

Archipelago-wide episodic recruitment of the file fish *Pervagor spilosoma* in the Hawaiian Islands as revealed in long-term records

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Received 19 July 2003 Accepted 19 February 2004

Key words: reef fish, density, long-term census, archipelago, pelagic juveniles

Synopsis

The endemic filefish, *Pervagor spilosoma*, has long been known to recruit infrequently but in large numbers to shallow water habitats in Hawai'i. When it does recruit, as it did in 1944, 1975 and 1982–1987, it becomes the most abundant or one of the most abundant species on Hawaiian reefs. At these times of high abundance, juvenile individuals also become abundant in the off-shore pelagic environment and in deeper benthic habitats. The results of two previously published studies and this one show that the last heavy recruitment occurred throughout the Hawaiian Island chain in the period from 1982–1988. The earliest strong recruitment in this interval occurred on the leeward, or northwest Hawaiian Islands in 1982, then on O'ahu in 1983, then on the island of Hawaii, at the southeast end of the island chain in 1985. At the Kane'ohe Bay, O'ahu, sampling site, strong recruitment occurred in 1983–1987. Fish that had recruited in the summer of a year survived less than a year at these shallow (<15 m) sites or moved off the reefs. No other fish species among the 30 species censused in a 20 year period at Kane'ohe Bay has shown the extremes of abundance displayed by this species, nor did any other species recruit so strongly in the 1983–1987 period. The latter event suggests that the pattern of recruitment in this species was not solely due to a particular pattern of ocean circulation, because if that were the case, other species would also show strong recruitment. The rarity of large recruitment events in this species, the high density of the recruits, the length of individuals at recruitment, the observation by others of juveniles and possibly young adults in the water column, and the sequential nature of the recruitment down the length of the island chain may in part be the result of metamorphosis in the pelagic environment and a pelagic juvenile stage in this species.

Introduction

Long-term temporal changes in the population sizes of reef fishes have seldom been monitored (Sale et al. 1984, Walsh 1987, Doherty & Fowler 1994b, Milicich & Doherty 1994, Robertson & Kaufman 1998, Tolimieri et al. 1998). Long-term records could provide important ecological insights, such as how much inter-annual variation in abundance is possible, and could lead to the development of hypotheses about the control of reef fish abundance. Observations of cyclic fluctuations in small mammal abundance (Chitty

1960) and the cycles in predator–prey interactions (Elton & Nicholson 1942) stimulated research into explanations for these cycles. Long-term studies of fluctuations in the abundance of insects were used to identify regulatory factors (Varley & Gradwell 1960). Long-term records of the fluctuations of fisheries resources such as anchovy have led to insights into the joint effect of climate change and human impacts on fisheries yields (Chavez et al. 2003).

While recruitment of reef fishes is known to be variable in time (Sale et al. 1984, Walsh 1987, Doherty & Fowler 1994b, Milicich & Doherty

1994, Robertson & Kaufman 1998, Tolimieri et al. 1998), the common species at a site can generally be found to have some recruitment each year. For example, long-term studies by Doherty & Fowler (1994a, b) show that two species of pomacentrids recruited in each of 9 years on the seven study reefs, although particularly strong recruitment occurred in some years. Robertson & Kaufman (1998) followed three acanthurids over 16 years at San Blas and found recruitment in each year. Russ et al. (1996) reported strong recruitment in particular years in some reef fish species, but some recruitment occurred in all species in all years. In a 20 year study of abundance of 30 species of reef fish at a site in Kane'ohē Bay, O'ahu, (J. Stimson, unpublished data), the Hawaiian endemic *Pervagor spilosoma* stood out in that it had strong recruitment and high abundances in only one period of five consecutive years in the mid-1980s. In years of high abundance, *Pervagor spilosoma* became the most abundant species in shallow reef communities in the southeast or main Hawaiian Islands (Hobson & Chess 1996), yet in most other years this species has been virtually absent from the community. Such exceptionally high abundances were reported in 1944 (Titcomb & Pukui 1972), in 1975 (Reed 1977, Hutchins 1986) and in the early to mid 1980s (this study, Schroeder 1989, Hobson & Chess 1996).

Pervagor spilosoma is regarded as a reef fish (Hobson 1974, Randall 1978, Hutchins 1986) and has been reported to be able to feed on coral polyps (Hobson 1974), but it has also been reported that in years of high abundance it can metamorphose in open water, where it evidently feeds on plankton (Hobson & Chess 1996) and itself becomes prey to pelagic predators (Hobson & Chess 1996) including tunas (Brock 1985). It is not clear where adult populations of this Hawaiian endemic reside in years of low abundance.

This study reports on the recruitment of this fish over a 20 year period on four small reefs in Kane'ohē Bay, O'ahu, near the southeastern end of the Hawaiian chain. The timing of large recruitments of this species and the subsequent adult abundances were recorded and compared to published records of abundance at Midway Atoll, which lies at the northwest end of the Hawaiian Island chain (Schroeder 1989), and at Hawai'i Island at the southeast end of the chain (Hobson &

Chess 1996). The spatial and temporal patterns of abundance reported here make it possible to examine some explanations for the episodic outbreaks of this species.

Methods

Censuses of *Pervagor spilosoma* for this study were conducted on 4 small patch reefs in central Kane'ohē Bay, O'ahu, Hawai'i (Figure 1). These patch reefs are truncated cones; their bases are at approximately 17 m depth in the silty bay bottom. Each reef is at least 200 m from any other reefs. Their tops (reef flat) are at the levels of the low tides. The reef flats are circular or oval and their perimeters (reef crest) range in length from 67 to 167 m (Table 1). The reef slopes consist primarily of rubble, sediment, macroalgae, and corals (Table 1). Corals and macroalgae are most abundant on the upper third of the reef slope. Vertical relief on the slopes and reef flats of these reefs is small, on the order of 30–40 cm. These reefs were chosen for censusing because they were relatively small; the smallest has a surface area of $\sim 1500 \text{ m}^2$ (Brock et al. 1979).

The censuses reported here were begun in 1982 and were all carried out by the author. No censuses were conducted on any reef from January 1990 to June 1990. One reef, reef #19, was censused in every year, and was censused more intensively each year than were the other reefs. The censuses of other reefs had large gaps, particularly prior to 1987. Fish were counted in a strip transect centered on the reef crest and extending around each reef; the transect included the outer 3 m of the reef flat and the upper 5 m of the reef slope. *P. spilosoma* tended to associate with small coral outcrops on the slope. Individuals of this species are somewhat distinctive because of the bright orange of their tail, their head shape and their habit of remaining relatively still in the water column. All the individuals counted were within 2 m of the surface of the reef slope and none were seen higher off the reef or further out in the water column. Censuses were only conducted if visibility was sufficient to see 5–6 m down the reef slope, but some of the variability in the censuses is attributable to variability in visibility. A complete list of

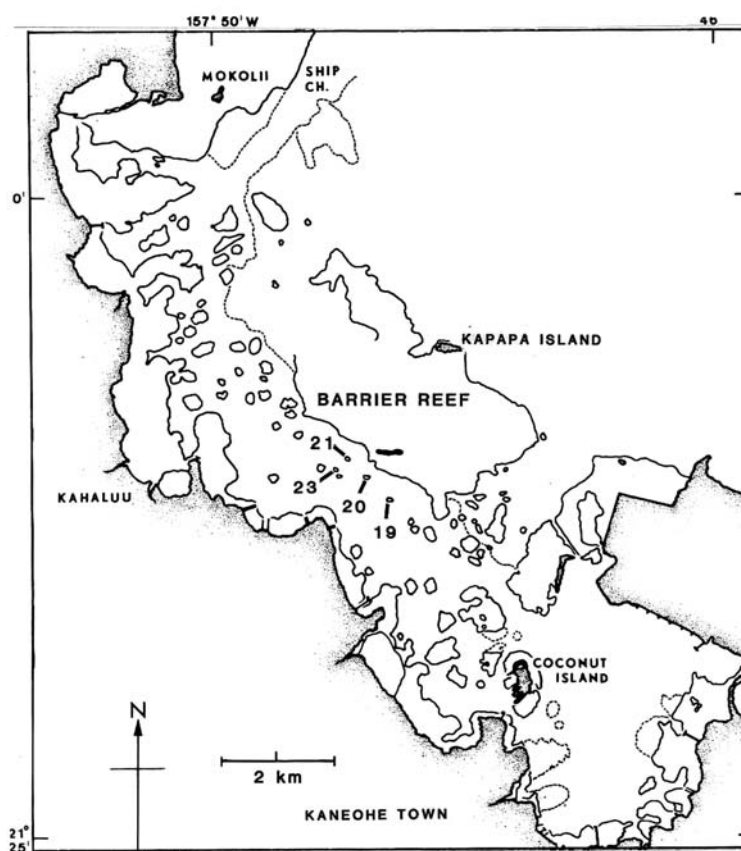


Figure 1. Map of Kane'ohe Bay, O'ahu showing patch reefs (numbered) on which fish censuses were performed. The characteristics of the reefs are given in Table 1.

Table 1. Characteristics of the study reefs.

Reef #	Circumference (m)	Distance to nearest reef (m)	Percent cover	
			<i>Dictyosphaeria</i>	Coral
19	96	425	29	2.5 ^a
20	115	350	55	1.5 ^a
21	67	198	40	12.0 ^a
23	167	76	57	17 ^b
			46	11.0 ^a
			43	23 ^b

Cover of coral and of the green alga *Dictyosphaeria cavernosa* are for the upper 3 m of the reef slope. Reef numbering system and dimensions are from Roy (1970).

^aThis study, surveyed in 1992.

^bBooth (1991), surveyed in 1987.

species inhabiting these reefs can be found in Brock et al. (1979).

Counts on each of the four reefs were converted to counts per 100 m of reef perimeter (measured at

the outer edge of the reef flat) to allow comparison of abundances among reefs. These counts can be converted to approximate densities by using the width of the transect, 8 m (3 m of reef flat and 5 m

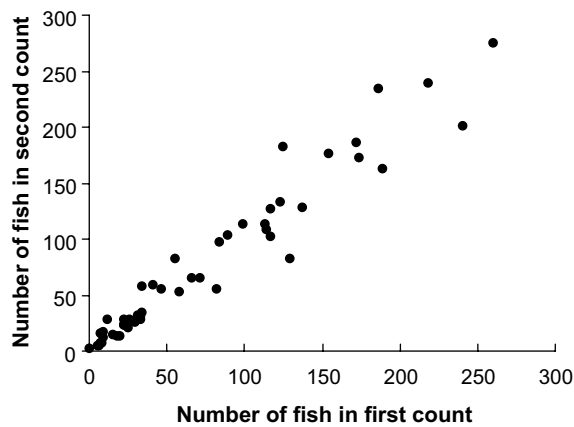


Figure 2. Correlation between counts of individual reef fish species made at consecutive times on the same reef. Each point represent the abundance of a species in two counts performed on the same or consecutive days. Correlation coefficient is 0.97, sample size is 52.

of reef slope). These visual counts of fishes are regarded as estimates, not the actual numbers of fishes in the transects. The relationship between visual counts and actual numbers of fish on Kane'oh'e Bay reefs has been estimated by other investigators (Brock 1982). The repeatability of counts made in this study was examined by re-surveying reefs on the same day or consecutive days without tallying the previously recorded count for each species. The degree of correlation of counts repeated on the same or consecutive days is high (Figure 2).

The censuses described above did not include estimates of the lengths of the *P. spilosoma*, but another less extensive set of census does provide information about how the size frequency distribution of these fish changes over the course of a year. In the period from July 1980 to August 1982 fish were sampled on 10, 6 m long transect lines which were set down the reef slope on the four reefs described above. The upper ends of the transect lines originated from points equidistantly positioned around the perimeter of the reef flat of each reef. Twenty centimeter long sections of plastic pipe, marked with rings at every 5 cm along their length, were distributed along each transect line to act as references to aid in estimating fish lengths. An observer floating above one of these lines, counted all the fishes which crossed the

transect line during a 20 min period and estimated the total length of each individual to the nearest cm. These counts are referred to as 'fixed point' censuses and are included here because they show the change in average size of *P. spilosoma* over the course of a year.

No obvious changes in the benthic communities of these reefs occurred during the 20 year survey period, but the reefs have been subject to three factors which could have caused changes in their biotas. (1) There has been an increase in the use of reef #21 by green sea turtles, which create ledges and pockets on the reef's slope which they then use as resting sites. The turtles first began appearing on this reef in the early 1980s. In creating resting ledges and pockets, they break the fragile coral and generate down-slope slides. These processes may have increased the proportion of rubble on the slope of this reef and reduced coral cover, both of which could in turn reduce shelter for fishes. (2) Two of the four patch reefs were used for two experiments which potentially could have influenced results presented here. In the first, muraenid eels were removed from reef #19 from September 1980 to September 1981, and then removed from reef #20 for the next year. The second experiment was the removal of almost all *Chaetodon miliaris* from reef #19 in the spring of 1988. (3) Kane'oh'e Bay is the site of a substantial amount of subsistence and recreational fishing, and some commercial fishing. These fisheries are primarily directed at octopus, pelagic species, goatfishes, and parrotfishes (Everson 1994).

Results

Pervagor spilosoma were abundant on these four reefs from 1983 to 1987 (Figure 3). One other small peak of abundance occurred in 1993 on all four reefs. During each of the annual peaks in the 1980s, fish that recruited from the plankton during the early summer (Figure 3) first appeared at a size of ~5 cm (Figure 4A), grew rapidly during the summer and fall to a length of ~12 cm and then disappeared by the winter (Figure 4B). This pattern of abundance is best shown on reef #19, which had the greatest frequency of sampling. The pattern of growth is illustrated by the data on fish censused and measured in the fixed-point censuses

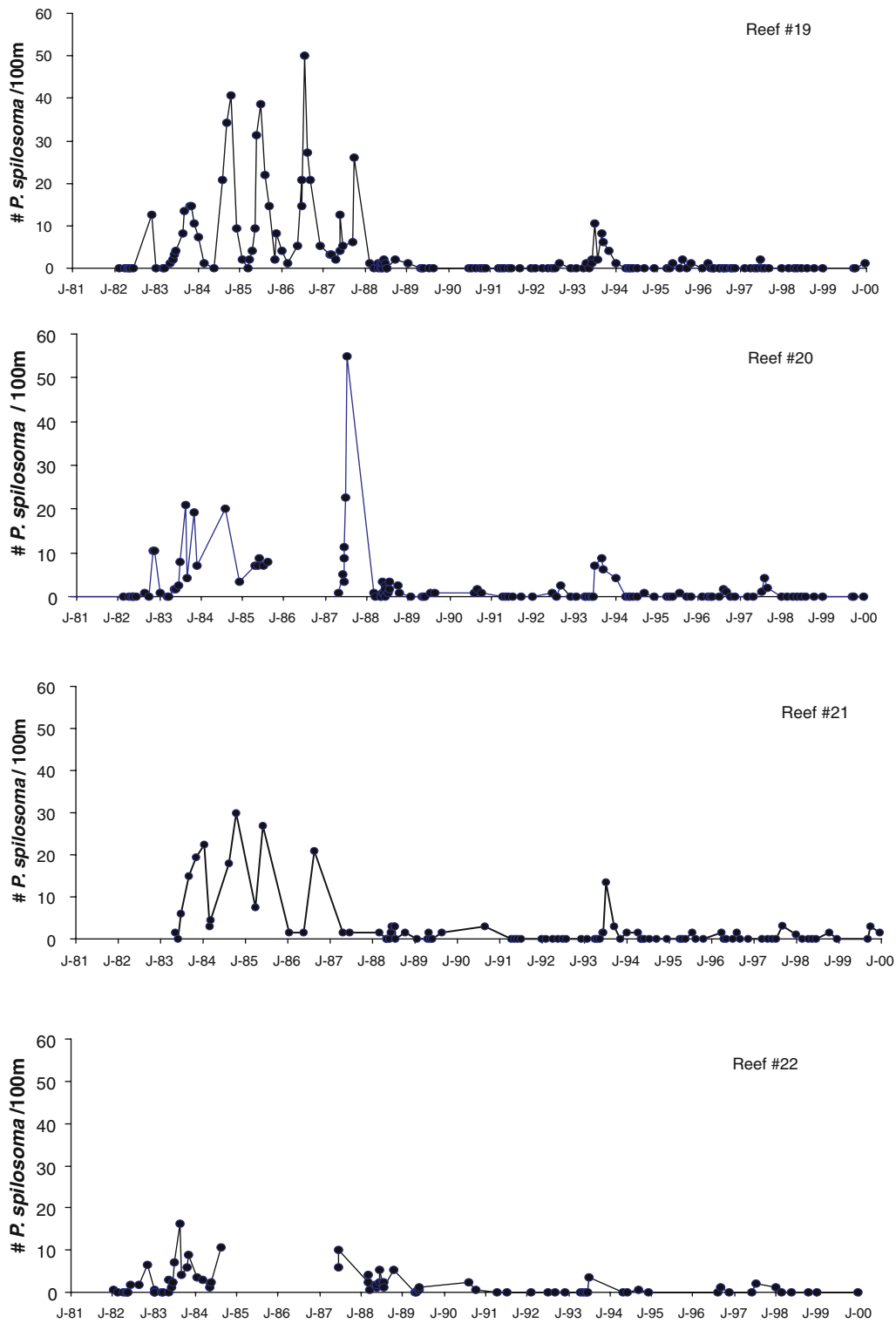


Figure 3. Pattern of abundance of *P. spilosoma* on four small patch reefs through time. Absence of points indicates no counts were made on a reef at that time. Tick marks and the letter J refer to January of each year.

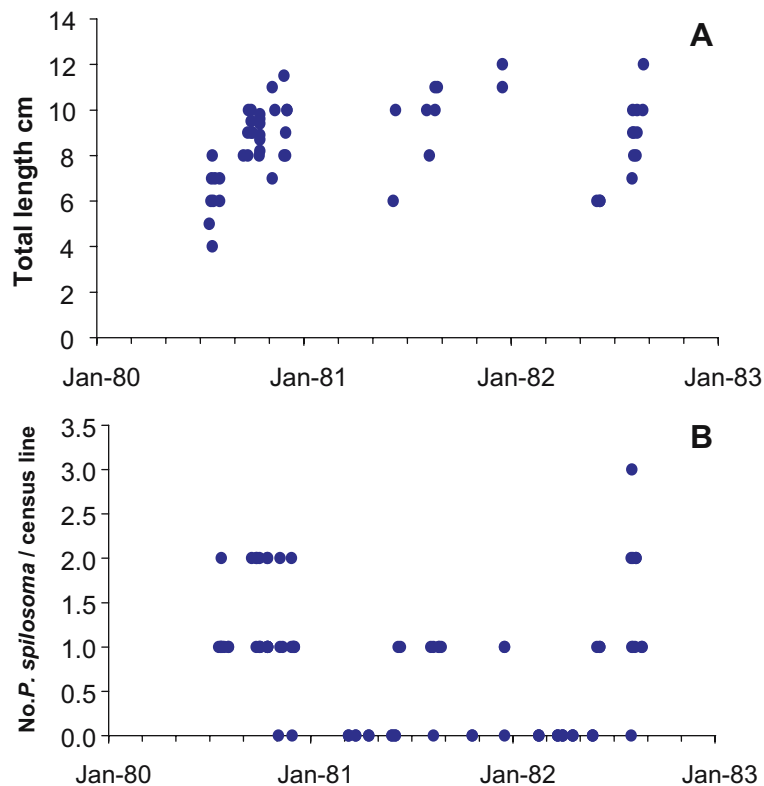


Figure 4. (A) Change in size of *P. spiliosoma* through time based on fixed-point counts performed in 1980–1982. (B) The relative abundance of *P. spiliosoma* on reefs expressed as the number of fish crossing a 6 m long line in 20 min.

conducted during the period from 1980 to 1982 when densities were much lower (Figure 4A). Each succeeding summer, the first *Pervagor spiliosoma* were about half the length of the individuals seen in the previous December. The fact that there were no large fish in June indicates that the peaks in abundance each year are the result of the recruitment of fish during the summer of each year. Very few or no fish persisted on the patch reefs from one year to the next and none were seen in the nearby water column. The large *P. spiliosoma* of the winter either died or moved off the reefs. *P. spiliosoma* were also caught in traps set on these reefs to capture eels. These *P. spiliosoma* were only caught in the months from August through December when the fish were large enough to be retained by the mesh of the traps, even though traps were set throughout the year from July 1980 to July 1982. No *P. spiliosoma* were captured from December 1980 until May 1981 or from December 1981 until May 1982.

It is not known whether the difference in density among the four reefs is due to differences in recruitment strength, in subsequent survival of juveniles, or in the frequency of sampling. Peak densities on the frequently-sampled reef #19 are higher, but last for a very short time, so the fact that peaks on the other reefs are lower may be because the actual peak densities were missed because of the lower frequency of sampling or the timing of the censuses.

Two other species have shown ‘outbreaks’ which are similar in some regards to the ‘outbreaks’ in *Pervagor spiliosoma* reported here. In the August of 2003, the priacanthid, *Priacanthus meeki*, suddenly became abundant on the four reefs used in this study. Densities on some reefs exceeded 1000 fish per 100 m of reef perimeter, making this species the most abundant fish on the reef. This species had not been seen on these reefs by this investigator during the period from 1981 to 2003. There are reports that the species recruited at many

shoreline sites on O'ahu and that it has been abundant in the pelagic fish community 5–30 km offshore in water of >100 m in depth. This recruitment is similar to the events of the years of heavy recruitment of *P. spilosoma*: sudden recruitment of individuals >5–6 cm in total length, appearance of large numbers in open-water non-reef habitats, abundances which exceed that of any of the usual ichthyofauna of the reefs. By the fall of 2003 the numbers of this fish on Kane'ohē Bay reefs had declined substantially. The second species is *Zanclus cornutus*, the Moorish Idol, which reached densities of 50–90 fish per 100 m of reef perimeter in 1988–1989 on all four study reefs and again reached this level in September and October of 2003. This level of density is at least five times higher than the usual densities of this species on these reefs over 20 years. Similar to the *Priacanthus meeki* and *Pervagor spilosoma*, the first individuals of *Z. cornutus* which appeared on the reef were large, 7–8 cm (total length) relative to adult size, suggesting these fish recruit as juveniles.

Discussion

Pervagor spilosoma is unusual and almost unique among the reef fish found on the patch reefs of Kane'ohē Bay because in the period from 1981 to 2000 it has been very abundant only during the 5 consecutive years from 1983 to 1987. None of 30 other fish species censused with equivalent effort on these reefs in the interval from 1981 to 2000 were particularly abundant in this time period, and none showed such large inter-year changes in abundance or went from being one of the rarest species on the reef to virtually the most abundant (J. Stimson, unpublished data). These results suggest that the episodic recruitment of this species is not due to a particular oceanographic feature which affects many species (Polovina et al. 1994), but is evidently the result of an interaction between some feature of the life history of this species (e.g. prolonged pelagic juvenile life or the ability to metamorphose in the pelagic environment), and some oceanographic phenomenon (for example, the development of a particular current).

The phenomenon of rare, strong recruitment and high abundance in this species has been reported previously (Jordan & Evermann 1903).

Particular years of high abundance in Hawai'i were: 1944 (Titcomb & Pukui 1972), the mid 1950s (University of Hawai'i Sea Grant Newsletter, July 1985), 1975 (Reed et al. 1977, Hutchins 1986), and 1985 to 1987 (Hobson & Chess 1996).

These peaks in recruitment and abundance of *Pervagor spilosoma* have not given rise to strong year classes, as has been observed in other species (Russ et al. 1996). Instead the consecutive peaks have been the products of annual recruitments. Individuals that recruited in the spring and summer did not survive on the same reefs through the winter (Figure 3), and the first individuals censused in the summer of a peak year were smaller than the last individuals censused or trapped in the previous winter. The patch reef individuals died within the year, or they emigrated from the study reefs. Similarly, Hobson & Chess (1996) saw no increase in size in their consecutive annual samples, a situation which also suggests annual recruitment and poor survival. Fish may have returned to the water column, as suggested by Hobson & Chess (1996), although in Kane'ohē Bay adult *P. spilosoma* have not been seen in the water column near the patch reefs.

This species was censused at a variety of sites in the Hawaiian archipelago in the course of other multi-year studies conducted during the last 30 years. These studies provide information on the extent and timing of recruitments of *P. spilosoma* down the length of the archipelago (Figure 5) and suggest a sequential appearance of recruits down the 2500 km length of the island chain. (1) Schroeder (1989) censused these fish at Midway Atoll, 2100 km WNW of Oahu, four times a year from May 1981 to August 1985. During this interval the species was only abundant on the eight sampled patch reefs in mid-1984, and had not appeared as of the August 1985 census (Figure 6A). (2) A study of feeding behavior of jacks conducted in the Northwestern Hawaiian Islands from French Frigate Shoals to Midway Atoll (900–2100 km WNW of Oahu), over the period September 1978 to March 1983, detected large numbers of *P. spilosoma* in visual censuses conducted on reefs and in the stomachs of jacks (Sudekum et al. 1991). The bulk of the *P. spilosoma* encountered in the analysis of the diets of the jacks (25 of the 28 sampled jacks), were detected in the latter part of this period (June 1982 and March 1983) so

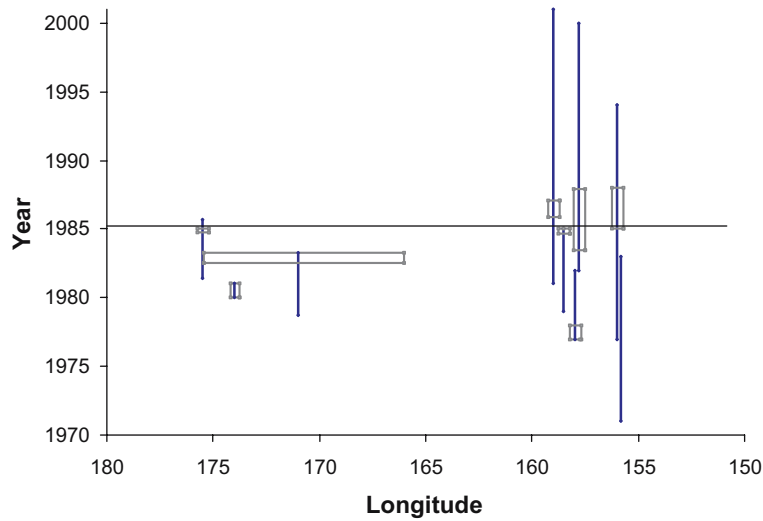


Figure 5. Timing of the peaks of abundance of *P. spilosoma* over the length of the Hawaiian Archipelago. Vertical lines represent the period of observation in each study. Boxes represent the timing and duration of peak abundances of *P. spilosoma*. The broad box represents the time of occurrence of peak abundance recorded in one study which sampled a set of sites over a geographic range, but did not refer peak abundance's to particular sites. The 1977 and 1980 peaks were of a lesser magnitude and possibly less extensive than the 1983–1987 peaks.

P. spilosoma were abundant in the Northwestern Hawaiian Islands 1 (1983) or 2 (1982) years before Schroeder's (1989) record at Midway (Figure 6A). (3) Hobson (1984) surveyed 13 sites (142 transects) over the length of the Hawaiian Island chain from 1977 to 1982. Hobson (1984) and Hobson & Chess (1996) reported that *P. spilosoma* were abundant (more than 10% of the fish counted) on Neva Shoals (near Lisianski Island, 1700 km WNW of Oahu) in 1980 (the only year the site was censused), and were abundant on leeward O'ahu in 1977 (more than 5% of the fish counted). No other sites censused by Hobson (1984) had an abundance of *P. spilosoma* greater than 1%. (4) Surveys performed at a power plant at Kahe on the Wai-anae, or southwest coast of O'ahu from 1979 to 1984 (E. DeMartini, NMFS, Honolulu, personal communication) showed a high abundance of *P. spilosoma* in 1984 and smaller peaks in the early 1980s (Figure 6B). (5) Two other sites on the southwest coast of O'ahu have been censused from 1981 to 2001 in the course of contracted surveys. High numbers of *P. spilosoma* (approaching 1 m^{-2}) were reported in 1985, 1986 and early 1987 at these sites (Figure 6C) but fewer than 0.03 m^{-2} were seen in years prior to or following these three

years (Russo 1989, Water Resources Research Center Reports, Univ. of Hawai'i). (6) Hobson & Chess (1996) censused this species annually (September) at three sites on the west coast of the island of Hawai'i, 250 km SE of Oahu, from 1977 to 1994, and found the fish were particularly abundant in 1985, 1986 and 1987, and about one tenth as abundant in 1988 (Figure 6D). They described the initial appearance of this species in their censuses as explosive and reported that in the peak years it was among the dominant species at all three sites. (7) A study of recruitment and the abundance of juvenile reef fishes was conducted at Keei on the island of Hawai'i (250 km SE of Oahu) by Walsh (1987) from 1977 to 1983; he found no significant numbers of *P. spilosoma* in this period, as was the case in the study by Hobson & Chess (1996). (8) Hobson & Chess (1996) refer to two personal communications which noted that the species was abundant off O'ahu in the pelagic environment in 1985 and 1986 and that it was a major prey of pelagic predators off the Island of Hawai'i in 1985, 1986 and 1987.

These multi-year studies show that *P. spilosoma* recruited heavily throughout the 2500 km length of the Hawaiian archipelago during the 1983–1988

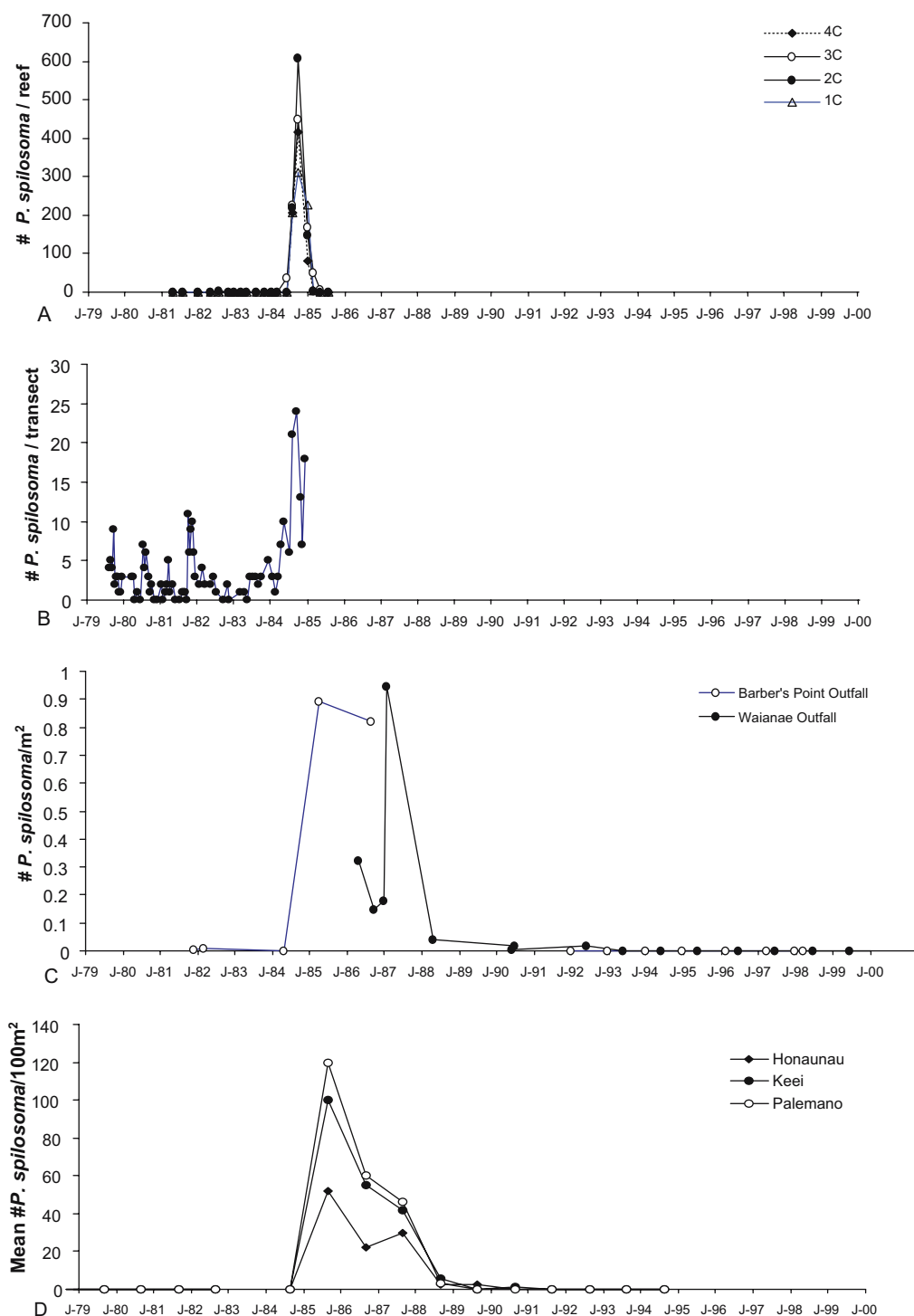


Figure 6. Pattern of abundance of *P. spilosoma* at (A) a Midway Atoll lagoon patch reef (Schroeder 1989) (B) Kahe, Oahu, (De Martini, pers. comm.) (C) two sites on the leeward coast of O'ahu (Russo 1989, reports of the Water Resources Research Center, Univ. Hawaii). A third leeward O'ahu site, Sand Island Outfall had no *P. spilosoma* from 1991 through 1996. (D) Three sites on the Kona Coast of the island of Hawai'i (Hobson & Chess 1996). These censuses were performed over time periods which overlap the censuses reported in this paper. X-axis marks indicate January of the year.

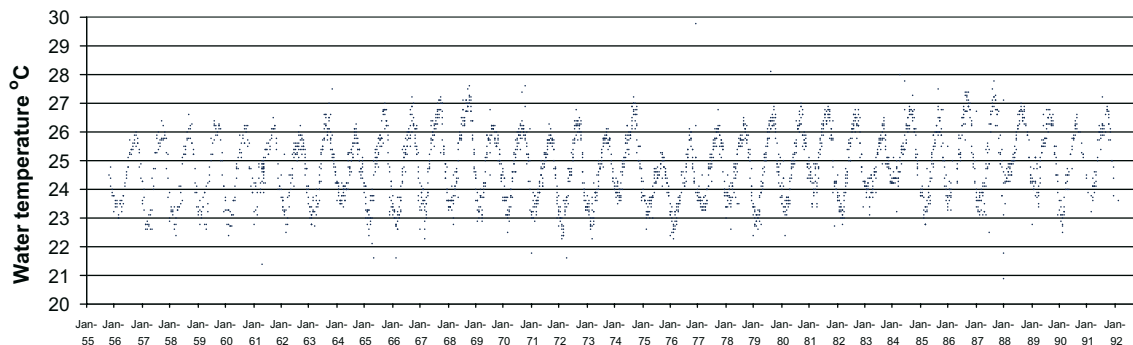


Figure 7. Seawater temperature record from Koko Head, O'ahu, Hawai'i collected by the National Marine Fisheries Service approximately twice weekly. Water samples were taken from a cliff by bucket, and are reported to be representative of off-shore values.

period and that heavy recruitment possibly occurred sequentially from NW to SE (Figure 5). In the Northwestern Hawaiian Islands (i.e., NW of Kauai) there is evidence of recruitment at Midway in 1984, but not in August of 1985 (Schroeder 1989, Figure 6A), and the observation of large numbers of *P. spilosoma* in censuses and in diets of jacks in 1983 or even 1982 (Sudekum et al. 1991). Recruitment in the northwestern islands seems to have occurred toward the beginning of the years of peak abundance on O'ahu (1983–1987, Kane'ohē Bay, Figure 3; 1984–1987, Leeward O'ahu, Figure 6B and C). Recruitment on the west coast of Hawai'i Island peaked in 1985–1987 (Figure 6D), toward the end of the sequence of years of peak abundances on O'ahu as measured in Kane'ohē Bay. These results suggest that whatever factor favored the settlement of large number of *P. spilosoma* in shallow water acted over a very large area and acted at consecutively later times on more south-easterly islands in the chain. The recruitments of 1977 (Hobson & Chess 1996) and 1980 (Hobson 1984) were smaller and less extensive and do not seem to be a part of this more extensive pattern in the mid-1980s.

It is possible that the spatial and temporal patterns of recruitment of this species could be correlated with some large-scale oceanographic feature which, over the period 1983–1988, moved through the archipelagic waters from NW to SE. A seawater temperature record collected weekly at Koko Head, O'ahu, Hawai'i from 1955 to 1992 (National Marine Fisheries Service, Honolulu) does show that water temperatures were warmer

than normal ($>27^{\circ}\text{C}$) in 1984–1988 (Figure 7). This 1984–1988 warm period is a component of the Pacific Decadal Oscillation (Polovina et al. 1994). A similar warm period appears in the record from 1966 to 1968, but no published reports of unusually high abundances of *P. spilosoma* have been found for this period. There are records of a 1975 outbreak on the islands of Kauai and Oahu (Reed et al. 1977) where *P. spilosoma* constituted 49 and 60% of the fish fauna respectively, but the Koko Head temperature record does not show high water temperatures at that time (Figure 7). A second long-term seawater temperature record collected at French Frigate Shoals from 1981 to the present by a NOAA buoy¹ does not show elevated temperatures in the mid 1980s corresponding to the peaks in the Koko Head record. Though the surface temperature records alone do not support this idea, the involvement of a large-scale physical oceanographic factor is suggested by the overlap in the settlement peaks among the islands distributed over the length of the Hawaiian chain and the apparent sequential appearance of peak years from west to east in the chain. The NW to SE direction of the sequential appearance of *P. spilosoma* does agree with the simulated dispersal of lobster larvae through the chain using geostrophic flow generated by sea surface height differences in the period 1993–1996 (Polovina et al. 1999).

The possibility was investigated that the sporadic heavy recruitment of *P. spilosoma* observed

¹<http://ilikai.soest.hawaii.edu/HILO/buoys/ndbc.html>.

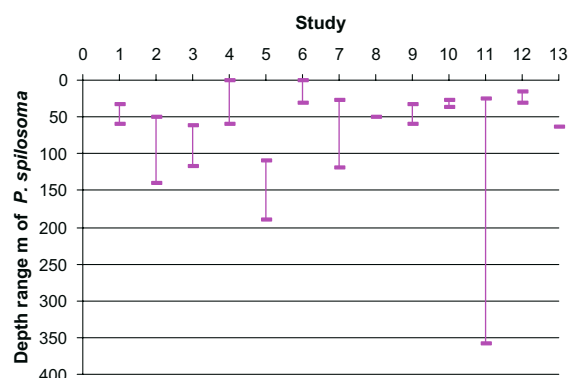


Figure 8. Depth distribution of *P. spilosoma* reported in the literature. (1) Fowler (1928), Hawaiian Islands. (2) Chave & Mundy (1994), Johnston Atoll, Hawaiian Islands. (3) Haight et al. (1993) Penguin Banks. (4) Hutchins (1986), Hawaiian Islands. (5) Jordan & Evermann (1903), Bird Island. (6) Hobson (1984), Lisianski. (7) Uchida & Uchiyama (1986), Necker. (8) Uchida & Uchiyama (1986), French Frigate Atoll. (9) Uchida & Uchiyama (1986), Brooks. (10) Uchida & Uchiyama (1986), Maro Reef. (11) Uchida & Uchiyama (1986), Laysan. (12) Uchida & Uchiyama (1986), Lisianski. (13) Uchida & Uchiyama (1986), Kure.

in shallow waters is the result of the expansion of the species range from deep into shallow water. Tinker (1982) states that *P. spilosoma* is characteristically found in 'deeper waters' and that it periodically appears in shallow waters. Many of the collection depth records for this species are from depths greater than 15 m (Figure 8), and *P. spilosoma* are reportedly taken by snappers (1982–1983) caught in more than 50 m of water (Haight et al. 1993), but most of these records of occurrence at deep-sites are from the peak years of 1984–1987. Examination of the sightings of *P. spilosoma* made from research submarines working between 50 and 400 m depth in Hawai'i show that *P. spilosoma* does occur down to depths of 140 m or more, but all of the sightings of this species (22 dives) in waters deeper than 50 m are in the period from January 1985 to April of 1987, when they were also abundant in shallow water. Thirty-eight dives made at the same sites in the balance of the years of submarine operation (between 1981 and 1998) did not report any *P. spilosoma*, (unpublished Hawai'i Undersea Research Laboratory data). This suggests that when *P. spilosoma* becomes abundant in shallow water it also becomes abundant in deep water and that it is

not characteristically a deep-water benthic species. The failure of this species to persist for more than a year in shallow water on the Kane'ohe Bay reefs and at Kona (Hobson & Chess 1996), its apparent lack of permanent deep-water reef populations, and its generally low levels of abundance make it unclear how this species generates such high abundances over large areas in outbreak years.

This species apparently has an exceptionally lengthy pelagic juvenile stage (Hobson & Chess 1996) and belongs to an order (Tetraodontiformes) which apparently has a number of instances of recruitment to the benthos as juveniles (Leis & Carson-Ewart 2000). This pattern may be part of the answer to why this species has seasonally disappeared from reefs during the peak years and why it infrequently has years of high abundance. The pelagic juvenile stage may greatly extend the larval/pelagic phase of this fish's life. The pelagic juvenile stage may also favor early survival due to the presumably lower risk of predation in the pelagic environment (Leis & Carson-Ewart 1998). A long pelagic juvenile stage in *P. spilosoma* is consistent with the fact that the species is known to be able to feed on planktonic food (Hobson & Chess 1996) and could explain their virtual disappearance from the study reefs from December to May, the period when the species may exist as pelagic juveniles. Hobson & Chess (1996) reported that individuals of about 8 cm (in September) showed signs of developing gonads, and individuals reach a length of 12 cm by December (Figure 4B). *P. spilosoma* may be spawning between September and December, and the next 4–5 months may be spent in the pelagic environment. The maximum length of individuals of this species is evidently 18 cm (Randall 1996), but individuals of this length have not been seen at this study site. The presumably long pelagic life of this species may allow for wide dispersal and may result in their interaction with oceanographic features such as oceanic fronts or eddies (Olsen et al. 1994, Polovina et al. 2001). These features could make it less predictable whether the juveniles will settle and could concentrate the pelagic stage and thereby make settlements very large. Finally, the years of heavy juvenile recruitment may be followed by the operation of a strong density dependent factor, which could explain the poor survival (or

emigration) seen in this study and that of Hobson & Chess (1996).

The production of pelagic juveniles in reef fishes may be a characteristic of benthic species that occasionally show very heavy recruitment. Like the Tetradontiformes (Leis 1978, Leis & Moyer 1985, Randall 1996), priacanthids have also been reported to remain pelagic as juveniles (Caldwell 1962). There are no published reports that *Z. cornutus* has a pelagic juvenile stage, but it is reported that individuals of a congener metamorphose from post-larvae to juveniles at a length of 7 cm (Krupp 1995); and when individuals of this species first appear in the fish community in Kaneohe Bay they are approximately this length. In support of this generalization, Doherty (2002) observed an extremely heavy recruitment in Moorea by *Ctenochaetus striatus*, a species which is not known to have pelagic juveniles, but which belongs to the acanthurids which can have relatively large pelagic juveniles (Randall 1956, Krupp 1995, Leis & Carson Ewart 2000).

Relatively few studies of the abundance of tropical reef fish extend for more than about three or four years (Doherty & Fowler 1994b, Robertson & Kaufman 1998) or over a very broad geographic scale. As a result, we know little about how much variability there is temporally and spatially in recruitment and abundance, and what we do know is based on a small sample of reef fish species. The long-term record of the abundance of the endemic species *P. spilosoma* seems to show an unusual pattern through time, but there is relatively little data available for comparison on change in abundance through time in reef fishes. The pattern observed here may be a result of the existence of a pelagic juvenile stage. The broad geographical extent of this recruitment is evidently not unusual (Fowler et al. 1992), but again there are few records for comparison.

Acknowledgements

This study was made possible through access to the facilities of the Hawaii Institute of Marine Biology. I thank Bruce Mundy, Ed DeMartini and William J. Walsh for commenting on earlier versions of this manuscript. Boulderson Lau ably assisted in organizing the data for analysis.

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