps (Barbados Coastal Conservation Project, 1983). Using the map scale ($2cm=100m^2$) a 4 cm piece of paper (equivalent to $10000m^2$) was weighed. Each reef was traced from the map onto identical paper. The reefs were then cut out and weighed. The ratio of reef weight to square weight multiplied by 10000 m^2 gave the planar area of the reef.

4.2.3 Population Composition

Density surveys provide information on the proportion of the population that is terminal phase adults compared to initial phase adults. They do not allow separation of either initial phase or terminal phase adults into gonochores or hermaphrodites. These aspects of population composition were determined by subsampling populations twice on North Bellairs reef, every three months on Paynes Bay, Golden Palms, Glitter Bay, Greensleeves, and Sandridge, and once per month on Heron Bay. Subsampling was conducted between October 1984 and October 1985. To subsample, fish were captured using a 2 litre glass jar filled with a crushed sea urchin (Diadema antillarum) placed at elevated areas on the reef surface. Five sites randomly chosen on the reef were each fished twice during each monthly sample. The jar was left for a maximum of 5 minutes during each fishing attempt. The same locations on the reef were used for each monthly sample. This sampling technique was size selective for larger fish, over 98% of the fish caught being either at or over the size of sexual maturity (about 30mms S.L. and 3 months of age; (Victor 1986a). However, there is no evidence to suggest that gonochores and hermaphrodites of a given size, whether they are initial phase or terminal phase, differ in their susceptibility to the capture technique. For each fish caught, type (i.e. initial phase or terminal phase; transitional fish with blue colouration were treated as terminal phase), standard length (to the nearest mm), and total weight and gonad weight (to the nearest 10^{-2}gm) were recorded. From these measurements the following were obtained: (1) the within-population overlap in size of initial phase and terminal phase individuals, (2) the proportion of gonochores to hermaphrodites in both initial phase and terminal phase fish, and the variation in the proportion with fish size. Separation of gonochores from hermaphrodites required histological examination of gonads. In the case of terminal phase individuals, the technique for separating gonochores and hermaphrodites (i.e. primary from secondary males) is described by Reinboth (1962, 1980), (3) the mean size of transition from initial phase to terminal phase for gonochores and hermaphrodites and (4) the population sex ratio. To determine size at sex change in hermaphrodites, the proportion of gonad devoted to testes in a female was investigated by direct histological examination, and expressed as 0%, 25%, 50%, 75% or 100% devoted to testes. The proportion of the gonad that was ovary multiplied by the total weight of the gonad gave the approximate weight of ovary in transitional gonads.

4.2.4 Growth and Mortality Rates

Growth rates were determined by dating the otoliths of approximately 600 bluehead wrasse taken in monthly samples on Heron Bay and collected as described in Section 3.2.2. Mean growth rates were determined for gonochores and hermaphrodites, when in primary phase and when in terminal phase. An effect of density on growth rates was investigated by dating otoliths of gonochores and hermaphrodites on two additional reefs (about 50 fish/reef) ; a high density reef (Greensleeves, density=1.72 N/m^2) and a low density reef (Golden Palms, density=1.04 N/m^2). To date otoliths, two pairs of the larger otoliths (sagittae and lapillae) were removed from the ear canals of each fish. Minimal preparation is needed to view and read otoliths in <u>T.bifasciatum</u> (see also Victor 1982). The otoliths were rinsed in 90-100% ethanol and then cleared for 24 hrs in xylene. Pairs of otoliths were then mounted with mounting medium on glass slides. They were viewed with polarization under 400x magnification with a compound microscope. An index of relative mortality rates of hermaphrodites and gonochores was determined by comparing the proportions of gonochores and hermaphrodites in each size class of initial phase fish.

4.3 RESULTS

4.3.1 Population density and size

Most of the reefs off the west coast of Barbados are large fringing reefs ranging from $10{,}000m^2$ to $70{,}000m^2$ in area (Barbados Coastal Conservation Project 1983, this study). The estimated areas of the study reefs and the mean of the monthly population densities of bluehead wrasse on each area are shown in Table 10. The highest mean density (1.72 N/m^2 on Greensleeves) was >1.5 times that of the lowest mean density (1.04 N/m^2) on North Bellairs and Golden Palms reefs. Population size was estimated by multiplying mean population density by reef area (Table 10). Population size varied from 16,000 on the smallest reef (North Bellairs) to 69,000 on the largest reef (Sandridge). Population size increased linearly with reef area, but the largest reef (Sandridge) had a smaller population size than predicted by reef area (Fig. 19a). More surprisingly, mean population density was higher on larger reefs (Fig. 19b). The principal exception was the largest reef (Sandridge) which had a lower density than expected by reef area.

4.3.2 Per capita mating success.

Spawning in the bluehead wrasse was more common between January and June (termed the reproductive season) than between July and December (the non-reproductive season; Section 3.3.1). The indices of monthly per capita mating success of terminal phase males, initial phase males and females on Heron Bay reef are shown separately for the two seasons in Table 11. The index for terminal phase males did not differ between seasons (Mann-Whitney U test, $z=1.20$, $P>0.05$; Table 11).

TABLE 10

Reef area, mean population density and population size of *Thalassoma bifasciatum* on seven fringing reefs in Barbados.

REEF	(1a) REEF AREA(m^2)	(1b) MEAN POPULATION DENSITY (N/m^2)	(1c) POPULATION SIZE (N)
North Bellairs (NB)	16,226	1.04	16,875
Golden Palms (GP)	23,962	1.04	24,921
Glitter Bay (GB)	19,198	1.24	23,806
Sandridge (SD)	52,547	1.31	68,837
Paynes Bay (PB)	25,943	1.49	38,655
Heron Bay (HB)	27,264	1.51	41,169
Greensleeves (GS)	33,584	1.72	57,765

Figure 19a. Mean population size (N) of *Thalassoma bifasciatum* vs reef area (m^2) on seven fringing reefs in Barbados.

NB = North Bellairs
GB = Glitter Bay
GP = Golden Palms
PB = Paynes Bay
HB = Heron Bay
GS = Greensleeves
SD = Sandridge

T indicates 95% confidence limits

Figure 19b. Mean density (N/m^2) of *Thalassoma bifasciatum* vs reef area (m^2) on seven fringing reefs in Barbados. Reef names as for Fig. 19a.

T indicates 95% confidence limits

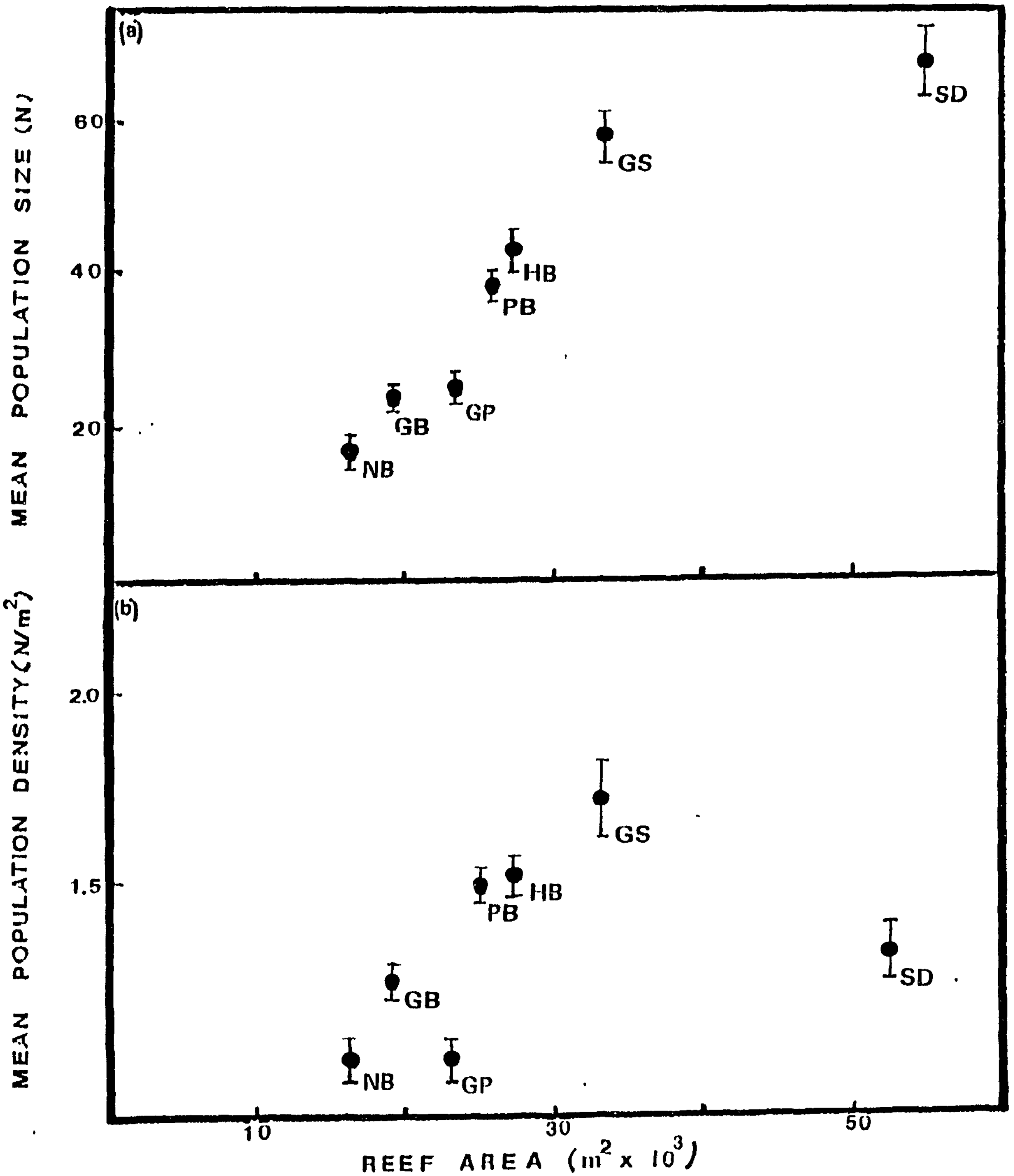

(a)
MEAN POPULATION SIZE (N)
60
40
20
SD
GS
HB
PB
GP
GB
NB
(b)
MEAN POPULATION DENSITY (N/m^2)
2.0
1.5
GS
HB
PB
SD
GB
NB
GP
10
30
50
REEF AREA (m^2 x 10^3)

TABLE 11

Indices of monthly per capita mating success of terminal phase males (TP), initial phase males (IP) and females in the reproductive and non-reproductive seasons, for Thalassoma bifasciatum on Heron Bay reef in Barbados. Secondary initial phase males are excluded from the analysis.

		INDEX OF PER CAPITA MATING SUCCESS		
SEASON	MONTH	TP	IP MALE	FEMALE
(1984)				
NON-REPROD.	NOVEMBER	84.9	6.2	7.9
	DECEMBER	43.3	6.7	6.7
(1985)	JANUARY	62.5	27.3	27.3
	FEBRUARY	228.6	46.4	25.4
REPROD.	MARCH	112.1	49.5	45.5
	APRIL	108.3	94.5	54.0
	MAY	265.0	70.2	59.5
	JUNE	860.0	55.9	32.1
	JULY	163.0	36.4	19.5
NON-REPROD.	AUGUST	190.0	16.6	24.9
	SEPTEMBER	129.7	23.3	24.9
	OCTOBER	60.3	38.8	29.5

However, the index of monthly per capita mating success of both females and initial phase males was significantly higher in the reproductive season than in the non-reproductive season on Heron Bay reef (Mann-Whitney U test; for females, z=2.64, P<0.05; for IP males, z=2.48, P<0.05; Table 11).

The index of monthly per capita mating success of terminal phase males on Heron Bay reef was significantly higher than that of females and initial phase males in both seasons (Wilcoxon paired-sample test (Zar, 1984); vs females for reproductive, z=-2.20, P<0.05; for non-reproductive, z=-2.20, P<0.05; vs IP males for reproductive, z=-2.20, P<0.05; for non-reproductive, z=-2.20, P<0.05; Table 11.) Moreover, the per capita mating success of terminal phase males on North Bellairs reef did not differ between seasons (Mann-Whitney U test; z=0.08, P>0.05; Table 12), and was significantly higher than that of initial phase fish in both seasons (Wilcoxon paired-sample test; for reproductive, z=-2.20, P<0.05; for non-reproductive, z=-2.20, P<0.05; Table 12).

About 5% of the initial phase population is secondary IP males i.e. hermaphrodites who have changed sex and are reproducing as IP males. If these individuals are excluded, female per capita mating success does not differ from initial phase male per capita mating success in the non-reproductive season on Heron Bay reef (Wilcoxon paired-sample test; z=0.11, P>0.05; Table 11), but tends to be lower than that of IP males in the reproductive season (Wilcoxon paired-sample test; z=1.78, P=0.08; Table 11). If secondary IP males are included, female per capita mating success and initial phase male per capita mating success do not differ in either the non-reproductive

TABLE 12

Indices of monthly per capita mating success of terminal phase males (TP) and initial phase fish (IP) in the reproductive and non-reproductive seasons, for Thalassoma bifasciatum on North Bellairs reef in Barbados.

		INDEX OF PER CAPITA MATING SUCCESS	
SEASON	MONTH	TP	IP
(1984)			
NON-REPROD.	NOVEMBER	63.3	5.6
	DECEMBER	33.3	6.2
(1985)	JANUARY	64.0	6.4
	FEBRUARY	45.0	4.0
REPROD.	MARCH	83.3	6.4
	APRIL	73.9	4.5
	MAY	370.0	9.9
	JUNE	252.2	11.9
	JULY	90.0	5.6
NON-REPROD.	AUGUST	94.3	7.0
	SEPTEMBER	115.2	5.9
	OCTOBER	106.7	3.4

(Wilcoxon paired-sample test; z=0.67, P>0.05; Table 13) or reproductive seasons (Wilcoxon paired-sample test; z=0.73, P>0.05; Table 13). Per capita mating success of initial phase males and females was not compared on North Bellairs reef since the sex ratio of the initial phase population was not known for all months.

4.3.3 Effects of density or population size on mating success.

4.3.3.1 Between-reef comparisons

Effects of density or population size on per capita mating success were investigated by comparing mating success on Heron Bay reef (a high density reef of large population size; Table 10) with that on North Bellairs reef (a low density reef of small population size; Table 10). Since monthly terminal phase mating success did not differ between seasons for either Heron Bay or North Bellairs reefs, the comparison of terminal phase per capita mating success between reefs was made across all months. The results suggest that monthly terminal phase mating success did not differ significantly between reefs (Mann-Whitney U test, z=1.12, P>0.05).

A more direct approach to assessing whether the extent to which mating success of terminal phase fish exceeds that of initial phase fish differs on reefs of different density and/or population size is to compare the ratio of per capita TP mating success to per capita IP mating success on the high density reef with that on the low density reef across all months (Table 14). The ratio of per capita terminal phase male mating success to per capita initial phase mating success did not differ between reefs (Mann-Whitney U test; z=0.28, P>0.05).

TABLE 13

Indices of monthly per capita mating success of terminal phase males (TP), initial phase males (IP) and females in the reproductive and non-reproductive seasons, for _Thalassoma bifasciatum_ on Heron Bay reef in Barbados. Secondary initial phase males are included in the analyses as IP males.

		INDEX OF PER CAPITA MATING SUCCESS		
SEASON	MONTH	TP	IP MALE	FEMALE
(1984) NON-REPROD.	NOVEMBER	84.9	6.2	7.9
	DECEMBER	43.3	5.8	6.7
(1985) REPROD.	JANUARY	62.5	20.8	27.3
	FEBRUARY	228.6	35.1	25.4
	MARCH	112.1	42.1	45.5
	APRIL	108.3	51.1	54.0
	MAY	265.0	63.5	59.5
	JUNE	860.0	50.0	32.1
NON-REPROD.	JULY	163.0	38.7	19.5
	AUGUST	190.0	14.3	24.9
	SEPTEMBER	129.7	18.8	24.9
	OCTOBER	60.3	27.2	29.5

TABLE 14

Monthly ratios of per capita terminal phase male mating success to per capita initial phase mating success (TP m.s / IP m.s) in 1984 and 1985 on a low density reef (North Bellairs) and a high density reef (Heron Bay), for *Thalassoma bifasciatum* in Barbados.

	PER CAPITA TP M.S. / PER CAPITA IP M.S.	
MONTH	NORTH BELLAIRS	HERON BAY
(1984)		
NOVEMBER	11.3	38.6
DECEMBER	5.4	14.0
JANUARY	10.0	5.7
FEBRUARY	11.3	23.8
MARCH	13.0	5.9
APRIL	16.4	4.7
MAY	37.4	10.6
JUNE	21.2	59.3
JULY	16.1	17.9
AUGUST	13.6	25.6
SEPTEMBER	19.6	15.4
OCTOBER	31.3	4.8

Although the extent to which per capita TP mating success exceeded that of IP mating success was not lower in the more dense (and/or larger) population than in the less dense (smaller) population, the total pair spawning events to total group spawning events was lower in the more dense population over all months (Fig. 20; Mann-Whitney U test, z=2.28, $P<0.05$). Pair spawning made up 40% of the total spawning events observed (n=1161) on the low density reef (NB) and only 25% of all the spawning events observed (n=1524) on the high density reef (HB). Together, Table 14 and Fig. 20 suggest that the proportion of terminal phase to initial phase fish must differ between the two reefs (see Section 4.3.4).

4.3.3.2 Within reef comparisons.

Adult density varied during the year on both North Bellairs and Heron Bay reefs, being low between March and May and higher for the rest of the year (Section 3.3.2). Possible effects of density on the relative per capita mating success of TP males and IP males on Heron Bay reef were investigated by correlating the ratios of per capita TP mating success/per capita IP male mating success in a given month with adult density in that month. The ratio of per capita TP mating success/per capita IP male mating success in a given month was not correlated with adult density in that month (Spearman's Rank Correlation, $r_s=0.27$, $P>0.05$; Fig. 21a). However, on any reef, adult density in a month is only an accurate predictor of total spawning activity in that month if spawning activity per fish does not change seasonally. Spawning activity per fish on Heron Bay reef was highest between March and May (Section 3.3.2), months in which adult density tended to be lowest. The ratio of per capita TP mating

Figure 20. The monthly pair to group spawning ratio (P/G) for *Thalassoma bifasciatum* over a fourteen month period on two reefs of different density in Barbados.

●-● = North Bellairs reef (low density)

▲-▲ = Heron Bay reef (high density)

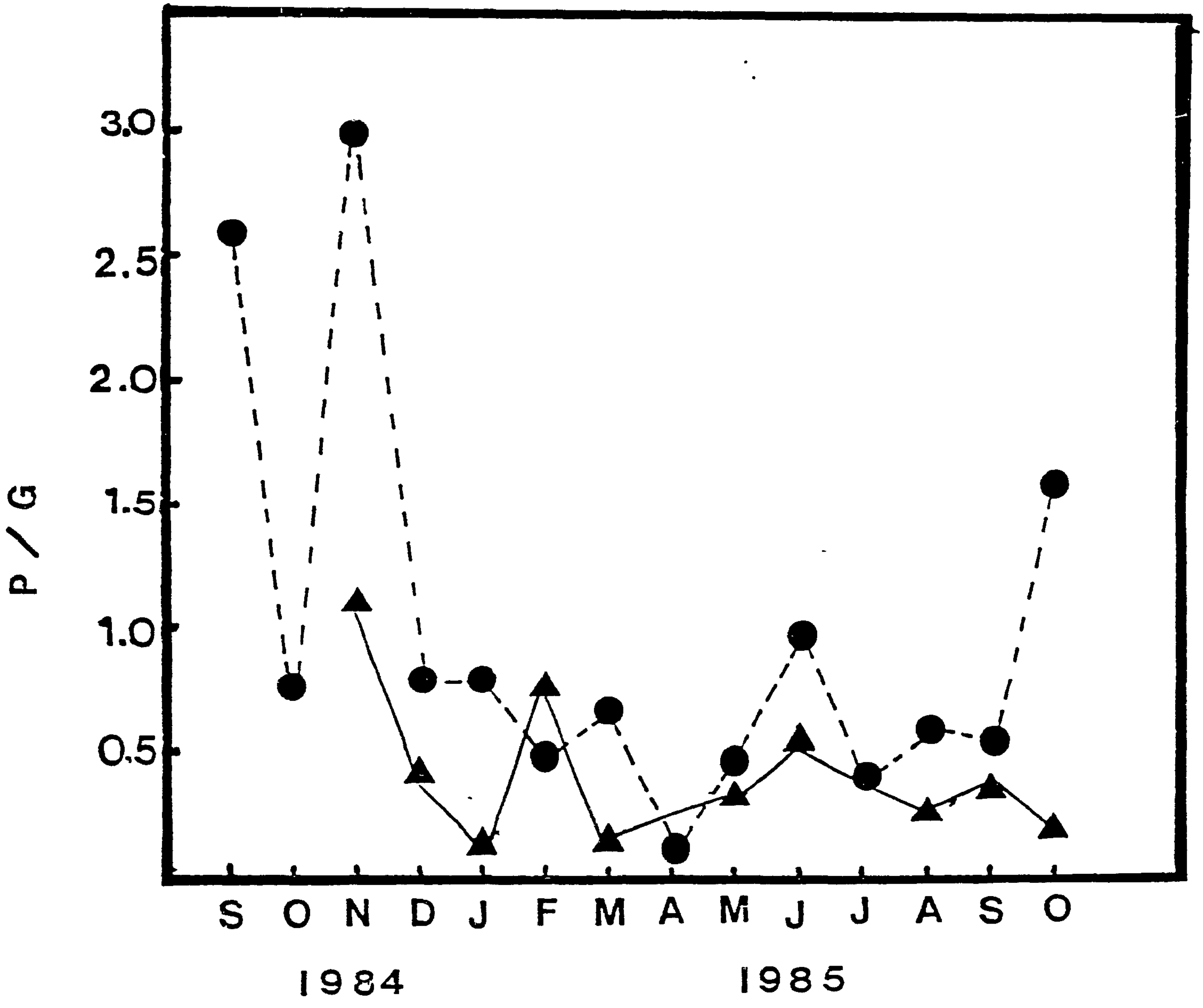
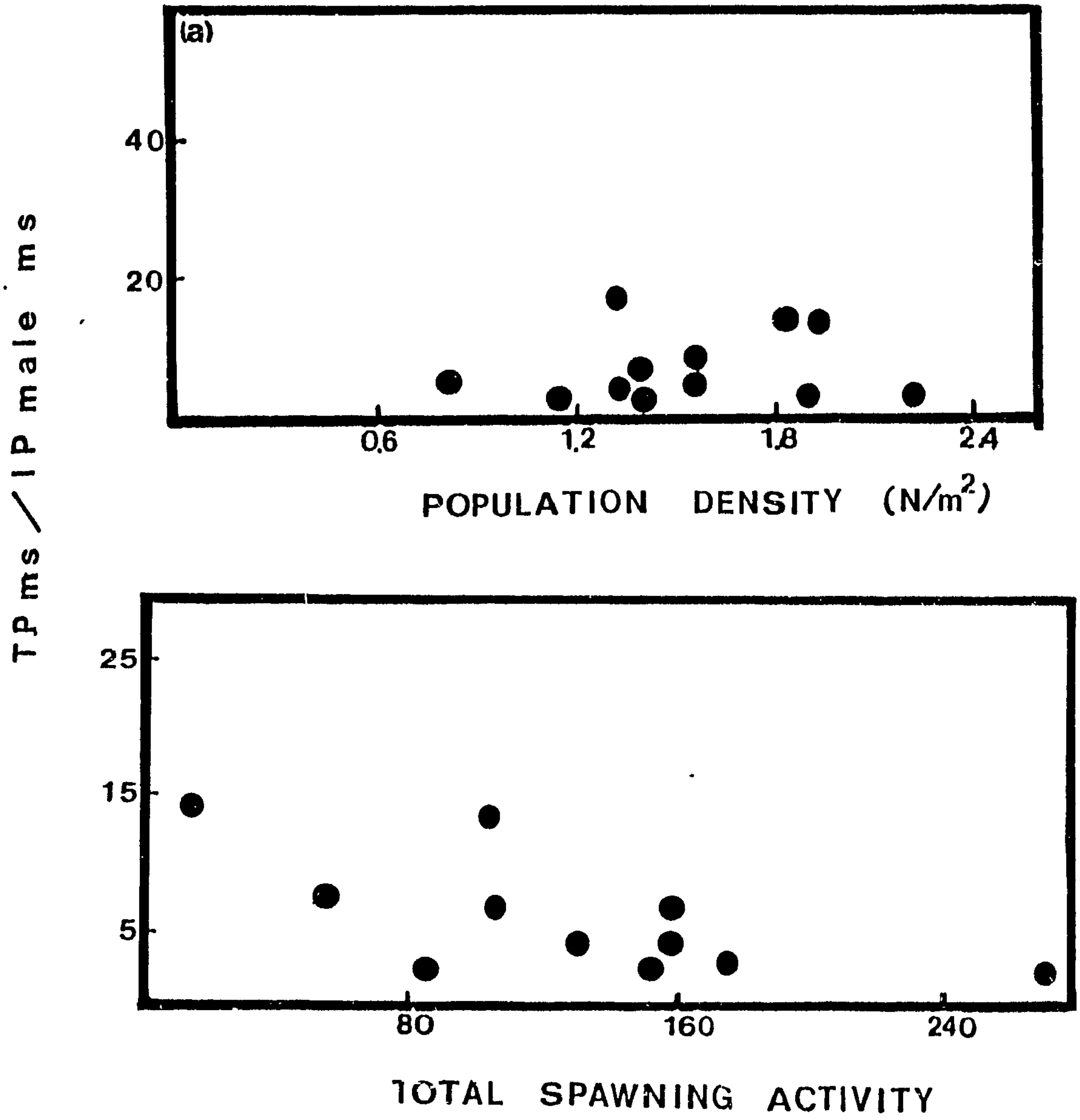

3.0
2.5
2.0
1.5
1.0
0.5
P / G
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1984
1985

Figure 21. The ratio of (a) per capita terminal phase mating success to per capita initial phase male mating success (TP/IP male) vs density (N/m^2) and (b) per capita terminal phase mating success to per capita initial phase male mating success (TP/IP male) vs total spawning activity for Thalassoma bifasciatum on Heron Bay reef, Barbados. The data are from the period September, 1984 to October, 1985.


(a)
40
20
0.6
1.2
1.8
2.4
POPULATION DENSITY (N/m2)
TPms / IP male ms
25
15
5
80
160
240
TOTAL SPAWNING ACTIVITY

success/per capita IP male mating success in a given month was negatively correlated with total spawning activity in that month (Spearman's Rank Correlation, $r_s=-0.67$, $P<0.05$; Fig. 21b). In short, per capita mating success of IP males improves relative to TP males the greater the total spawning activity on the reef.

4.3.4 Effects of Density on Population Composition

The mean colour phase ratio of adults (terminal phase : initial phase), determined from density censuses for all seven reefs, was 1:22 (n~21,000 fish). This TP/IP ratio is considerably smaller than that reported for bluehead wrasse in Panama (Warner and Robertson 1978). The TP/IP ratio on a given reef tended to be lower the higher the density on the reef (Spearman Rank Correlation, $r_s=-0.62$, $P=0.09$), but was not affected by either population size (Spearman Rank Correlation, $r_s=0.07$, $P>0.05$) or reef area (Spearman Rank Correlation, $r_s=-0.07$, $P>0.05$) (Figs. 22a-22c). The proportion of TP males in the total population dropped from approximately 8% to 2% between the lowest and highest density reefs respectively.

Sex ratio was investigated by subsampling six of the study reefs. Of the 1608 fish examined (both initial phase and terminal phase individuals), 51% were males and 49% were females. This ratio did not differ significantly from 1:1 ($X^2=1.32$, $P>0.05$). The population sex ratio on a reef did not change with population density on a reef (Spearman Rank Correlation, $r_s=-0.05$, $P>0.05$; Fig. 23a), with population size (Spearman Rank Correlation, $r_s=0.17$, $P>0.05$; Fig. 23b) or with reef area (Spearman Rank Correlation, $r_s=0.55$, $P>0.05$; Fig. 23c). It did not differ significantly from 1:1 on any reef (P>0.05 in

Figure 22. The ratio of terminal phase individuals to initial phase individuals (TP/IP) vs (a) mean population density (N/m^2), (b) mean population size (N) and (c) reef area (m^2) for <u>Thalassoma bifasciatum</u> on six fringing reefs in Barbados.

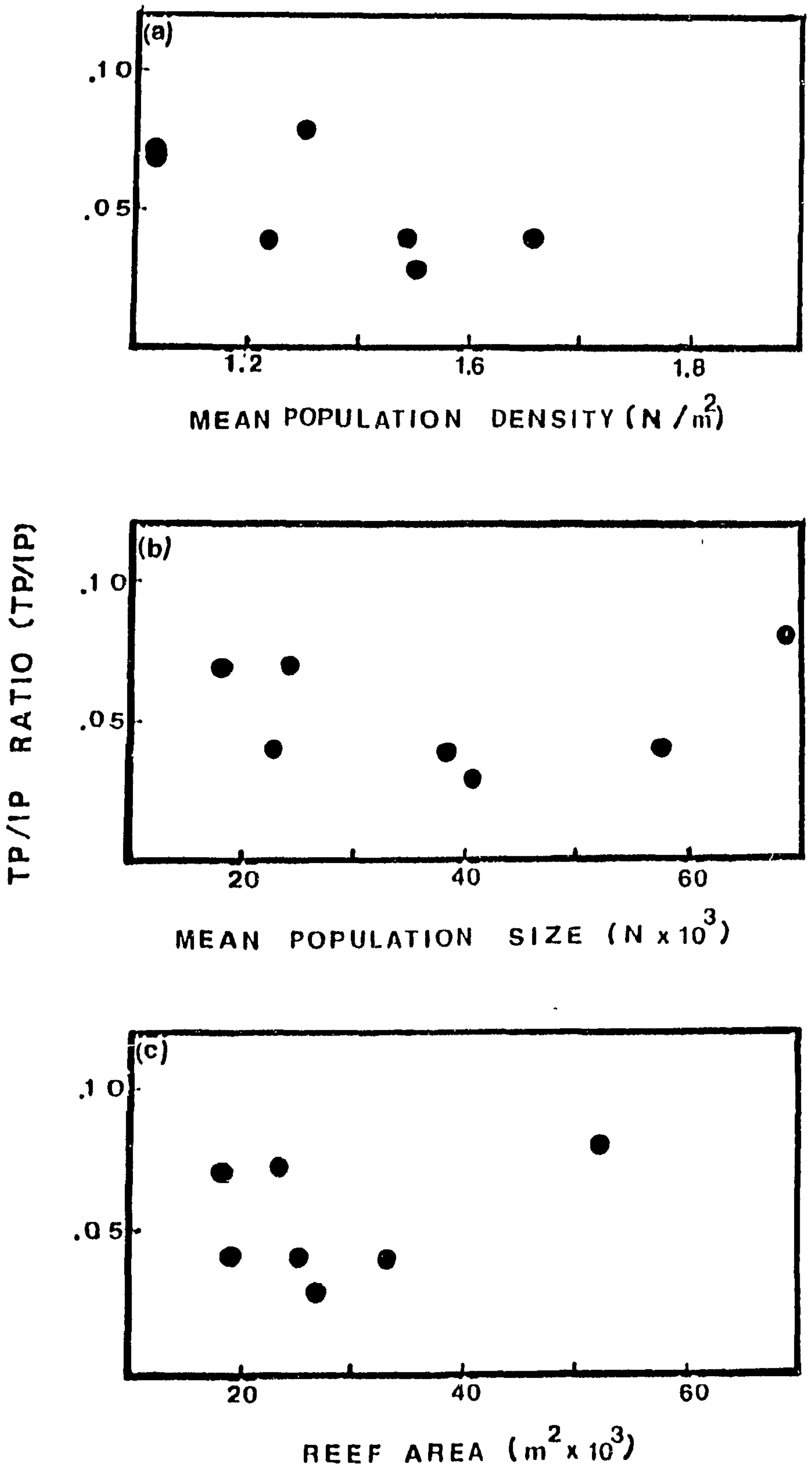
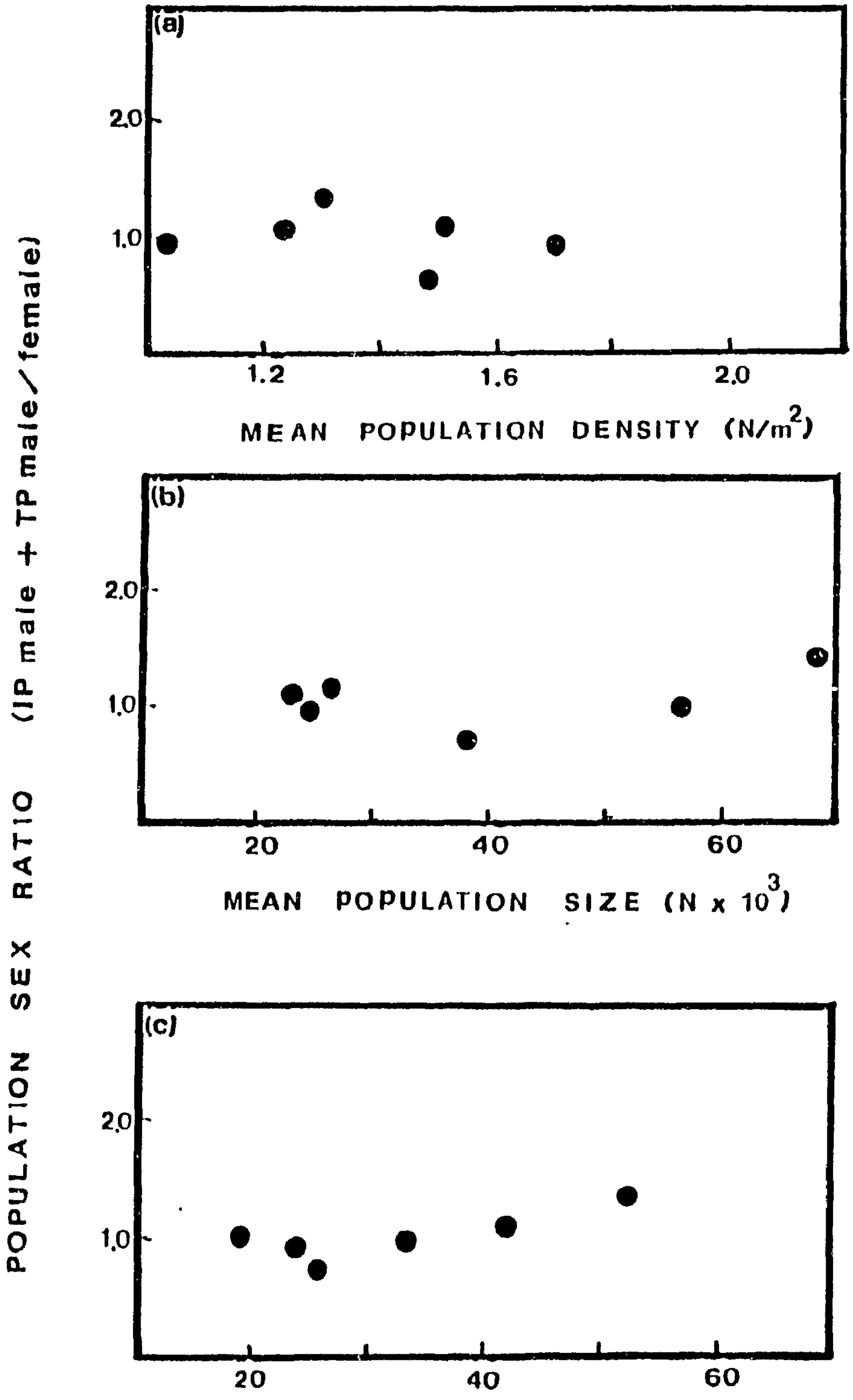

(a)
.10
.05
1.2
1.6
1.8
MEAN POPULATION DENSITY (N/m²)
TP/IP RATIO (TP/IP)
(b)
.10
.05
20
40
60
MEAN POPULATION SIZE (N x 10³)
(c)
.10
.05
20
40
60
REEF AREA (m² x 10³)

Figure 23. The adult population sex ratio (TP & IP males/ female) vs (a) mean population density (N/m^2), (b) mean population size (N) and (c) reef area (m^2) for Thalassoma bifasciatum on six fringing reefs in Barbados.


POPULATION SEX RATIO (IP male + TP male/female)
(a)
2.0
1.0
1.2
1.6
2.0
MEAN POPULATION DENSITY (N/m²)
(b)
2.0
1.0
20
40
60
MEAN POPULATION SIZE (N x 10³)
(c)
2.0
1.0
20
40
60
REEF AREA (m² x 10³)

all cases). Of the fish examined in the initial phase population, 55% were females and 45 % males. This is a significant sex ratio bias towards females (X^2=14.4, P<0.001). Sex ratio was significantly different from a 1:1 ratio on all reefs (P<0.05 in all cases). The initial phase sex ratio on a reef did not change with population density on the reef (Spearman Rank Correlation, r_s=-0.14, P>0.05; Fig. 24a), with population size (Spearman Rank Correlation, r_s=0.2, P>0.05; Fig. 24b) or with reef area (Spearman Rank Correlation, r_s=-0.25, P>0.05; Fig.24c).

4.3.5 Seasonal variation in Population Composition

The proportion of females in the population varied seasonally, being highest in the summer on all reefs (Fig. 25a). Conversely, the proportion of initial phase males in the population was lowest in the summer on all reefs (Fig. 25b). The proportion of terminal phase males was low and did not vary seasonally (Fig. 25c). The proportion of total males (i.e. initial phase males plus terminal phase males) in the population therefore followed the same seasonal pattern as initial phase males (Fig. 25d). Interestingly, the proportion of females tends to increase during months of recruitment into the adult population, reaching its highest values when adult population density is approaching its maximum (Section 3.3.2). This may suggest that sex ratio at recruitment into the adult population is biased towards females, and that mortality following recruitment into the adult population is higher for females than males (see Section 4.3.6 and 4.3.9).

Figure 24. The initial phase sex ratio (IP male/female) vs (a) mean population density (N/m^2) (b) mean population size (N) and (c) reef area (m^2) for Thalassoma bifasciatum on six fringing reefs in Barbados.

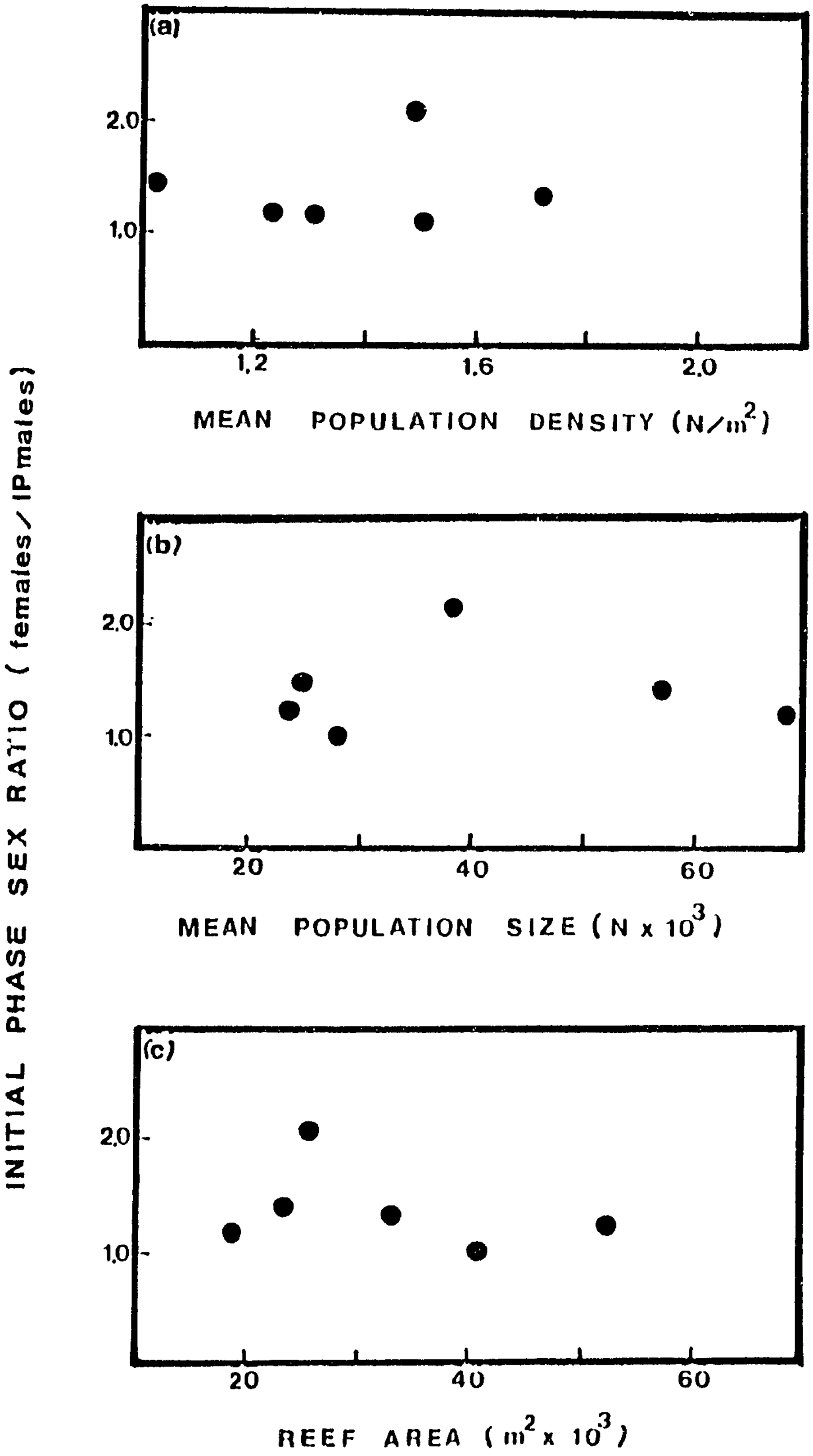
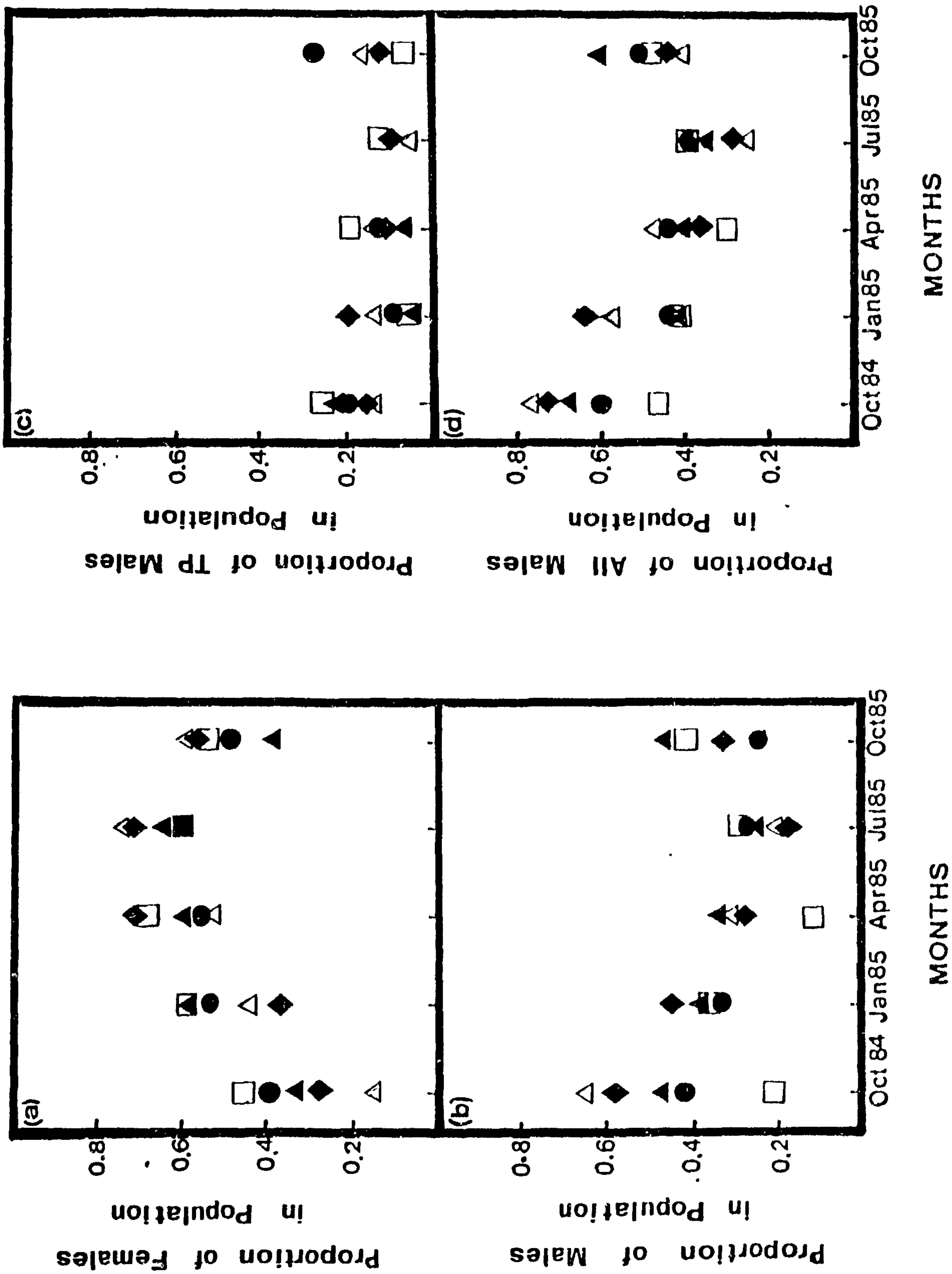

INITIAL PHASE SEX RATIO (females / IP males)
(a)
2.0
1.0
1.2
1.6
2.0
MEAN POPULATION DENSITY (N/m²)
(b)
2.0
1.0
20
40
60
MEAN POPULATION SIZE (N x 10³)
(c)
2.0
1.0
20
40
60
REEF AREA (m² x 10³)

Figure 25. Seasonal variation in population composition of *Thalassoma bifasciatum* on five fringing reefs in Barbados. (a) Proportion of females, (b) proportion of initial phase males, (c) proportion of terminal phase males and (d) proportion of all males.

● = Glitter Bay
△ = Sandridge
◆ = Greensleeves
▲ = Golden Palms
□ = Paynes Bay


(a)
(b)
(c)
(d)
Proportion of Females in Population
Proportion of Males in Population
Proportion of TP Males in Population
Proportion of All Males in Population
0.8
0.6
0.4
0.2
Oct84
Jan85
Apr85
Jul85
Oct85
MONTHS

4.3.6 Population composition by body size.

Population composition by body size is shown for all reefs combined in Figure 26. For initial phase fish, females (hermaphrodites) were more numerous than males (gonochores) in the smaller size classes, but gonochores outnumbered hermaphrodites (females and secondary IP males) in the larger size classes (Fig. 26). This change in population composition with body size occurred on all reefs . On 4 of the 7 reefs, the difference in composition between the smallest IP size class and the largest IP size class was significant (X^2test,<0.05 in all cases). These data support the suggestion that female (hermaphrodite) mortality may be heavier than male (gonochore) mortality following recruitment into the adult population (see Sections 4.3.5 and 4.3.9). Note that only 5% (74 of 1425) of initial phase males were secondary males (hermaphrodites). Among terminal phase fish, primary males (gonochores) were more numerous than secondary males (hermaphrodites) (Fig.26,$X^2=7.4$,$P<0.01$).

4.3.7 Size at Transition

Colour changes accompany the transition between initial phase and terminal phase in the bluehead wrasse. Characteristic blue-green colouring on the head region of the fish and dark vertical body stripes are two common indications of phase change (Roede 1972). Mean size at transition for the bluehead wrasse in Barbados was 65.01mm+0.47 ; determined by calculating the mean size of all fish with transitional colouring (n=36). Size at transition did not differ for male and females (IP males, $\bar{x}$=65.5mm± 0.53, n=17; IP females, $\bar{x}$=64.9mm ±0.43, n=19; t-test, t=0.013, P=0>0.05).

Figure 26. Population composition by body size for :

(a) terminal phase individuals

▨ = secondary males (hermaphrodites) in terminal phase

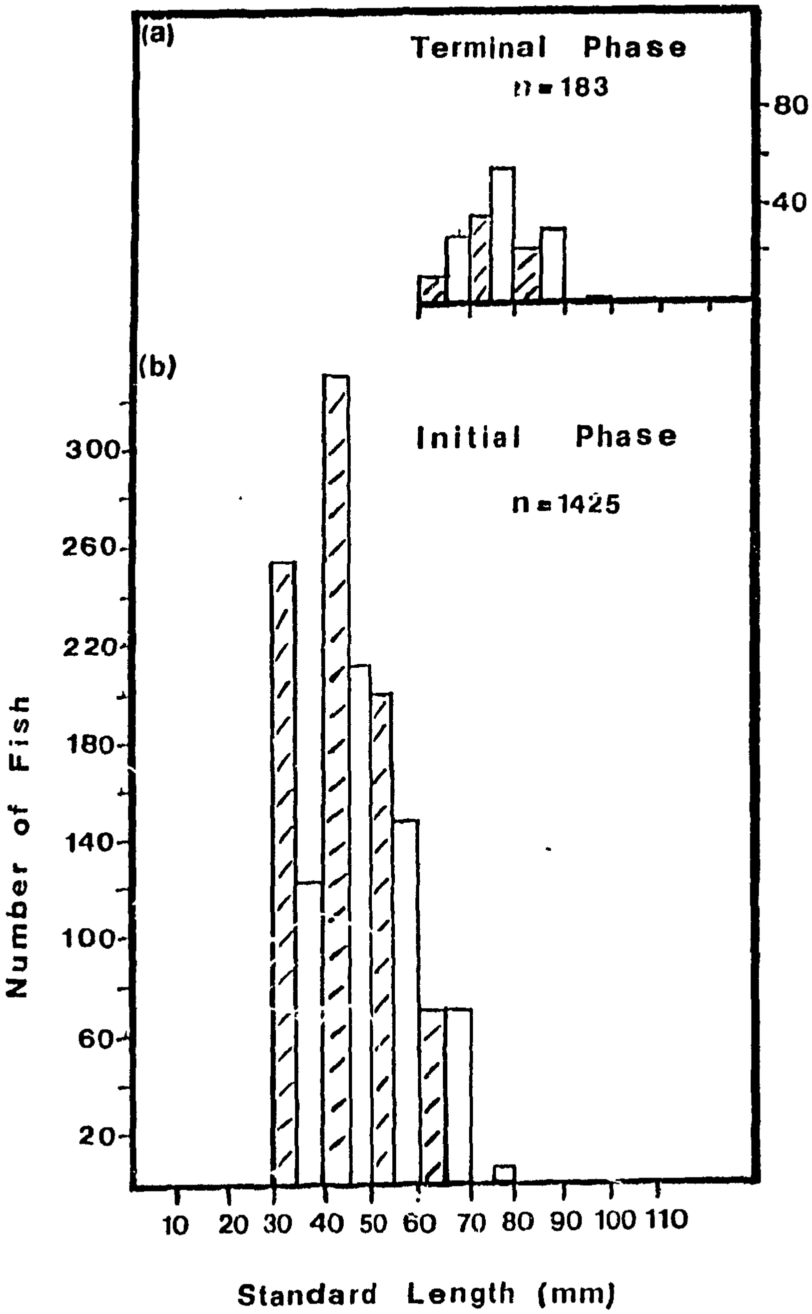
☐ = primary males (gonochores) in terminal phase

(b) initial phase individuals

▨ = females (hermaphrodites) in initial phase

☐ = males (gonochores) in initial phase

for *Thalassoma bifasciatum* for all reefs studied in Barbados.


(a)
Terminal Phase
n = 183
80
40
(b)
Initial Phase
n = 1425
300
260
220
180
140
100
60
20
Number of Fish
10 20 30 40 50 60 70 80 90 100 110
Standard Length (mm)

Since reefs of higher population density have a smaller proportion of terminal phase fish (Section 4.3.4), the effect of density on size at transition to terminal phase was investigated. Three approaches were used. First, the largest initial phase fish on a reef was correlated with the mean population density on the reef. Second the smallest terminal phase fish on a reef was correlated with the mean population density on the reef. Third the mean size of all fish in the size classes over which both initial phase and terminal phase fish were observed (i.e. the overlap size range between IP and TP fish) was investigated on the different reefs. There was a tendency for the largest initial phase fish to be bigger on reefs of higher population density (Spearman's Rank Correlation, r_s=0.77, P=0.08; Table 15). Moreover, the size of the smallest terminal phase male was greater on reefs of higher population density (Spearman's Rank Correlation, r_s=0.83, P=0.06; Table 15). Finally, the mean size of fish in the overlap zone differed significantly between reefs (One-way ANOVA, F=4.51, P<0.005; Table 15). Mean size increased with increasing mean population density (Spearman's Rank Correlation, r_s=0.77, P=0.08) and was smaller on the lower density reefs than on the higher density reefs (SNK test, (NCSS,1985, P<0.05). These results suggest that the smaller proportion of terminal phase fish on higher density reefs results, in the proximate sense, from fish transforming from initial to terminal phase at larger sizes on higher density reefs.

4.3.8 Size at Sex Change

The overlap zone between two colour phases has been used to determine the size of sex change in monandric fish (e.g. Shapiro

Table 15

Standard lengths of (a) the largest initial phase fish (b) the smallest terminal phase fish and (c) mean size of all fish in the overlap zone between initial phase and terminal phase fish, for *Thalassoma bifasciatum* on six fringing reefs in Barbados.

REEF	Mean Population Density (N/m^2)	Largest Initial Phase (mm)	Smallest Terminal Phase (mm)	Mean Size in overlap zone (mm)
Golden Palms	1.04	68.6	57.3	64.1
Glitter Bay	1.24	69.8	60.8	65.4
Sandridge	1.31	69.4	62.7	67.8
Paynes Bay	1.49	74.8	64.9	68.8
Heron Bay	1.51	75.0	64.2	68.1
Greensleeves	1.72	73.2	64.3	67.9

1984). This approach is inappropriate for the bluehead wrasse which is diandric and in which sex change begins, and is often completed, prior to phase change (pers. obs., Warner and Robertson 1978). Size at sex change was determined by investigating the proportion of the gonad devoted to ovaries. The proportion of ovary:testes in each gonad was assessed on a scale of 1 to 0 by microscopic examination of whole gonads. A female was defined as having changed sex when >50% of the gonad is devoted to testes, and as having completed sex change when 100% of the gonad is devoted to testes. The percentage of females that had changed sex in each size class, and the percentage that had completed sex change in each size class, are shown in Figs. 27a and 27b for Heron Bay reef. The results suggest that sex change may begin at a relatively small size, with about 10% of all females already having 50% of their gonad devoted to testes in the smallest size class investigated (30-40mm). However, in the largest initial phase size class (60-70mm), only 20% of the females had completed sex change (100% testis) and fewer than 40% had >50% of their gonad converted to testis. This may suggest that most females in the largest IP size class are not going to become terminal phase males.

4.3.9 Growth and Mortality

4.3.9.1 Growth

Growth rates were determined by dating of otoliths from monthly samples of fish collected on Heron Bay reef. Sizes at age for initial phase males and for females are shown in Fig. 28a and 28b. The slopes for initial phase males and females do not differ (Student t-test for comparison between slopes of regression lines (Zar 1984) ; t=0.23, P>0.50), suggesting no difference in growth between IP males

Figure 27. (a) Percentage of females that had changed sex (>50% testes) in each size class (including terminal phase fish) (b) percentage of females that had completed sex change (100% testes) in each size class (including terminal phase fish) for Thalassoma bifasciatum on Heron Bay reef in Barbados.

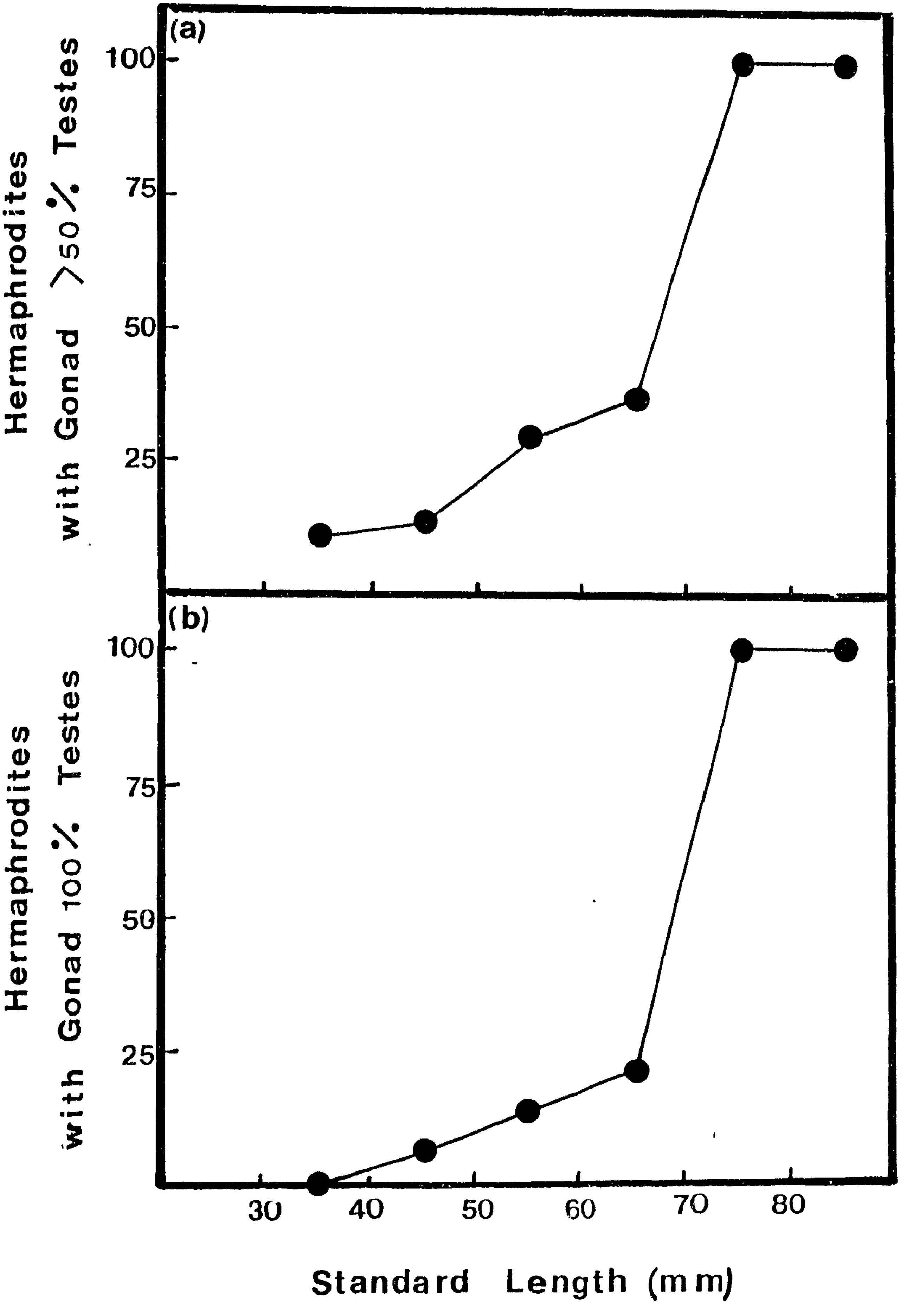
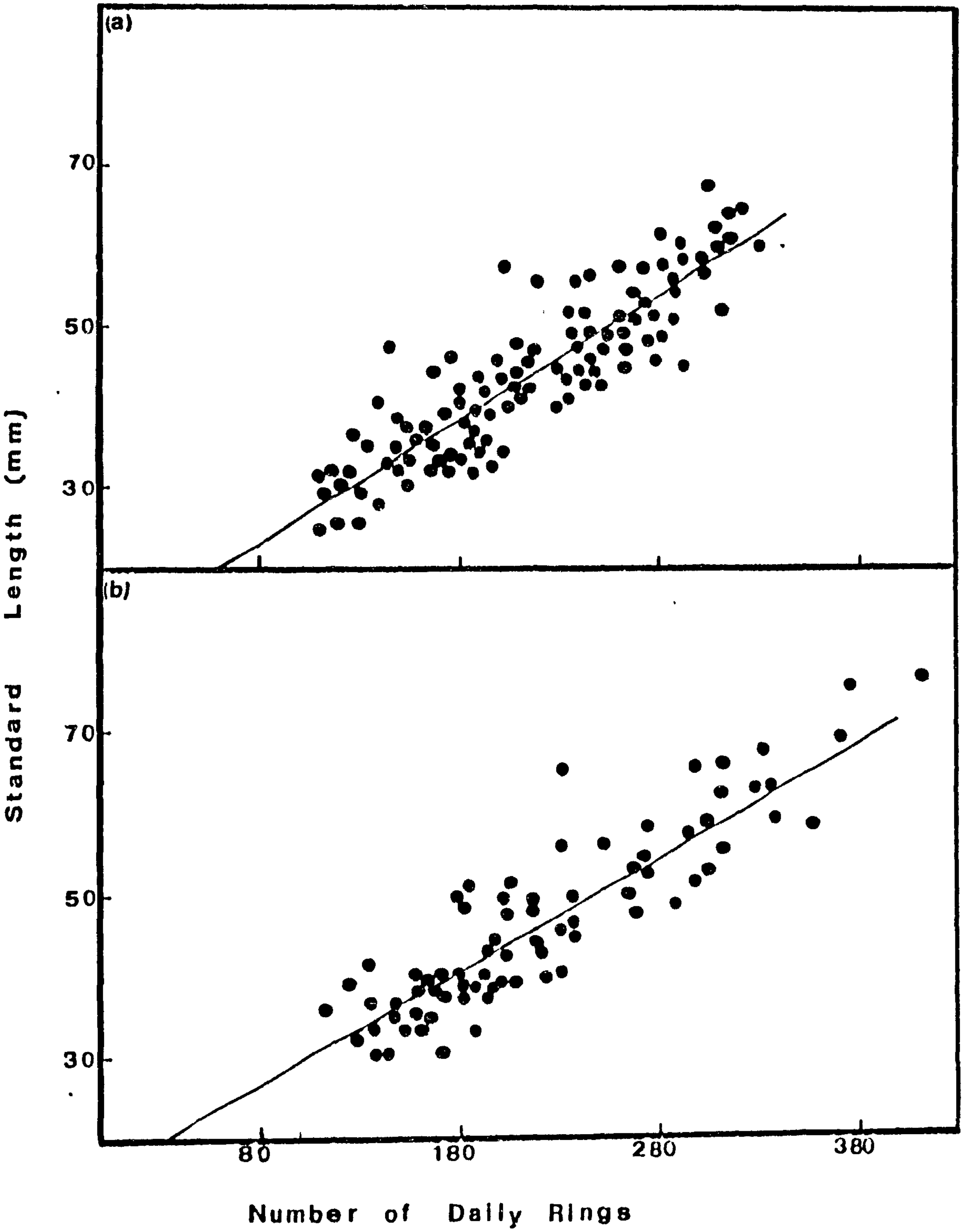

(a)
Hermaphrodites with Gonad >50% Testes
100
75
50
25
(b)
Hermaphrodites with Gonad 100% Testes
100
75
50
25
30
40
50
60
70
80
Standard Length (mm)

Figure 28. Standard length (mm) vs number of daily rings (from otolith counts) for (a) females and (b) initial phase males between 30-75mm, for Thalassoma bifasciatum on Heron Bay reef, Barbados.

(a) $Y=0.157x + 10.18$, $r=0.89$, $P<0.05$

(b) $Y=0.140x + 15.15$, $r=0.89$, $P<0.05$


(a)
(b)
70
50
30
70
50
30
Standard Length (mm)
80
180
280
380
Number of Daily Rings

and females. Mean size at age and mean growth rates within 5mm size classes and for all size classes combined are shown in Table 16 for females, initial phase males, terminal phase primary males and terminal phase secondary males. There is no difference in growth between initial phase males and females (mean growth of the former is 0.205 mm/day, that of the latter 0.211 mm/day; t=1.59, P>0.05; Table 16). To the extent that gonadosomatic index reflects the proportion of resources allocated to reproduction as opposed to growth, the observation that GSI values of initial phase males and females do not differ (Table 17; comparison of mean GSI values, t=0.46, P>0.05), is consistent with the observation that IP males and females do not differ in growth.

For terminal phase fish, size at age of primary males did not differ from that of secondary males on Heron Bay reef (comparison of mean growth of categories, t=1.29, P>0.05). Note that this is consistent with the observation that initial phase males and females do not differ in growth rate on this reef. Growth rate as determined from all initial phase individuals (mean=0.207 mm/day) did not differ from that as determined from all terminal phase individuals (mean=0.198; t=0.27, P>0.05; Table 16). This suggests that there is little change in growth rate as individuals move from initial phase to terminal phase.

Growth rates for females and for initial phase males were compared on three reefs differing in reef area, population density and population size (Table 18). Growth rates of neither initial phase males nor females differed between reefs (One-way Anova; for males, F=1.63, P>0.05; for females, F=0.93, P>0.05).

Table 16

Mean size at age and mean growth rates within 5mm size classes and for all size classes combined for females, initial phase males, terminal phase primary males and terminal phase secondary males for *Thalassoma bifasciatum* on Heron Bay reef in Barbados.

	INITIAL PHASE MALE				FEMALE			
Size Range	n	Mean SL (mm)	Mean Age (d)	Mean Growth rate (mms./day)	n	Mean SL (mm)	Mean Age (d)	Mean Growth rate (mm/day)
30.0-35.0	12	32.6	155.6	0.209	21	33.0	165.5	0.199
35.1-40.0	24	37.8	177.8	0.212	28	37.2	172.9	0.215
40.1-45.0	8	42.7	227.5	0.187	29	42.5	210.5	0.201
45.1-50.0	17	48.3	231.1	0.209	28	47.5	252.1	0.188
50.1-55.0	11	52.2	275.6	0.189	13	52.5	263.3	0.199
55.1-60.0	10	56.9	290.6	0.202	11	57.2	274.6	0.208
60.1-65.0	4	63.7	309.3	0.205	8	62.3	317.3	0.196
Combined	86	47.7	238.2	0.200	138	47.5	236.6	0.200
	PRIMARY TERMINAL PHASE				SECONDARY TERMINAL PHASE			
70.0-75.0	5	72.6	353.4	0.205	7	72.2	366.0	0.197
75.1-80.0	1	77.6	405	0.191	4	77.8	367.0	0.211
Combined	6	75.1	379.2	0.198	11	75.0	366.5	0.205

Table 17

Gonad weights and gonadosomatic indices (gonad weight as a percentage of body weight) for initial phase males, females, primary terminal phase males and secondary terminal phase males of _Thalassoma bifasciatum_ in Barbados (means and standard deviations are shown).

INITIAL PHASE MALE			FEMALE		
n	Gonad weight (g)	GSI (%)	n	Gonad weight (g)	GSI (%)
194	0.073±0.07	3.31±1.35	299	0.063±0.05	3.25±1.31
PRIMARY TP MALE			SECONDARY TP MALE		
12	0.04±0.03	0.98±0.23	28	0.09±0.040	1.61±1.20

Table 18

Mean growth rates of initial phase males and females between the size range 30-60mm for *Thalassoma bifasciatum* on three reefs differing in population density, population size and reef area.

				IP MALE	FEMALE
Reef	Reef Area (m^2)	Mean Population Size (N)	Mean Density (No/m^2)	Mean Growth Rate (mm/day)	Mean Growth Rate (mm/day)
Golden Palms	23,962	24,921	1.04	0.24±0.01	0.22±0.01
Heron Bay	27,264	41,169	1.52	0.21±0.03	0.21±0.02
Greensleeves	33,584	57,765	1.72	0.22±0.01	0.22±0.01

4.3.9.2 Mortality

Comparative mortality of hermaphrodites (primarily females, but also secondary IP males) and gonochores (primary IP males) was investigated by examining changes in the sex ratio of the initial phase population with fish size (Fig. 29). For most reefs separately, and for all reefs combined, the proportion of hermaphrodites was highest in the smallest size classes, declining to about 0.5 in the size class 50-60mm; the size class below that at which transition to terminal phase typically occurs (Section 4.3.7). For Sandridge, Greensleeves, Paynes Bay and Golden Palms, as well as for all reefs combined, the proportion of hermaphrodites in the smallest initial phase size class was significantly greater than the proportion of hermaphrodites in the largest initial phase size class (Sandridge, X^2= 3.55, $P<0.05$; Greensleeves, X^2=16.39, $P<0.001$; Paynes Bay, X^2=6.11, $P<0.05$; Golden Palms, X^2=3.18, P=0.07; all reefs combined, X^2= 14.77, $P<0.005$). Since growth rates of females (hermaphrodites) and initial phase males (gonochores) do not differ, the decline in proportion of hermaphrodites with increasing fish size suggests that mortality of hermaphrodites may be higher than that of gonochores prior to transition.

The question of whether female mortality increases relative to male mortality during sex change or phase transition was addressed by investigating the rate of decrease in proportion of hermaphrodites (i.e. primarily females when IP; secondary males when TP) from the smallest IP size class to the largest TP size class (Fig. 30). Most sex changing females complete sex change as they move from size class 60-70mm to size class 70-80mm and the decrease in proportion of

Figure 29. Proportion of hermaphrodites (primarily females, but also secondary males) in the initial phase population of Thalassoma bifasciatum as a function of fish size (10mm size classes) for six reefs separately and combined in Barbados.

GP = Golden Palms
GB = Glitter Bay
SD = Sandridge
PB = Paynes Bay
HB = Heron Bay
GS = Greensleeves
CB = Combined

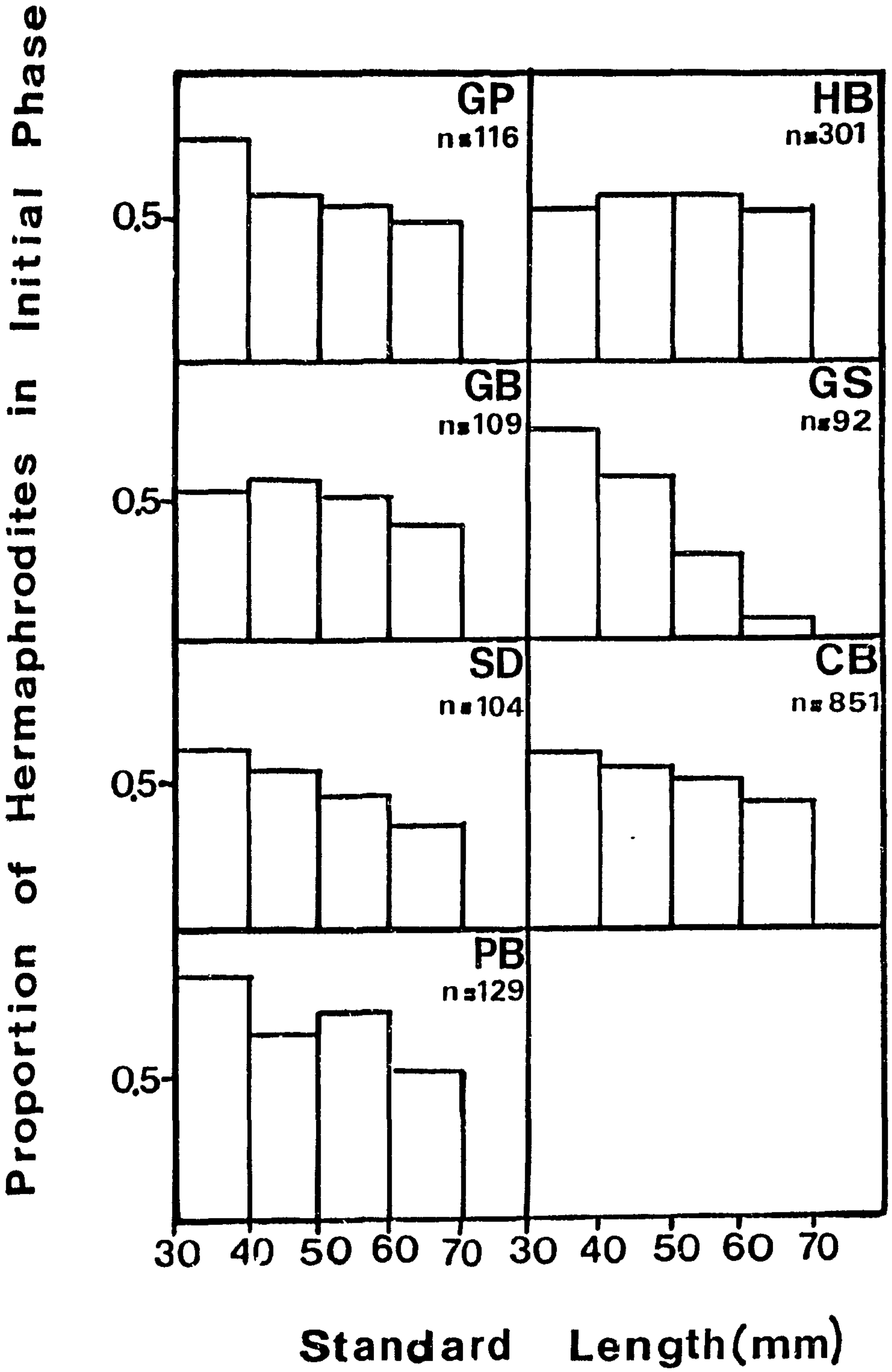
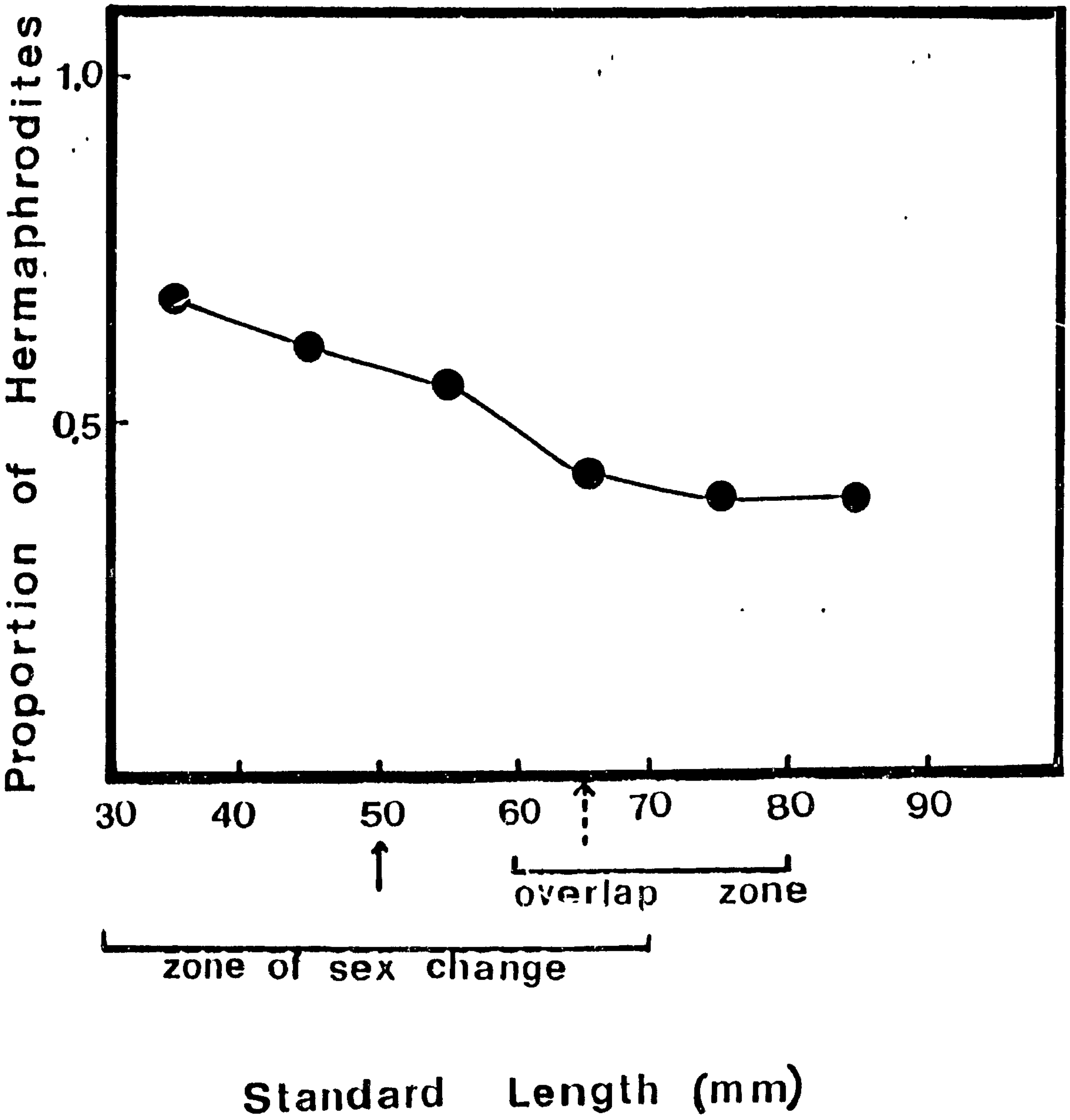

Proportion of Hermaphrodites in Initial Phase
GP
n=116
HB
n=301
GB
n=109
GS
n=92
SD
n=104
CB
n=851
PB
n=129
0.5
0.5
0.5
0.5
30 40 50 60 70 30 40 50 60 70
Standard Length(mm)

Figure 30. Proportion of hermaphrodites in the initial phase and terminal phase populations vs fish size (10mm size classes) for <u>Thalassoma bifasciatum</u> in Barbados.

↑ = mean size of sex change

⇡ = mean size of phase change


Proportion of Hermaphrodites
1.0
0.5
30
40
50
60
70
80
90
overlap zone
zone of sex change
Standard Length (mm)

hermaphrodites is not particularly marked over these size classes(Fig.30). However, sex change may begin when initial phase females are relatively small (Section 4.3.8). Hence, the possibility that the higher mortality of hermaphrodites relative to gonochores results from the sex change that occurs over all IP size classes can not be discounted. This is supported by the observation that in the largest TP size classes where sex change is complete (i.e. all individuals are males), there is no further decrease in the proportion of hermaphrodites relative to gonochores (Fig.30).

The suggestion that mortality is higher for hermaphrodites than gonochores (IP males) is supported by the observation that, on all reefs, more terminal phase individuals are primary males (gonochores) than secondary males (hermaphrodites); but there are more females (hermaphrodites) than males (gonochores) in the initial phase population (Table 19). For all reefs combined, the percentage of females in the smallest adult initial phase size class (62% , Fig. 26) and the percentage of females in the whole initial phase population (49%) are significantly higher than the percentage of terminal phase fish that are secondary males (37% ; smallest IP size class vs TP, X^2=30.5, P<0.001; all IP vs TP, X^2=19.05, P<0.001). These results suggest that the probability of a hermaphrodite (female) becoming terminal phase is significantly lower than the probability of a gonochore (IP male) becoming terminal phase.

Table 19

Percentages of primary males in the initial phase and terminal phase populations of *Thalassoma bifasciatum* on six reefs in Barbados.

				INITIAL PHASE		TERMINAL PHASE	
Reef	Reef Area (m^2)	Mean Population Size (N)	Mean Density (N/m^2)	N	Primary Male (%)	N	Primary Male (%)
Golden Palms	23,962	24,921	1.04	190	41.0	32	59.4
Glitter Bay	19,198	23,806	1.24	194	45.8	25	52.0
Sandridge	52,547	68,837	1.31	188	44.1	28	71.4
Paynes Bay	25,943	38,655	1.49	181	32.0	31	74.2
Heron Bay	27,264	41,169	1.51	505	40.3	62	53.0
Greensleeves	33,584	57,765	1.72	159	42.1	24	62.5

4.4 Discussion

The index of per capita mating success of terminal phase males in bluehead wrasse populations in Barbados was significantly higher than that of either initial phase males or females. This is consistent with the results obtained for the bluehead wrasse in Panama (e.g. Warner et al 1975; Warner 1984), and with the size-advantage hypothesis for sex reversal and phase transition (Ghiselin 1969; Charnov 1982; Warner 1988a,b). Initial phase males and females become terminal phase because this allows a sharp increase in per capita mating success. Indeed, given the high mean per capita mating success of terminal phase males, their rarity in bluehead wrasse populations (2%-8% in Barbados; 1% to 12% in Panama; Warner and Hoffman, 1980a) is somewhat surprising. The constraint to becoming terminal phase may lie in the high variance in mating success of terminal phase males, and the observation that body size explains a major component of the variance. Large terminal phase males may have twenty times the mating success of small terminal phase males in Panama (Hoffman et al 1985), and a correlation between body size and mating success of terminal phase fish has also been found in Barbados (Giraldeau et al Unpub. MS). In short, the frequency of transition/sex reversal in bluehead wrasse populations may be constrained by the fact that more frequent transition may imply earlier transition, and smaller terminal phase fish may have little mating success. The advantage of being terminal phase in the context of the mean per capita mating success of TP fish must therefore be discounted by the time lag between transition and reaching the size at which the mean mating success of TP fish is attained, and by the probability of dying during this time period. Warner (1988a) estimates that secondary males in Panama spend at least 120 days as males before achieving any appreciable mating success. Hoffman et al (1985) made a similar observation but developed the argument further by suggesting that the cost of transition/sex change is a heavy investment in growth at the expense of current reproduction as a means of rapidly attaining the size necessary for successful reproduction as a terminal phase fish. However, there was no evidence of accelerated growth following transition in bluehead wrasse in Barbados. Mean daily growth rate based on terminal phase fish was not significantly higher than mean daily growth rate based on initial phase fish (Section 4.3.9.1). Note that, in the case of hermaphrodites, an additional disadvantage of becoming terminal phase may be that it requires sex change, and there is some evidence in the present study to suggest that sex change may increase mortality.

Warner and Hoffman (1980a) suggested that the mating success of terminal phase males relative to initial phase males varied with reef size. On 'larger reefs' (population size > 200 fish), mating success of terminal phase males was lower and mating success of initial phase higher than on smaller reefs (population size < 200 fish). They suggested that this explained the observation that the percentage of terminal phase fish in the population decreased with increasing population size in Panama. The reefs and populations studied in Barbados were considerably larger (range of population size 16,000 - 53,000) than those in Panama. In Barbados, terminal phase spawning made up 40% of all spawning events observed on the low density/small population size reef, but only 25% of spawning events observed on the high density/large population size reef. Moreover, the percentage of terminal phase males in the population decreased with increasing population density. These results support the suggestion of Warner and Hoffman (1980 a,b) that the advantage of being a terminal phase male rather than an initial phase male decreases with increasing competition for spawning sites and/or females. In Panama, this 'competition effect' occurred on 'larger reefs'; in Barbados it occurred on reefs of higher population densities. More accurately, the key factor influencing the extent to which it pays to be a terminal phase male rather than an initial phase male is probably degree of spawning activity per unit reef area. At any given time of the year, this will be higher for reefs of higher population density. On a given reef, this will be highest during reproductive months i.e. when spawning activity per fish is high. Interestingly, the proportion of matings that are initial phase rather than terminal phase is highest on Heron Bay reef in months when spawning activity per fish is highest, even though density on the reefs is lowest in these months (Section 4.3.3.2).

It is worth noting that since the proportion of terminal phase males is lower on reefs of higher density (i.e. fewer individuals transform to terminal phase), the per capita mating success observed for terminal phase males need not be lower, nor that of initial phase males higher, on reefs of high density. Indeed, in the present study, because the proportion of terminal phase males was higher on low density reefs, the extent to which their per capita mating success exceeded that of initial phase males did not differ from that on high density reefs.

The observation that the percentage of terminal phase fish decreases on reefs of higher density implies either that fish grow slower and hence take longer to reach transition size on such reefs, or that transition size is larger on these reefs. Victor (1986a) found growth of bluehead wrasse to be slower on high density reefs in Panama. However, somewhat surprisingly, growth of neither initial phase males nor females differed on reefs of different density in the present study. The difference in results of the two studies may result from the difference in density ranges characteristic of Panama and Barbados reefs, the latter having densities two to three times higher than the former (Section 3.4.4). The inhibitive effect on growth of any increment in density may decline on reefs of extreme densities.

In this study, there was evidence too suggest that transition size is larger on higher density reefs (Section 4.3.7), indicating that this is the proximate cause of the lower proportion of terminal phase fish on these reefs. This result is consistent with the increasingly accepted perspective that the size or age at sex change is not rigidly determined genetically, but is modified in response to local conditions (e.g. Shapiro 1984, 1987, 1988).

The mean size of transition for bluehead wrasse in Barbados is smaller (~65mm; age about 0.7 years) than that in Panama (~75mm; age about one year, Warner 1984), and terminal phase fish are smaller in Barbados (max. size ~ 85mm) than in Panama (>100mm; Hoffman et al 1985). This is interesting, given the much higher population density of bluehead wrasse in Barbados compared to Panama, and the fact that, within the Barbados population, size at transition increases with increasing density. In short, one might have expected transition at smaller size on the lower density reefs in Panama. These data may therefore suggest that populations of the bluehead wrasse in Panama and Barbados are genetically distinct. Within both populations, optimal size at transition may increase with increasing density but the trajectory of transition size vs density differs between the populations, such that transition size at any given density is smaller for the Barbados population.

The difference in size of terminal phase fish between Barbados and Panama may result partly from differences in growth. Although growth rates on the more dense of the Panama reefs are similar to growth rates in Barbados, overall growth is probably faster in Panama (Victor 1986a; Section 4.3.9.1 this study). Perhaps more importantly, life span of the bluehead wrasse is shorter in Barbados (1.5 years) than in Panama (2.5 years; Hoffman et al 1985), suggesting that total mortality is greater in Barbados. If the higher mortality results from external environmental factors characteristic of the Barbados environment, it could be a causal factor in the evolution of the difference in the transition size vs density trajectory observed between Barbados and Panama populations. Higher extrinsic mortality typically selects for higher reproductive effort and earlier reproduction (e.g. Stearns 1976), and in the case of the bluehead wrasse, may select for earlier age at sex change and transition. It is of interest in this context that the gonadosomatic index of initial phase males in Panama (~2.64; Warner and Robertson 1978) is lower than that of initial phase males in Barbados (~3.31; Section 4.3.9.1). Note, however, that since sex change may have a mortality cost, the earlier sex/phase change observed in Barbados populations may itself contribute to higher total mortality and hence to the shorter life span observed in these populations.

The overall population sex ratio (i.e. terminal phase males plus initial phase males vs females) for the bluehead wrasse in Barbados was 1:1. It is of interest that this is consistent with the spirit of Fisher's (1930) original hypothesis for the evolution and maintenance of population sex ratios. If total males are rare relative to females, per capita mating success of females will be low relative to males, and it will pay females to change sex until the total population sex ratio approaches 1:1. At this point, per capita mating success of males must equal that of females. In this study, total population sex ratio did not differ from 1:1 on any of the study reefs i.e. it was independent of population density, population size and reef area over the range of those parameters observed. Note the potential advantage that the option to change sex gives to hermaphrodites over gonochores, since the former can in principle adjust sex to maximize mating success if reefs were to differ in breeding sex ratio.

Given that the total population sex ratio is 1:1, the initial phase sex ratio must be biased toward females. In Barbados, the initial phase population sex ratio was 1.22 females to 1 male (i.e. 55% female). This ratio did not differ between study reefs, and was similar to that observed in Panama on reefs of similar size (Warner and Hoffman 1980 a,b). These authors reported strong sex ratio skews (~80%) towards females on small reefs (population < 500). How such skews may occur is not clear, although Warner and Hoffman (1980a) suggested that males may actively avoid small reefs when recruiting from the plankton. Given that the great majority of wrasses live in populations > 500, the importance of such sex ratio deviations in the population and evolutionary dynamics of wrasses may be limited.

An issue addressed by Warner et al (1975), Warner and Hoffman (1980a) and Charnov (1982) is why gonochores (IP males) are retained in bluehead wrasse populations. The answer may lie in frequency dependent selection coupled with the cost to females of changing sex and becoming terminal phase. If males and females were equivalently common in the initial phase population, the per capita mating success of the former would be less than the latter, since some females pair spawn with terminal phase males. Consistent with this, males are more rare then females in the initial phase population, and the proportion of males to females is such that the per capita mating success of the two types does not differ. Note that in principle hermaphrodites (females) could continue to depress the per capita mating success of gonochores as the latter become proportionately more rare by increasing their rate of transition to either secondary initial phase males or secondary terminal phase males. However, at the point when per capita mating success of initial phase males equals that of females, it will not benefit a female to change sex and become a secondary initial phase male, particularly if there is a mortality cost to sex change. Nevertheless, in this situation , given the high mean per capita mating success of terminal phase fish, a female might in principle benefit from becoming terminal phase, and this could continue to depress the per capita mating success of initial phase gonochores. The constraint here may lie again in the cost of changing sex, as well as in the cost of becoming terminal phase at small body size previously discussed. Note that the cost of changing sex is higher mortality, and the consequence of this is that hermaphrodites have a lower probability of becoming terminal phase than gonochores; 62% of terminal phase wrasses in Barbados are primary males. In short, gonochores are retained in bluehead wrasse populations because (1) their per capita mating success in initial phase increases relative to hermaphrodites as they become more rare, and (2) they have a higher probability of becoming terminal phase than do hermaphrodites. Both (1) and (2) may result, at least in part, from the mortality cost of changing sex. In the case of (1), this is supplemented by the potential cost of changing phase.

One may reasonably ask why hermaphrodites are retained at present proportions in bluehead wrasse populations in Barbados. If they were to become more rare, the decline would be checked by frequency dependent selection; their per capita mating success increasing relative to gonochores the more rare they become. However, given that the per capita mating success of initial phase males and females does not differ in Barbados populations, but that the former have a higher probability of becoming terminal phase than the latter, the question becomes, why is the proportion of hermaphrodites as high as observed in Barbados populations? A possible answer may lie in the advantage that the flexibility to change sex may give to hermaphrodites in the longer term. In the present study, if secondary initial phase males are excluded, the per capita mating success of females (hermaphrodites) is lower than that of initial phase males (gonochores). However, in such circumstances, a hermaphrodite can increase mating success by becoming a secondary initial phase male. The present results suggest that this occurs to the point where per capita mating success of initial phase males (primary and secondary) equals that of females. In a more general context, breeding sex ratios may oscillate through time. If they do, hermaphrodites, by adjusting sex in response to the prevailing sex ratio, may be able to markedly increase per capita mating success relative to gonochores during periods of sex ratio skews. This advantage of hermaphrodites over gonochores need not be observed if per capita mating success of the two types is compared at any instant in ecological/evolutionary time.

In the present study, growth rates of initial phase males and females did not differ, and growth rates of neither sex differed between study reefs. Warner (1984) also found no difference in growth between initial phase males and females on large reefs (N>120) in Panama, but claimed that males grew twice as fast as females on small reefs (N<110). Again, given that most wrasses live in populations>120, the importance of accelerated male growth on small reefs in the population and evolutionary dynamics of wrasses is unclear. Other questions of interest remain. For example, in contrast to the present results, Warner (1984) reported no differences in mortality between initial phase males and females in bluehead wrasse populations in Panama. Warner and Hoffman (1980a) claimed that only 25% of terminal phase fish are primary males in Panama (compared to 62% in the present study). Given that about 35% of initial phase fish are males in Panama (Warner and Hoffman 1980a), that mortality of initial phase males is reported to be similar to that of females

(Warner 1984), and that initial phase males grow as fast as or faster than females (Warner 1984), it is not clear why only 25% of the terminal phase population is primary male. In both Panama and Barbados, the factor primarily constraining attempts to further comprehend the ecological and evolutionary dynamics of the bluehead wrasse is ignorance of the genetics of sex determination. Direct attempts to address this issue through breeding experiments are severely constrained by the relatively long planktonic larval phase characteristic of wrasses.

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