Diel, Lunar, and Seasonal Periodicity in the Reproductive Behavior
of the Pomacanthid Fish, *Centropyge potteri*,
and Some Other Reef Fishes in Hawaii¹

PHIL S. LOBEL²

ABSTRACT: The reproductive behavior of five Hawaiian coral reef fishes are
described for the first time: an angelfish (Pomacanthidae), three butterflyfishes
(*Chaetodon fremblii*, *C. multicinctus*, *C. unimaculatus*), and a goatfish (*Parupeneus multifasciatus*). The angelfish, *Centropyge potteri*, was examined in
detail. It was determined that every month from December until May it spawns
each evening during the week preceding a full moon. On extensive coral reefs
*C. potteri* occurs mostly in pairs, whereas on patch reefs a single male may
control access to several females. Thus, males on patch reefs seem to enjoy
greater reproductive success than males on extensive reefs. The advantages
potentially associated with spawning synchronized at dusk between the first
quarter and full moon primarily involve reduced mortality of offspring. The
annual reproductive period, which is shared by several other Hawaiian shore
fishes, is correlated with a semiannual shift in ocean currents that may retain
larvae in the vicinity of the Hawaiian reefs at that time.

REPRODUCTIVE BEHAVIOR OF MARINE FISHES
has been scarcely described for any but a few
taxa (Breder and Rosen 1966), e.g., some
pomacentrids (Clarke 1970, Helfrich 1958,
Myrberg, Brahy, and Emery 1967, Sale 1971,
Stevenson 1963, Swerdloff 1970, Walters
1967) and some labrids and scarids (Potts
1974, Randall and Randall 1963, Reinboth
1973, Roede 1972, Youngbluth 1968). De­
spite numbers field studies, the reproductive
activities of many reef fishes remain un­
known. Most observations on the activity of
reef fishes have been during midday and thus
have missed peaks of reproductive activity at
dusk, where and when such peaks occur.
A similar situation existed with predatory
activities until observations were made during
the crepuscular periods (e.g., Hobson 1965,
1968, 1972, 1974). This article reports the
spawning behavior and periodicity of a
pomacanthid, *Centropyge potteri*, which
spawns at dusk. Also included are observa­tions of other species that spawn at the same
time, notably three chaetodontids, one mul­
lid, and three acanthurids.

METHODS

Direct Observations

Fishes were watched under water using
scuba equipment during approximately 300
hr at all times of day and night, including 30
hr immediately before sunset, from June
1974 to June 1975. I soon recognized that the
reef fishes were spawning predominantly
during dusk. To minimize the influence of
my presence on this activity, I positioned
myself on station at least 30 min before the
fish began courtship. The sudden appearance
of a diver (or a large fish) caused many fishes
to cease spawning activity. I remained on
station until convinced that all activity had
ceased and that the fishes had retired for the
night [for approximate timing of various
species, see Hobson (1972)]. Spawning activ-
### TABLE I

**SIZE AND RATIO OF THE SEXES OF *Centropyge potteri* ON PATCH REEF AREAS**

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>DEPTH (m)</th>
<th>NUMBER OF FISH SAMPLED</th>
<th>NUMBER, MALE: FEMALE</th>
<th>RATIO, MALE: FEMALE</th>
<th>STANDARD LENGTH, MEAN AND RANGE (mm)</th>
<th>PATCH HABITAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outside Kaneohe Bay</td>
<td>16</td>
<td>14</td>
<td>3:11</td>
<td>1:3.67</td>
<td>76.5 (61–87)</td>
<td>Fish from two rubble areas 2 meters apart; total area approximately 24 m²</td>
</tr>
<tr>
<td>Waikiki (Oahu)</td>
<td>8.3</td>
<td>4</td>
<td>1:3</td>
<td>1:3</td>
<td>76.5 (63–91)</td>
<td>Solitary coral cluster approximately 3 meters from extensive reef; patch approximately 1 meter diameter</td>
</tr>
<tr>
<td></td>
<td>16–20</td>
<td>7</td>
<td>1:6</td>
<td>1:6</td>
<td>65 (45.5–83)</td>
<td>Three rocks, 0.6 meter at greatest length; close together with scattered rubble</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>8</td>
<td>2:6</td>
<td>1:3</td>
<td>76 (61–94)</td>
<td>Three rocks, 1 meter at greatest length; spaced 1 meter apart with rubble around</td>
</tr>
<tr>
<td></td>
<td>25–30</td>
<td>5</td>
<td>1:4</td>
<td>1:4</td>
<td>63 (54–68)</td>
<td>Single coral cluster 1.4 m²; 0.6 meter high</td>
</tr>
<tr>
<td></td>
<td>25–30</td>
<td>7</td>
<td>1:6</td>
<td>1:6</td>
<td>71 (59–89)</td>
<td>Patch of large rock rubble approximately 16 m²</td>
</tr>
<tr>
<td>Totals</td>
<td>8.5–30</td>
<td>45</td>
<td>9:36</td>
<td>1:4.28 ± 1.39</td>
<td>71 (45.5–94)</td>
<td></td>
</tr>
</tbody>
</table>

Note: The difference between sex ratios between patch and extensive reefs (Table 2) was significant (*t* statistic, two-tail level of significance; 0.01 < *P* < 0.02).

### TABLE 2

**SIZE AND RATIO OF THE SEXES OF *Centropyge potteri* ON EXTENSIVE REEF AND RUBBLE HABITATS**

<table>
<thead>
<tr>
<th>LOCATION</th>
<th>DEPTH (m)</th>
<th>NUMBER OF FISH SAMPLED</th>
<th>NUMBER, MALE: FEMALE</th>
<th>RATIO, MALE: FEMALE</th>
<th>STANDARD LENGTH, MEAN AND RANGE (mm)</th>
<th>EXTENSIVE REEF AND RUBBLE HABITAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mahukona (Hawaii)</td>
<td>11–16</td>
<td>26</td>
<td>12:14</td>
<td>1:1.17</td>
<td>62 (47–81)</td>
<td>Extensive reef with dense layers of coral including <em>Porites lobata, Porites compressa, Pocillopora meandrina</em></td>
</tr>
<tr>
<td>Makaha (Oahu)</td>
<td>8.3–16</td>
<td>12</td>
<td>4:8</td>
<td>1:2</td>
<td>57.5 (38–71)</td>
<td>Vast area of large rubble on top and below a ledge</td>
</tr>
<tr>
<td>Makua (Oahu)</td>
<td>8.3–10</td>
<td>10</td>
<td>6:4</td>
<td>1:0.67</td>
<td>66 (55–81)</td>
<td>Large cave surrounded by rubble and coral; total area approximately 67,000 m²</td>
</tr>
<tr>
<td>Moanalua Bay (Oahu)</td>
<td>8.3–13</td>
<td>18</td>
<td>6:12</td>
<td>1:2</td>
<td>75 (51–98)</td>
<td>Scattered corals, mostly <em>Pocillopora meandrina</em>, and large rubble spaced less than 1 meter apart</td>
</tr>
<tr>
<td>Waikiki (Oahu)</td>
<td>16–30</td>
<td>58</td>
<td>24:34</td>
<td>1:1.42</td>
<td>73 (42–95)</td>
<td>Large rubble covering vast areas; rubble in some patches, but less than 1 meter part; very little live coral</td>
</tr>
<tr>
<td>Wreck buoy (Oahu)</td>
<td>8.3–10</td>
<td>50</td>
<td>20:30</td>
<td>1:1.5</td>
<td>77.5 (49–101)</td>
<td>Extensive region of large corals, mainly <em>Porites lobata</em> and <em>Pocillopora meandrina</em> corals spaced less than 1 meter apart</td>
</tr>
</tbody>
</table>

Totals 8.3–30 174 72:98 1:1.46 ± 0.51 68.5 (38–101)

Note: See note for Table 1.
TABLE 3
DIRECT OBSERVATION OF Centropyge potteri SPAWNING, 1975

<table>
<thead>
<tr>
<th>DATE OF FULL MOON</th>
<th>DATE OF OBSERVATION</th>
<th>REEF TYPE</th>
<th>NUMBER OF FISH SEEN SPAWNING</th>
</tr>
</thead>
<tbody>
<tr>
<td>27 January</td>
<td>25 January</td>
<td>Extensive</td>
<td>Six pairs</td>
</tr>
<tr>
<td>26 February</td>
<td>25 February</td>
<td>Patch</td>
<td>One male and six females, male spawned with three or four of six females each evening</td>
</tr>
<tr>
<td>27 March</td>
<td>22–26 March</td>
<td>Patch</td>
<td>One male and three females</td>
</tr>
<tr>
<td>25 April</td>
<td>19 April</td>
<td>Patch</td>
<td>Eight pairs spawned each evening</td>
</tr>
<tr>
<td>23 June</td>
<td>21 June</td>
<td>Extensive</td>
<td>One pair out of eight spawned</td>
</tr>
</tbody>
</table>

Note: All spawning occurred within 1 hr of sunset. Each female spawned once, although where more than one female was available, males spawned more than once. A total of 7 harem and 31 pair spawnings were observed (a pair spawning refers to a single spawning by a male with one female; a harem spawning refers to one male spawning repeatedly with two or more females).

Weights and Measures
Specimens were collected by spear. All weights were assessed on a Mettler electronic balance. Fishes were generally examined while fresh or frozen. Percentage gonad weight was determined by dividing the blot-dry gonad weight by the blot-dry total body weight of a fish and multiplying by 100. A total of 315 specimens of Centropyge potteri were examined.

Definitions
Reefs inhabited by Centropyge potteri were classified as either extensive or patch reefs. A patch of rock/coral with an area of less than 24 m² (the largest patch reef found), surrounded by sand, and at least 100 meters distant from neighboring reefs is defined as a patch reef. Patches near other reefs are defined as satellite reefs. Extensive reefs are characteristic of areas usually associated with the notion of coral reefs, a vast expanse of coral and rubble. Terms such as abundant, common, occasional, and rare are used as defined by Chave and Eckert (1974).

HABITAT EFFECT ON SEX RATIO
Adult Centropyge potteri inhabit reefs consisting of large corals and boulders within the 3- to 50-meter depth range. In such areas, this species is among the ten most frequently seen fishes (Hobson 1974).

The ratio of males to females differed between patch reefs and extensive reefs. There were approximately two to four more females per male on a patch reef than on extensive reefs (Tables 1, 2). This differential availability of females was evident during reproduction. Males on patch reefs spawned with each female, one at a time consecutively per evening, whereas males on extensive reefs did not spawn with more than one female per evening (Table 3).

The basis for these differing sex ratios has not been thoroughly tested; however, there were indications that it may be related to male defense of a spawning site. The most important aspect of such territory appears to be a towering rock or coral knoll over which the fish spawn (see details below). I introduced foreign males onto patch reefs on five occasions and each time the resident male attacked and kept the intruder over the sand beside the patch reef. Presumably it is dangerous for the fish to travel between reefs.

Study Areas
Study sites were located primarily on the reefs off Waikiki and the Waianae coast, Oahu Island, and the Kona coast, Hawaii Island. These reefs were typically composed of stony corals (Porites spp. and Pocillopora spp.) and rubble. Species composition of comparable regions has been reported by Hobson (1974).
The attacks by the resident were most persistent during the time of reproduction. *Centropyge potteri* is a herbivore and did not defend the territory against other species with similar food habits. During 20 hr of observation at midday only four agonistic encounters occurred between *C. potteri* and *Ctenochaetus strigosus* (Acanthuridae) and *Eupomacentrus fasciolatus* (= *Pomacentrus jenkinsi*, Pomacentridae). In the extensive coral reef habitat the availability of spawning sites, by inspection, was greater than on patch reefs, perhaps allowing more males to occupy spawning sites and giving females a broader choice of mates or merely reducing the ability of any one male to exclude other males from the large reef (see description of spawning site below). Individuals limit their movements to restricted, well-defined locations (Hobson 1974).

**SPAWNING BEHAVIOR OF Centropyge potteri**

The following generalized description of *Centropyge potteri* spawning is based upon 31 observations of pair spawning and 7 harem spawnings (Table 3). One sequence has been entirely recorded on super-8 mm movie film. The general sequence of behavior is presented diagrammatically in Figure 1.

Courtship was initiated by the male, who ceased feeding and began courting about 1 hr before sunset. The male swam toward a female in a vertical undulating style distinct from normal swimming motion. He stopped above her and erected all median fins while flapping the pectoral fins. This display continued as the male drifted slowly upward with his head diagonally up or with his side parallel to the substrate. If the female failed to follow, the male halted immediately and darted back to her. The male continued courtship by swimming around the female in the undulating fashion. In this way, the male approached the female as he swam forward while rising and dropping in a swooping, fluttering motion. Courtship continued until the female was enticed over to the prominent coral or rock tower and she rose above the tower with the male. This usually only required a few courting passes. Spawning occurred only over the tallest coral or rock in the immediate area. During courtship and spawning the overall blue color of both fish paled as the red color intensified.
During the first few encounters, the female rose up with the male and then darted back to cover when the male attempted to move to the spawning position. The male pursued her while continuing his courtship display. Spawning climaxed when the female remained in midwater, about 1 meter above the coral/rock tower. The male approached from underneath and appeared to press his snout against her abdomen (Figure 2). Such contact may signal or facilitate egg release. A single burst of eggs was broadcast. Because of the low light level I could not see sperm released in the field, but in aquaria spawnings of related _Centropyge fisheri_ it occurred simultaneously with egg release. Immediately after release of eggs and sperm, the pair darted to cover with the female chasing the male, apparently nipping at his caudal fin. Chasing by the female happened only after consummation of the spawning act and not during earlier episodes of courtship. Spawning was consummated before sunset, but the absolute time varied. Soon after sunset the fish retired into a cavity in the reef for the night.

During courtship various sounds, like clicks and grunts, were produced by these fish, although their precise role during reproduction was not examined.

Similar reproduction behavior was noted in aquarium spawnings of _Centropyge bispinosus_ (Bauer and Klay 1974, Lobel 1975), _C. fisheri_; _C. flavissimus_ spawned likewise during the full moon period of May 1975 at Enewetak Atoll, Marshall Islands.

**REPRODUCTIVE PERIODICITY**

The peak reproductive season for _Centropyge potteri_ began in December and continued through May (Figure 3). Development of the gonad within this annual season was correlated with the full moon; the female's ovary attained its greatest weight before spawning commenced—about 1 week before the full moon (Figure 4). _Centropyge potteri_ was observed to spawn only during the week preceding the full moon from January to April 1975 (Table 3). No observation dives were performed during the full moon period of May 1975. In June 1975, however, three dives during the full moon week revealed only one spawning event, although nine other pairs were in full view. Observation during other evenings of the lunar cycle and other times of the year gave no indications of spawning having occurred.

The question whether spawning occurs during the months of June to December may still be debated. However, it is evident that if spawning does occur at that time, the size of spawn will be very much less than during the months of December through May. The one male seen spawning in June did so only once, although he pursued two neighboring females that fled rather than respond to courtship. If spawning does occur during the off-season, it is probably infrequent.

**SPAWNING BEHAVIOR OF CHAETODONTIDS**

During the observations of _Centropyge potteri_, spawning was observed coincidentally in three species of chaetodontids: _Chaetodon fremblii_, _C. unimaculatus_ (three observations of each), and _C. multicinctus_ (six observations). All spawned within the hour preceding sunset during the week before the full moon, February and March 1975.

The reproductive behavior of _C. multicinctus_ appeared typical. Although more than two fish were present, only pairs
spawned. When spawning, *C. unimaculatus* and *C. fremblii* occurred solely as pairs. Aggregations of spawning *C. multicinctus* consisted four times of four individuals and two times of three individuals. One group of four *C. multicinctus* apparently included at least one female and two males. I did not spear any fish so that my actions would not disturb the behavior sequence. Female chaetodontids, obviously swollen with roe, led the group or pair as they swam along the reef. The sex of an individual was determined by observation as it spawned. Courtship among chaetodontids was less elaborate than among *Centropyge potteri*. As the chaetodontids swam along the reef, the female tilted her head slightly downward as she continued in front of the male. The male swam from behind and up alongside the female. As the male reached the female and placed his snout to her abdomen, both fish quivered and eggs and sperm were released (Figure 5). In one case, a male *Chaetodon multicinctus* approached a female in this fashion three times before spawning. The chaetodontid spawning posture was strikingly similar to that described for *Centropyge potteri*. Again, the nuzzling by the male may signal the female to release eggs. *Chaetodon multicinctus* and *C. unimaculatus* rose up approximately 0.5 meter above the substrate to spawn. *Chaetodon fremblii* rose into the water between 1 and 2 meters when it spawned.

At midday during the week before the full moon of May 1975 at Enewetak Atoll, Marshall Islands, a pair of *Megaprotodon trifascialis* were filmed in a brief encounter that culminated with the assumption of the spawning position, but spawning did not occur. *Megaprotodon trifascialis* are solitary territorial fish with males and females residing on neighboring *Acropora* sp. corals (Reese 1973).

*Forcipiger flavissimus* was also sighted in the chaetodontid spawning position although actual spawning was not seen. The position differed slightly because of the long snout. The male nuzzled with his forehead and kept his snout underneath. This single observation was made during the hour before sunset, 23 March 1975 (4 days before the full moon).

**SPAWNING BEHAVIOR OF A MULLID**

The mullid *Parupeneus multifasciatus* was sighted spawning four times at dusk on 25 March 1975, 2 days before the full moon.
An aggregation of approximately ten fish hovered about 1 meter above a sandy area next to a reef at 10 meters depth. The largest member, most probably the male, was a darker color than the others and darted conspicuously around and through the aggregation until another fish joined along its side. The pair ascended, side by side, to the surface, where they spawned while swimming forward just beneath the surface. After spawning, they separated and returned to the reef, whereupon I lost sight of them. This mullid was the most difficult of all fish to approach. When I came within 5 meters they ceased all spawning activity. In contrast, I was able to get within 1 meter of spawning *Centropyge potteri* and within 2 meters of the chaetodontids.

Randall and Randall (1963) also reported upward movement leading to spawning and large aggregations for the Caribbean mullid, *Parupeneus maculatus*.

### Spawning Behavior of Acanthurids

Three species of acanthurids spawned during the same time period as the previously described fishes during March and April 1975. A small aggregation of about a dozen individuals swam together until they suddenly darted upward a few meters, spawned...
and descended in unison. I noted several such group spawnings of *Acanthurus nigrorus*, *Ctenochaetus strigosus*, and *Zebrasoma flavescens*. Their reproductive behavior did not differ significantly from the reproductive behavior of acanthurids as described by Randall (1961b).

**DISCUSSION**

The schedule of reproduction among Hawaiian reef fishes reflects adaptation to a variety of ecological factors. Diel periodicity appears to be influenced primarily by the balance between the threats of diurnal planktivores feeding on eggs and newly hatched larvae and crepuscular piscivores attacking spawning adults. Spawning at dusk involves minimal risk to eggs and larvae, but it is the time of peak predation upon adult fishes. Lunar reproductive synchrony further reduces the probability of predation on individuals by creating a swamping effect [the selfish herd hypothesis, see Reaka (1976)]. The tide is outgoing during evenings shortly before a full moon and may aid in removal of eggs and larvae from the immediate vicinity of the reef where they are exposed to reef planktivores. The annual peak in reproductive activity is correlated with a shift in ocean current that retains pelagic larvae around the islands and ensures their return to Hawaiian reefs. These various factors exert their influence at different times (diel, lunar, and annual) and result in selection for reproductive cycles that overlap in many ways. Their relative effects on timing, however, are probably not as distinct as the categories presented below might imply.

**Reproductive Behavior and Coloration**

Pomacanthis and chaetodontids exhibited similar reproductive behavior and a mating position that is unlike other fishes whose behavior has been described. One difference between chaetodontids and pomacanthis is that the chaetodontids did not restrict their activity to specific locations on the reef. Whereas *Centropyge potteri* always spawned over the same spot and courtship was directed toward enticing a female to a specific tall rock/coral in the immediate territory, chaetodontids spawned wherever they might be in a general home range without apparent orientation to specific reef structures. Spawning did, however, take place on the seaward side of the reef. Reese (1975) has described other aspects of chaetodontid behavior. The taxonomic relationship of the Pomacanthidae and Chaetodontidae has been reviewed by Freihofer (1963) and Burgess (1974).

It is well known that chaetodontids, like many other fishes, transform into nocturnal colorations. Although the full significance of these nocturnal colors remains uncertain, the fact that chaetodontids wait until dusk to spawn agrees with Hobson's (1974) contention that recognition is important during both day and night. Hobson (1974) suggests: "It is logical that diurnal fishes would employ visual clues to identify one another. But the distinctive nocturnal colorations of many chaetodontids suggest that members of some species need to recognize each other after dark as well. Nocturnal colorations that occur among chaetodontids in Kona (Hawaii) tend to accentuate a contrast, thus making them more visible at lower light levels. Although the nocturnal colorations of some fishes, such as those that become mottled, make them more difficult to see in the dark (Schroeder 1964), certain chaetodontids in Kona seem to be effecting a nocturnal display" (p. 1022). Since at least three species spawn during dusk, these low-light-level, color-contrasting displays may aid in mate recognition. Probably the situation is similar in other species that change color when spawning at low light levels. Although, I noted color changes in these fishes when they spawned at dusk, I am not familiar enough with their nocturnal colorations to evaluate the similarities.

**Diel Reproductive Periodicity**

Diurnal planktivores are adapted for plucking small prey from midwater, while nocturnal planktivores, such as apogonids
and some holocentrids, possess large mouths and feed mainly on large plankton prey (Hobson 1974, Hobson and Chess 1976). By dusk, most diurnal planktivores have descended to the reef for the night (Collette and Talbot 1972, Domm and Domm 1973, Hobson 1972). Spawning at dusk may reduce the probability of eggs being eaten in two ways: (1) there are few active planktivores and (2) any planktivores that are still active may be quickly satiated by the simultaneous spawning by many fishes. In addition, there was an outgoing tide during the time of spawning of this study, which may aid in sweeping eggs and larvae from the reef and from the grasp of planktivores that are still active (Figure 6). At this time the difference in the height of the tide from high to low was greatest, which may influence the rate of flow. In the mornings the tide was incoming.

The reproductive activity of broadcast-spawning species was not evident in the reef areas where there were planktivores or other species spawning. The avoidance response by spawning fishes to planktivores has also been reported by Hobson (1965). Twilight is a visually difficult time for most reef fishes and is when predation is at its peak (Hobson 1972, 1974, Munz and McFarland 1973). It may be that the low level of reflected moonlight combined with sunlight just before sunset is sufficient for fishes to recognize mates, spawn, and also avoid potential predators, but is not enough for planktivorous fishes, requiring high visual acuity, to continue foraging.

The threat from predators may partially explain why a prominent reef structure towering in the home range of Centropyge potteri is important. While spawning in midwater, they were still close to a reef shelter to which they darted between encounters, after spawning, and when disturbed by other fishes. Similar orientation to a tall reef structure has been reported for Hypoplectrus chlorurus (Serranidae) when spawning (Barlow 1975).

The importance of such a towering coral/rock is evident on patch reefs, where it may be one factor limiting the number of spawning males. A male on a patch reef controlled a limited area and consequently access to resident females, while mostly pairs occurred on extensive reefs. Since females spawn only once nightly, the males on patch reefs very probably enjoy a greater reproductive success. This aspect of the biology of C. potteri should be further examined experimentally.

Spawning during the daytime is known to occur among some pomacentrids, labrids, and scarids (Helfrich 1958, Meyer 1977, Moyer 1975, Moyer and Bell 1976, Potts 1974, Reinboth 1973, Roede 1972, Sale 1971, Youngbluth 1968). Pomacentrids protect their nests against predators, and labrids and scarids release large numbers of eggs. Active predation of labrid eggs by planktivorous pomacentrids has been described by Meyer (1977). Eggs may be less likely to be eaten if they are toxic [as is known only for some tetraodontiform fishes and a cottid, Pillsbury (1957)] or float at the water’s surface where few fishes feed. The eggs of some nesting pomacentrids and balistids hatch predominantly during the dark (Allen 1972, Lobel and Johannes 1977). The eggs of the pomacentrid Amphiprion clarkii hatch between 34 and 70 min after sunset (Moyer and Bell 1976). These fishes would also share the advantages of fishes spawning at this time.
TABLE 4
FISHES WITH PELAGIC LARVAE SHOWED TO HAVE A PEAK SPawning SEASON
BETWEEN DECEMBER AND JUNE IN HAWAII

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>SPECIES</th>
<th>AUTHORITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthuridae</td>
<td>Acanthurus triostegus sandvicensis</td>
<td>Randall 1961a</td>
</tr>
<tr>
<td>Blenniidae</td>
<td>Entromacrodus marmoratus</td>
<td>Strasburg 1953</td>
</tr>
<tr>
<td></td>
<td>Istiblennius zebra</td>
<td>Strasburg 1953</td>
</tr>
<tr>
<td>Chaetodontidae</td>
<td>Chaetodon miliaris</td>
<td>Ralston 1975, 1976</td>
</tr>
<tr>
<td>Engraulidae</td>
<td>Stolephorus purpureus</td>
<td>Leary, Murphy, and Miller 1975</td>
</tr>
<tr>
<td>Kuhliidae</td>
<td>Kuhlia sandvicensis</td>
<td>Tester and Takata 1953</td>
</tr>
<tr>
<td>Labridae</td>
<td>Labroides phthirophagus</td>
<td>Youngbluth 1968</td>
</tr>
<tr>
<td>Muraenidae</td>
<td>Gymnothorax eurostus</td>
<td>Gosline and Brock 1960</td>
</tr>
<tr>
<td>Pomacanthidae</td>
<td>Centropyge poteri</td>
<td>This study</td>
</tr>
<tr>
<td>Pomacentridae</td>
<td>Abudefduf abdominalis</td>
<td>Helfrich 1958</td>
</tr>
<tr>
<td></td>
<td>Chromis ovalis</td>
<td>Swedluff 1970</td>
</tr>
<tr>
<td></td>
<td>Chromis verator</td>
<td>Swedluff 1970</td>
</tr>
<tr>
<td></td>
<td>Dascyllus albissela</td>
<td>Stevenson 1963</td>
</tr>
<tr>
<td></td>
<td>Eupomacentrus fasciolatus (= Pomacentrus jenkinsi)</td>
<td>Gosline 1958</td>
</tr>
</tbody>
</table>

NOTE: This table lists only those species with pelagic larvae. Spawning has been said to occur throughout the year in many of these fishes; however, all have been reported with peak reproductive seasons at this time. Details will be presented elsewhere (Lobel and Reaka 1977). All species listed are endemic to Hawaii except G. eurostus and E. fasciolatus.

Lunar Reproductive Periodicity

Annual and lunar spawning seasons have been described for many temperate zone fishes (e.g., Schwassman 1971), but reports on the spawning periods of tropical fishes are scattered and few.

In the Society Islands, Ctenochaetus striatus and Zebrasoma scopas spawned at dusk within 5 days preceding the full moon, and Acanthurus triostegus sandvicensis also spawns on a lunar cycle (Randall 1961a, b). Randall and Randall (1963) suggested that spawning occurred for Scarus rupripinne (Sacrdae) during the full moon and possibly during the new moon in the Caribbean Sea. Roede (1972) reported that peak reproductive activity for seven Caribbean labrids was pronounced at the full moon. She also found two other lower peaks during the lunar month, and she suggests that propagation in these labrids may continue throughout the month but with increased activity during the full moon period. Abudefduf abdominalis (Pomacentridae) spawned during full and new moon phases in Hawaii (Helfrich 1958), as does Amphiopion spp. (Pomacentridae) at Enewetak Atoll (Allen 1972). Allen (1972) reported 26 of 34 spawnings of Amphiopion spp. 6 days before or after the full moon, with 20 of 34 of the nests hatching within 1 week of the full moon. Two other pomacentrids also have spawning peaks on about the full moon (Moyer 1975, Moyer and Bell 1976). Johannes at Palau has determined full moon spawning synchrony for the nesting triggerfish, Pseudobalistes flavimarginatus (Lobel and Johannes 1977) Lunar periodicity has also been suggested for Extremeus micropus and Gnathodon speciosus (Carangidae) in Hawaii (Watson and Leis 1974). Kuhlia sandvicensis (Kuhliidae) is also suspected of spawning near the time of full moon in Hawaii (Tester and Takata 1953). In addition, many marine invertebrates are known to spawn during the full moon (Korringa 1947).

An explanation fully accounting for a peak period of spawning and hatching eggs during dusk on evenings of the first quarter to full moon is difficult to construct, however, several nonexclusive potential factors may be involved:

1. Reduced threat to eggs and larvae due to midwater planktivores which are generally inactive by dusk.
2. Eggs and larvae swept out to sea with retreating tide.
3. Lunar periodicity may act as a cue synchronizing simultaneous reproductive readiness within a species.
Reproductive Behavior of *Centropyge potteri*—LOBEL

Annual Reproductive Periodicity

While tropical fishes are generally believed to spawn throughout the year, a spring spawning peak during February through April is evident among Caribbean reef fishes (Munro *et al.* 1973). My observations suggest that reproductive activity in several Hawaiian reef fishes also peaks in the spring from December until June (Table 4). During this period in Hawaii there were generally lower surface temperatures and salinities that correlated with an abundance of all species’ eggs (Watson and Leis 1974). Water temperatures were also at their lowest during the reproductive peak in the Caribbean (Munro *et al.* 1973). Watson and Leis suggested that these physical changes in Hawaii reflect a shift in ocean currents and such a shift may increase the retention of pelagic eggs and larvae near the Hawaiian Islands (see also Jones 1968, Sale 1970). This is being further examined by Lobel and Reaka (1977) using the results of drift-bottle experiments by Barkley, Ito, and Brown (1964). Full moon phases during this season were associated with peak tidal changes and during this study spawning occurred at dusk, which coincided with an outgoing tide.

The seasonal change of ocean current direction has been assessed by the recovery of drift bottles released in the vicinity of the island of Hawaii (Barkley, Ito, and Brown 1964) (Figure 7). The current drift is roughly parallel to the Hawaiian Islands from January...
The populations of reefs which are adapted to unique situations are confronted with the problem of conserving their pelagic stages contrary to dispersing larvae into the major ocean current systems. Since many reef animals possess a pelagic stage in their life history, this selection pressure may be widespread where we find organisms (1) restricted to specific environmental circumstance, (2) in specific and very isolated places such as Hawaii, and/or (3) in a situation where the results of competitive interactions depend upon a large number of recruits (e.g., Sale 1974, 1977). Synchronization of reproduction with ocean currents favoring return of larvae to home reefs may be one mechanism by which reduced dispersal is accomplished. If the different ecological setting in Hawaii favors natural selection of those taxa with a mechanism assuring return of larvae to suitable reefs, we may expect a peak reproductive season between December and June to be evident among those species especially suited to Hawaiian habitats. If this proves true, we may predict such seasonality at least among the recognized endemic species [29 percent of the fishes (Randall 1976; see also Gosline 1968)], which are among the most numerous on Hawaiian reefs.

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