

Abstract.— Research and commercial trapping data show variation in recruitment to the fishery for spiny lobster *Panulirus marginatus* at Maro Reef, relative to Necker Island which is 670 km to the southeast. Recruitment to the fishery at Maro Reef is shown to be highly correlated with the difference in sea level 4 years earlier between French Frigate Shoals and Midway Islands. Geosat altimeter data indicate that the relative sea level between French Frigate Shoals and Midway is an indicator of the strength of the Subtropical Counter Current. Mechanisms linking the Subtropical Counter Current with larval advection and survival are discussed. The sea level index provides a forecast of recruitment 4 years later to the fishery at Maro Reef.

Variability in spiny lobster *Panulirus marginatus* recruitment and sea level in the Northwestern Hawaiian Islands*

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Significant correlations between commercial landings or recruitment estimates and one or more environmental indices are commonly reported in the fisheries literature, but few have served as accurate predictors of future population levels (Drinkwater and Myers 1987). However, such correlations can lead to the formulation or support of hypotheses regarding the factors responsible for population changes. For example, an inverse correlation between the survival of Pacific mackerel *Scomber japonicus* to age 1 and the strength of the California Current, and the lack of correlation between survival and plankton biomass, have been offered as evidence that advection, rather than starvation, controlled survival of the planktonic stages of this species (Sinclair et al. 1985).

Correlative studies on lobsters suggest that population size results from changes in survival and advection at the larval stage, but in at least one

instance, density-dependent mechanisms after postsettlement may dampen this variation (Pollock 1986). Fluctuations in sea-surface temperature appear to result in changes in larval survival and catches 6 years later for the clawed lobster *Homarus americanus* in Maine (Fogarty 1988). Variation in the strength of the Leeuwin Current, which may be linked to El Niño Southern Oscillation (ENSO) events, is suggested as a cause of variation in the number of larvae returned to the coast and subsequent recruitment to the fishery for the western rock lobster *Panulirus argus* (Pearce and Phillips 1988). Changes in recruitment levels of the California spiny lobster *P. interruptus* to the northern portion of its habitat may be episodic, influenced by large-scale, interannual El Niño events (Pringle 1986). Variation in postlarval recruitment in the South African rock lobster *Jasus lalandii* is thought to arise from changes in the paths and velocities of extensive offshore currents, which eventually return larvae to the coast. However, density-dependent phenomena influ-

encing juvenile and adult stages may substantially dampen this variation and produce fairly stable recruitment to the fishery (Pollock 1986).

In the Northwestern Hawaiian Islands (NWHI), a substantial drop in catches and catch-per-unit-effort (CPUE) of spiny lobster *P. marginatus* Quoy and Gaimard 1825 was recently documented (Polovina 1991). This study examines whether these declines in catches and CPUE are due to overfishing or to oceanographic factors which impact spiny lobster population dynamics.

NWHI lobster fishery

The NWHI region is an isolated range of islands, islets,

banks, and reefs that extend 2775 km northwest from Nihoa Island to Kure Atoll (Fig. 1). In 1977 after research cruises documented a substantial lobster population in the NWHI, a commercial trap fishery was initiated. The fishery targeted two species: the endemic spiny lobster *P. marginatus* and the slipper lobster *Scyllarides squammosus* Mike-Edwards 1837. A fishery management plan implemented in 1983 mandated that vessels submit logbooks recording daily catch and number of traps set (effort); the plan also established a minimum harvest size for spiny lobster and prohibited the harvest of egg-bearing females. Subsequent amendments to this plan added a minimum legal size for slipper lobster and required that traps have escape vents. In 1990, low catches and CPUE prompted a 6-month closure of the fishery (May–November 1991).

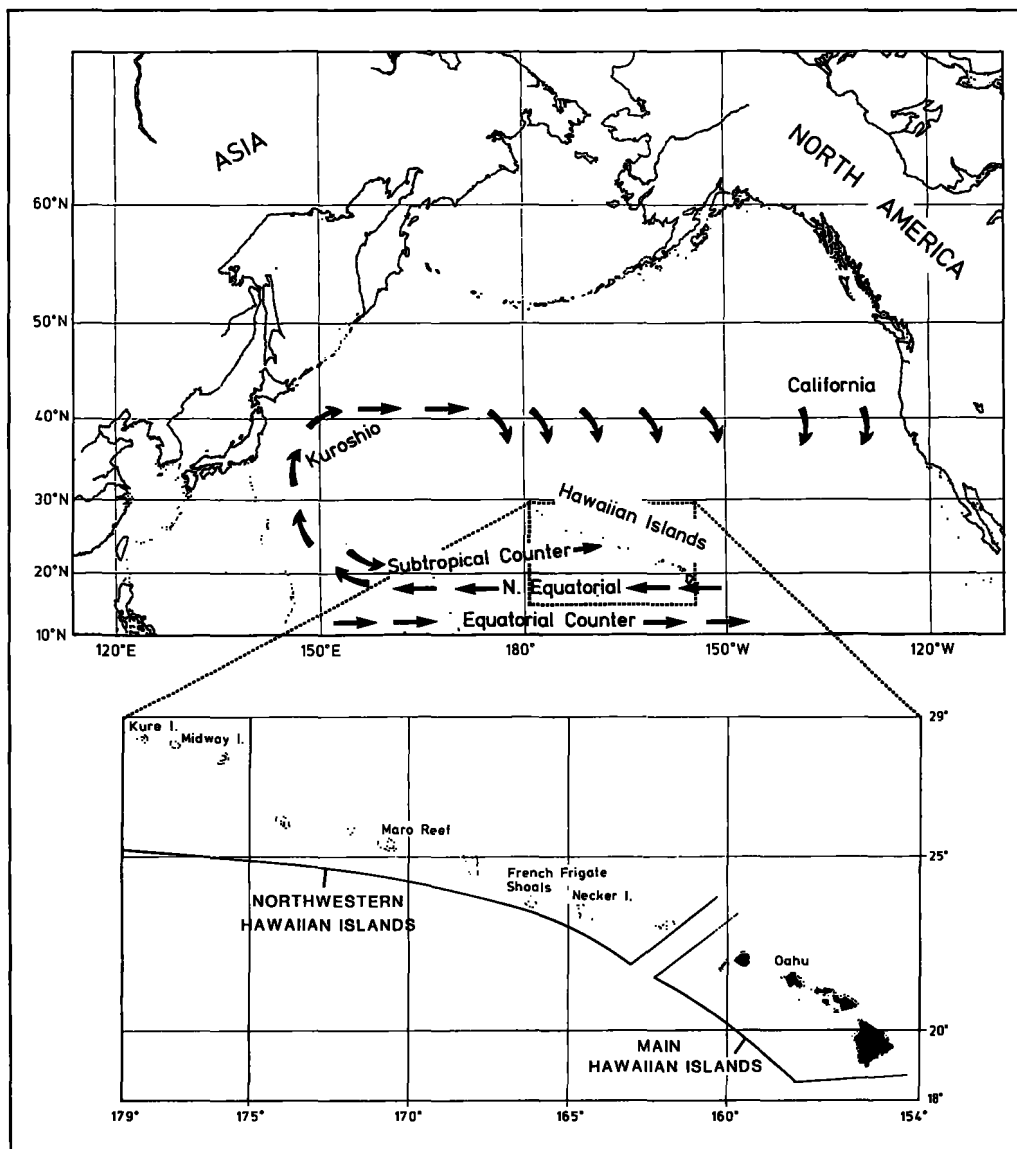


Figure 1
Pacific Ocean and major currents with an inset of the Hawaiian Archipelago, including the Northwestern Hawaiian Is.

Since 1983, the lobster fleet has been composed of 9–14 vessels (20–30 m long), each averaging 3 trips per year. The vessels set about 800 traps per day and remain at sea almost 2 months per trip. Landings in recent years have averaged almost 1 million lobsters, valued at about US\$6 million ex-vessel. Because of heavy fishing since 1986, the population has been fished down to the point that 3-year-old recruits comprised most of the fishery catches (Polovina 1991). Since 1988, about 80% of landings have been spiny lobster (Table 1). Two banks—Necker I. at the southeast end of the NWHI, and Maro Reef which is 670 km northwest of Necker I.—account for over 60% of the fishery's catches. There is no recreational lobster fishery in the NWHI.

Spiny lobster spawn over a broad spring, summer, and fall period. After hatching, the eggs are planktonic; the planktonic period for the larvae is estimated at 12 months based on spawning season and larval tow data (NMFS Honolulu Lab., unpubl. data). Further, the larval tow data suggest that mid- to late-stage spiny lobster larvae are close to the surface at night and move down to ~100 m during the day (Polovina, pers. observ.). Based on growth curves estimated from both tagging (MacDonald 1984) and length-based methods (Polovina and Moffitt 1989), spiny lobster reach the minimum legal size (which is slightly larger than the size at onset of sexual maturity) approximately 3 years after they settle onto benthic habitat. After settlement, the lobster probably do not move between banks since interbank depths exceed 1000 m.

Regional oceanography

The Hawaiian Archipelago lies within the subtropical gyre formed by the Kuroshio Current to the west and the north, the California Current to the east, and the North Equatorial Current to the south (Fig. 1). The speed of the gyre in the vicinity of the archipelago is slow (<5 cm/s; Roden 1991). An eastward-flowing current within the subtropical gyre, named the Subtropical Counter Current (SCC), was predicted by Yoshida and Kidokoro (1967) and subsequently confirmed by Robinson (1969) and Uda and Hasunuma (1969) (Fig. 1). More recent work has shown that, in at least the western portion, the interior of the subtropical gyre is composed

Table 1
Annual landings of spiny (*Panulirus marginatus*) and slipper (*Scyllarides squammosus*) lobsters, trapping effort, and percentage of spiny lobster in the landings, 1983–90.¹

Year	Lobster landings (10 ³)			Trap hauls (10 ³)	CPUE	% spiny lobster
	Spiny	Slipper	Total			
1983 ²	158	18	176	64	2.75	90
1984	677	207	884	371	2.38	78
1985	1022	900	1922	1041	1.83	53
1986	843	851	1694	1293	1.31	50
1987	393	352	745	806	0.92	53
1988	888	174	1062	840	1.26	84
1989	944	222	1166	1069	1.09	81
1990	591	187	778	1182	0.66	76

¹Data were provided to the NMFS Honolulu Lab., as required by the Crustacean Fishery Management Plan of the W. Pac. Reg. Fish. Manage. Council., Honolulu.

²April–December 1983.

of a quasi-stationary banded structure of easterly- and westerly-flowing currents (White and Hasunuma 1982). The SCC consists of two bands of eastward flow at 23° and 28°N, with mean annual speeds of 8 and 6 cm/s, respectively (White and Hasunuma 1982).

In addition to these large-scale features, the meso-scale oceanography around the Hawaiian Archipelago is a complex system of fronts and eddies resulting from both interactions between alternating east and west currents and interactions between current and the topography of the archipelago.

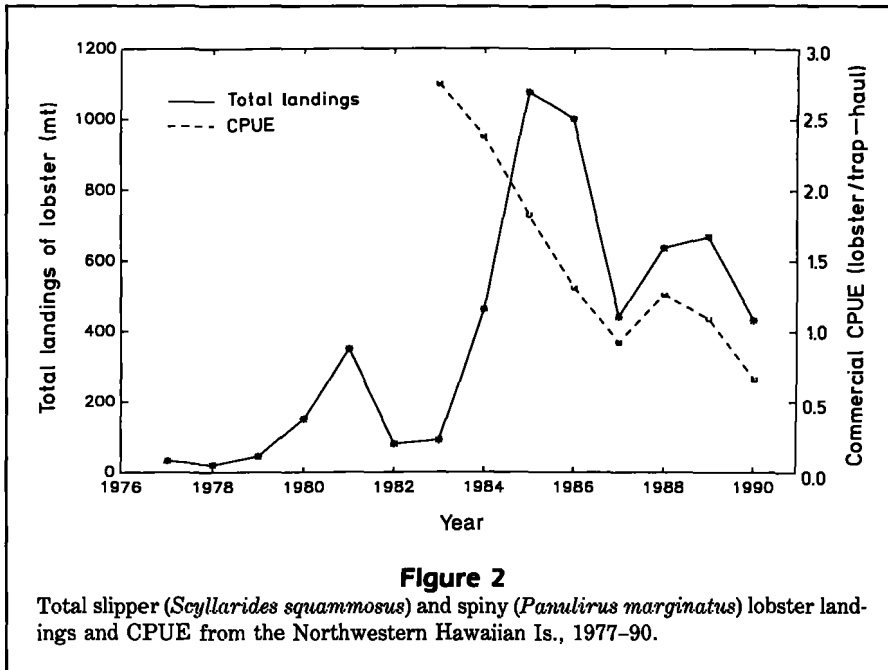
Data and analysis

Research data

Standardized trapping surveys, using the same traps set at the same sites, were conducted at Necker I. and Maro Reef during June and July of 1986–88 and 1990. The size-frequency data were converted to age-frequency data with a von Bertalanffy growth curve (MacDonald 1984). The age-frequency distribution was standardized for the number of traps deployed to estimate the relative age-frequency distribution of the population.

Fishery data

Although detailed catch and effort data were not available until after the logbook regulations were established in 1988, catch and effort were generally light and were concentrated around Necker I. from the inception of the fishery until 1984 (Fig. 2). The combined CPUE for slipper and spiny lobsters in 1983–90 generally declined from 2.8 to ~0.7 lobster per trap-



haul (Fig. 2), based on catch and effort data reported in the logbooks. Catch data in the logbooks are checked against landings by enforcement agents, so misreporting is not a problem. Common assessment approaches, such as length-based cohort analysis, are not applicable to this fishery, given the relatively short time-series of catch and effort data, the difficulty in routinely ageing lobsters, and the lack of information on the size-frequency from the landings and the nature of a stock-recruitment relationship. While a dynamic surplus production model has been applied to the data, an implicit assumption about the form of the stock recruitment relationship is required (Polovina 1991).

A more general approach is to begin with a model which expresses N_t as the number of exploitable lobsters at time t as a function of N_{t-1} , Z as the total instantaneous mortality from time $t-1$ to t , and r as the number which recruit and survive from $t-1$ to t as

$$N_t = r + N_{t-1} e^{-Z}$$

Using the relationship that the product of catchability (q) and $N_{(t)}$ is $CPUE_{(t)}$, this model becomes

$$CPUE_t = q * r + CPUE_{t-1} e^{-M-qr}$$

where M and f are annual instantaneous natural mortality and fishing effort, respectively, during the period $t-1$ to t . This CPUE model, a simple version of a size-structured model developed by Schnute et al. (1989), was used to estimate population parameters and to

evaluate the extent that fishing effort explains the observed variation in CPUE. This model assumes constant catchability and recruitment; hence, the differences between predicted and observed CPUE are interpreted as variation in recruitment, catchability, or both.

The commercial data do not indicate whether effort was directed at slipper or spiny lobster. However, the catches can be grouped into two periods based on the proportion of spiny to slipper lobsters. In period 1 (1983-84 and 1988-90), ~80% of the landings were spiny lobster; in period 2 (1985-87), ~56% of the landings were spiny lobster (Table 1). The change in proportion of spiny lobster catches is likely due to changes in targeting and abundance. The CPUE

model is modified so that a catchability coefficient can be estimated for each period. Our modified CPUE model regresses the CPUE of spiny lobster above the minimum size in month t ($CPUE_t$) on the CPUE of the same month in the previous year:

$$CPUE_t = R * Q_t e^{-\frac{(M+Q_t f_t)}{2}} + (CPUE_{t-12}) (e^{-M-Q_t f_t}) \left(\frac{Q_t}{Q_{t-12}} \right)$$

with

$$Q_t = q_1 I_{1,t} + q_2 I_{2,t}$$

where q_1 is the catchability of spiny lobster during period 1, q_2 is the catchability during period 2, M is the annual instantaneous natural mortality, R is the annual recruitment, f is the cumulative fishing effort during the period $(t-12, t-1)$, and $I_{i,t}$ ($i=1,2$) is the indicator or set function which takes the value 1 if t is within period i or otherwise takes the value 0. Estimates of R , q_1 , q_2 , and M were obtained by minimizing the sum of squares of the difference between the square root of the observed and predicted CPUE with a simplex algorithm.

Sea level data

To examine the relationship between lobster recruitment variation at Maro Reef and physical factors such

as variation in the SCC, we focused on the analysis of sea level data from the NWHI. Our choice of sea level was primarily a practical one. In comparison to current or upper-layer temperature records, the sea level records are of long duration, and the data are measured continuously and are available in nearly real-time. An additional advantage is that sea-surface height data from the Geosat satellite altimeter are available to provide a spatial description that complements the temporal description available from the sea level stations.

Data on the difference in sea level between the gauges at French Frigate Shoals (FFS) and at Midway Is. have been available since 1976 (Figs. 1,3). This sea level difference (denoted as FFS–Midway sea level) serves as an index of the geostrophic current anomalies across the NWHI in the region of Maro Reef. For example, an increase in the sea level height at FFS relative to Midway Is., measured from tide gauges, indicates the strengthening of a current that is across the gradient between the two locations and is flowing from the southwest to the northeast.

To interpret these flow anomalies as a manifestation of the variations in SCC strength, the spatial structure of the sea-surface height variation was examined by mapping the variability observed by the Geosat altimeter during November 1986–November 1988. These 2 years were selected because more accurate orbit estimates were available during this time-period and would result in more accurate sea-surface height fields. The Geosat geophysical data records were obtained from NOAA (Cheney et al. 1987) and were processed with software developed at the University of Hawaii.

Averages of the Geosat data over November 1986–November 1987 were subtracted from the averages over November 1987–November 1988. Before using the Geosat data, we checked that the resulting sea level differences from the altimeter were consistent with the corresponding sea level differences from tide gauges at FFS and Midway (not shown). Choosing these time-periods also allowed us to contrast conditions during the ENSO period of 1986–87, when the FFS–Midway sea level was low (~ 520 mm), with conditions during the normal period of 1987–88, when the FFS–Midway sea level was higher (~ 600 mm).

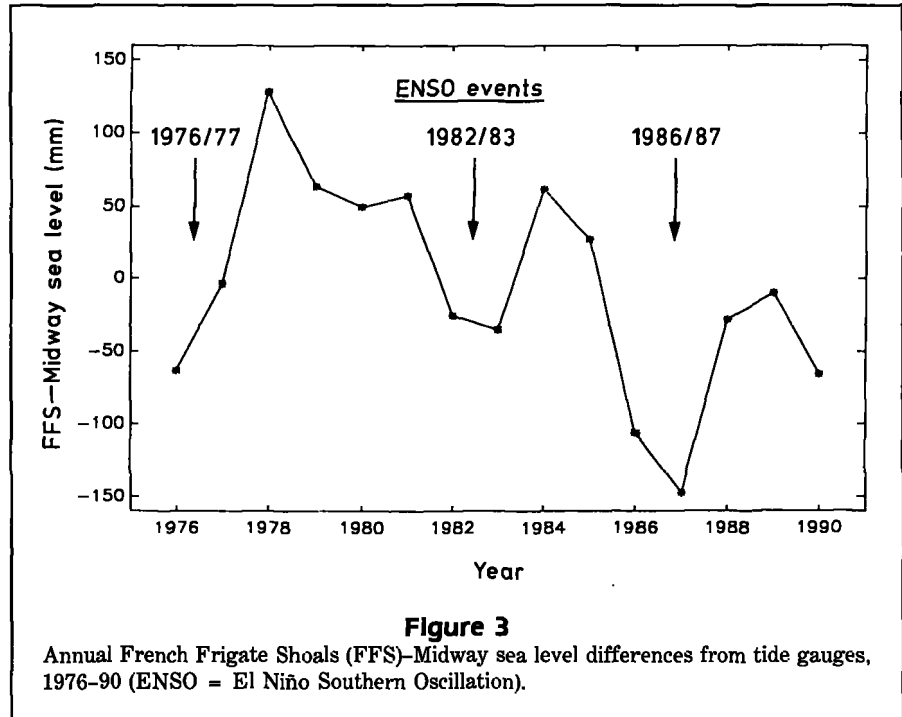


Figure 3
Annual French Frigate Shoals (FFS)–Midway sea level differences from tide gauges, 1976–90 (ENSO = El Niño Southern Oscillation).

Puerulus settlement

During the last planktonic stage (i.e., postlarval or puerulus stage), spiny lobster acquire the benthic morphological features of adults and become active swimmers seeking benthic habitat. MacDonald (1986) studied puerulus settlement in the Hawaiian Archipelago with traps known as Witham Collectors at Kure Atoll (north of Midway Is.) in 1979–83 and at FFS in 1981–85. He computed mean catch per collector over 12-month periods (June–May) at Kure Atoll and FFS. These data will be compared with the FFS–Midway sea level data.

Results

The fit of the model to the commercial CPUE data and the resulting residuals indicate the model fits the trend in CPUE, but considerable unexplained variation exists in CPUE within and between years (Fig. 4). For example, given the fishing effort, CPUE was greater than expected in 1988 but declined more than expected in 1990. Since the model assumes both constant recruitment and constant catchability, the residuals may reflect variation in these factors. From the fit of the model, $R = 1.2 \times 10^6$ adult lobsters/yr, $M = 0.71$ /yr, $q_1 = 1.2 \times 10^{-6}$, and $q_2 = 0.6 \times 10^{-6}$. Thus 1.2 million lobsters recruit to the fishery annually; with an M of 0.71/yr, only 50% of the 3-year-olds survive 1 year (in

the absence of fishing). Further, a CPUE of 1.2 spiny lobster/trap-haul means the exploitable population is 1 million spiny lobster. An independent estimate of M

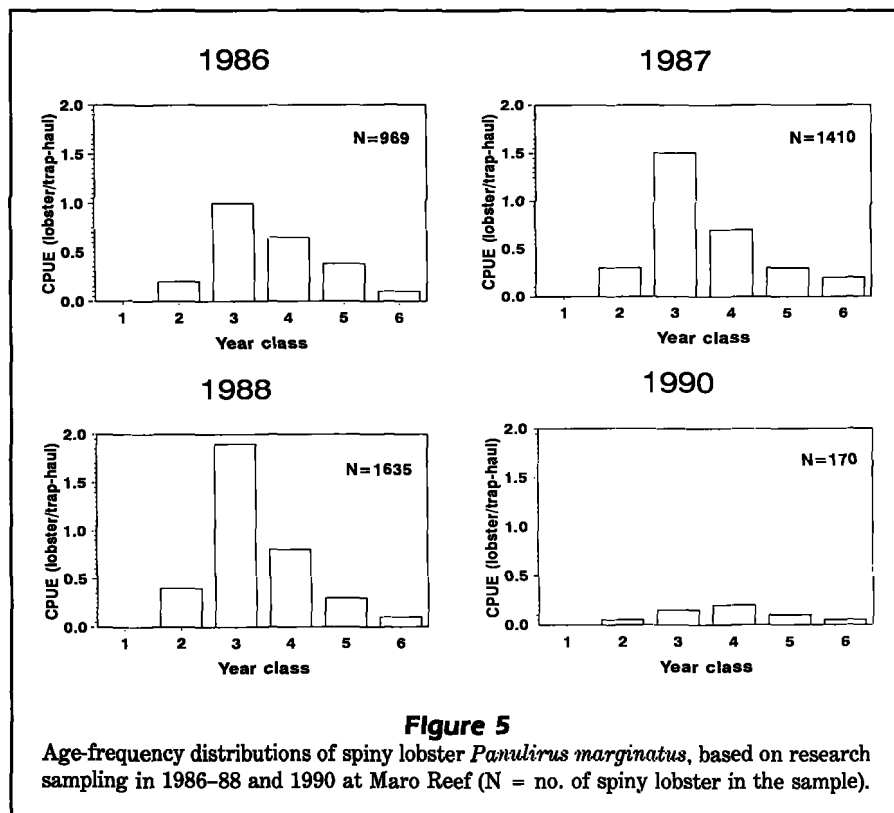
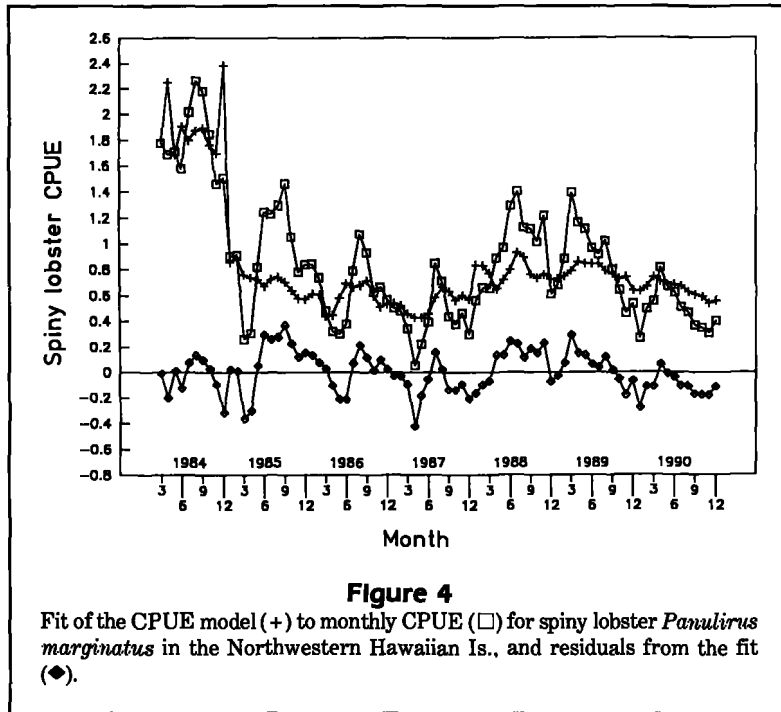
from tagging at FFS is 0.5/yr (MacDonald 1984).

Commercial trapping effort since 1985 has averaged about 1 million trap-hauls (Table 1); using the q_1 estimate as catchability, annual fishing mortality (F) is estimated as 1.2/yr or $1.7 \times M$. With these figures and the estimates of growth and age at onset of sexual maturity, the Beverton-Holt yield equation estimates the spawning-stock biomass per recruit, when effort is 1 million trap-hauls, is 40% of what it would be in the absence of fishing (Polovina 1991). Thus, the ratio of F to M and the relative spawning-stock biomass calculations suggest that the spawning biomass in 1985–86 was not fished down to a level that would cause the poor recruitment to the fishery 4 years later (1989–90).

Much of the variation in residuals from the CPUE model is due to variation in recruitment at Maro Reef. For example, for the entire NWHI in 1990, trapping effort increased 11% from the previous year while the catch declined 33%, resulting in a 39% decline in CPUE. However, the decline in CPUE was most striking at Maro Reef, where CPUE declined 42% even though effort decreased by 37%. At Necker I., CPUE also declined (40%) but effort increased 35%.

The estimated age-frequency distributions based on research cruises at Maro Reef show a strong 3-year-old class in 1988 and a striking absence of all age-classes in 1990 (Fig. 5). This is consistent with the hypothesis that recruitment of the 3-year-olds to the fishery was weak in 1990 and subsequent fishing reduced all older age-classes. Necker I. had many more 2-year-olds in the samples since some trapping sites include nursery habitat; but between years, the abundance of 2-year-olds was relatively constant, whereas older lobsters declined in 1990, likely because of the increase in fishing effort (Fig. 6).

The NWHI lobster fleet is very mobile and shifts its trapping locations according to abundance of lobsters. By 1985, both Maro



Reef and Necker I. had gone through a period of fishing down the pre-exploitation population; the relative change in catches between the two banks may reflect changes in their relative recruitment. Since both banks are not always fished each month, we pooled the catches by quarter. A 3-quarter moving average of the ratio of quarterly catches at Maro Reef to the combined quarterly catches at Necker I. and Maro Reef shows considerable variation (Fig. 7). For example, catches from Maro in 1985 and 1988 represented almost 80% of the catches from the two banks, but in 1990 they represented less than 20%. A 3-quarter moving average of the residuals from the CPUE model shows the same trend as the ratio of catches from Maro Reef relative to Necker I. and Maro Reef combined (Fig. 7). This suggests that the variation in recruitment, catchability, or both at Maro Reef is responsible for most of the variation not explained by fishing effort observed for the entire NWHI.

height of the sea level ridge stretching across the Pacific. The height and location of this sea level ridge

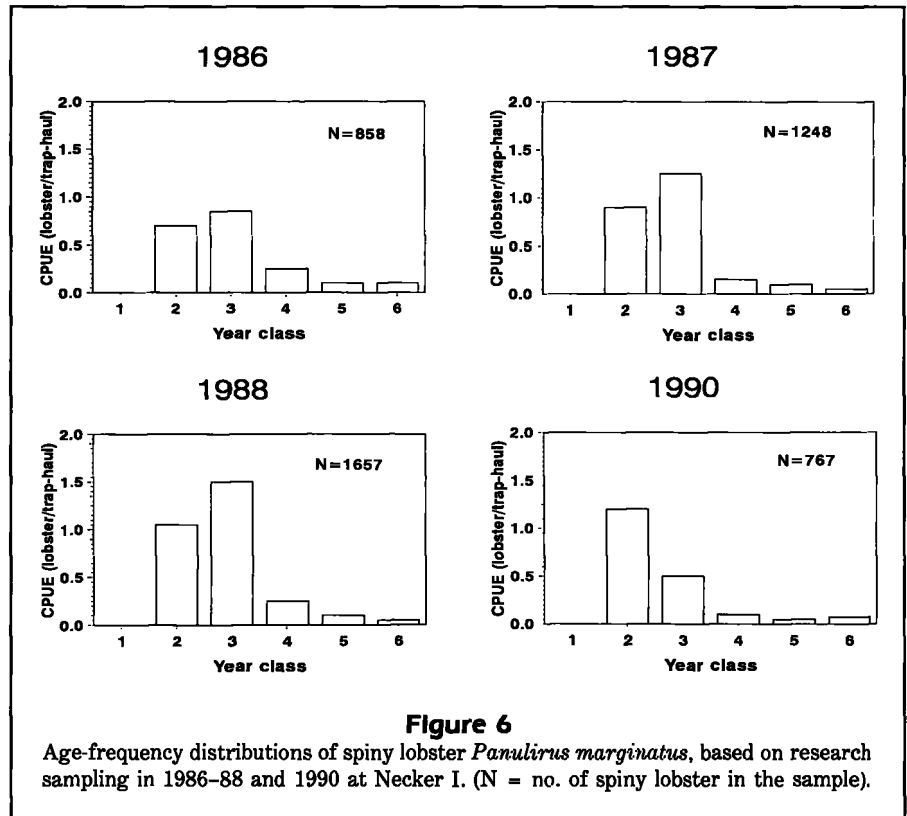


Figure 6
Age-frequency distributions of spiny lobster *Panulirus marginatus*, based on research sampling in 1986–88 and 1990 at Necker I. (N = no. of spiny lobster in the sample).

Variation between sea level and the SCC

Differences in sea level over the Pacific, between a year when the FFS–Midway sea level was high and a year when it was low, appear as a ridge of positive values, extending from southwest to northeast, that parallels a trough of negative values to the northwest (Fig. 8). Midway lies in the trough, Honolulu is on the ridge, and FFS lies on the gradient, which corresponds to the region of the most energetic geostrophic flow anomalies. This ridge and trough indicate that the change in the FFS–Midway sea level from low to high reflects the increase in a ridge extending across the western Pacific. The increase in the ridge and trough pattern represents an increase in the current flow along the gradient of this ridge. The path of this gradient or flow across the Pacific is consistent with the general path of the SCC. Thus FFS–Midway sea level measures a large-scale oceanographic feature which is represented by the

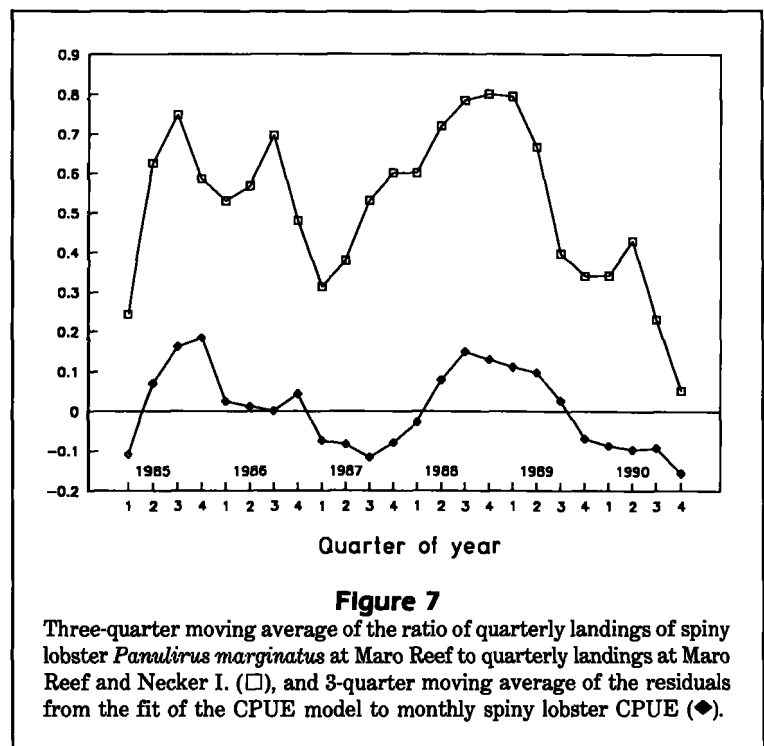


Figure 7
Three-quarter moving average of the ratio of quarterly landings of spiny lobster *Panulirus marginatus* at Maro Reef to quarterly landings at Maro Reef and Necker I. (□), and 3-quarter moving average of the residuals from the fit of the CPUE model to monthly spiny lobster CPUE (◆).

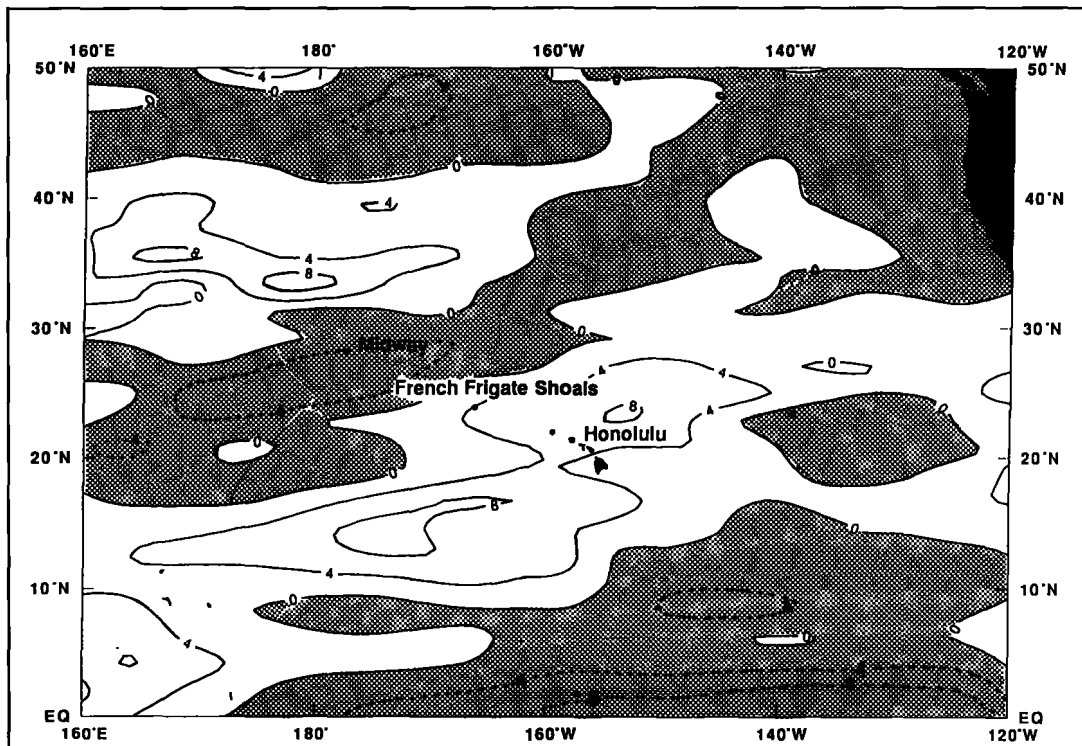


Figure 8

Differences between mean sea level during a non-ENSO (El Niño Southern Oscillation) period (Nov. 1987–Sept. 1988) and an ENSO period (Nov. 1986–Sept. 1987) from Geosat data. Negative values denoted by shaded areas.

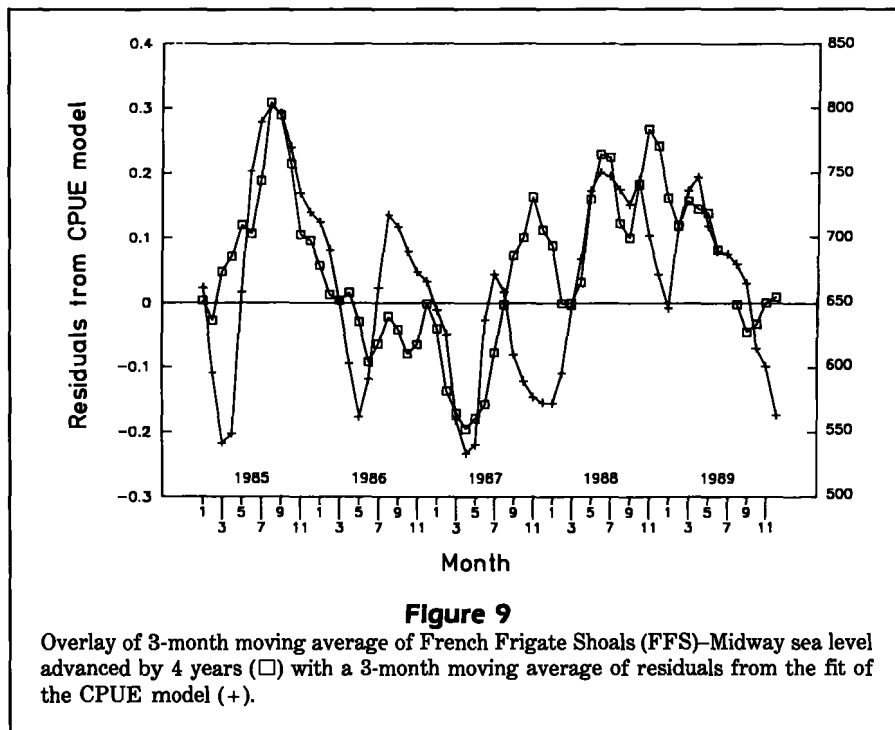


Figure 9

Overlay of 3-month moving average of French Frigate Shoals (FFS)–Midway sea level advanced by 4 years (□) with a 3-month moving average of residuals from the fit of the CPUE model (+).

correspond to the SCC strength and position, respectively.

Relationship between sea level and lobster abundance

Lagged cross-correlations between FFS–Midway sea level and the variables (i.e., the ratio of catches at Maro Reef to the combined catches at Maro Reef and Necker I., and the residuals from the CPUE model) have their strongest correlations (r 0.82 and 0.68, respectively) with sea level lagged by exactly 4 years. When sea level is lagged by 4 years and overlaid with these time-series, there is good agreement (Figs. 9, 10). Based on research samples pooled over 1986–88, the mean estimated age of lobsters caught by the fishery is 3.8 years (after settlement).

Based on the comparison of FFS–Midway sea level with the available puerulus settlement data from MacDonald (1986) in the same year, the FFS–Midway sea level correlates positively with mean puerulus catches at Kure Atoll (r 0.78, P 0.11) and shows no significant correlation with mean puerulus catches at FFS (r -0.37, $P > 0.25$) (Fig. 11).

ment differs between Necker I. and Maro Reef. At Maro Reef, large-scale oceanographic features appear to control the abundance of late-stage larvae, which in turn results in interannual variation in recruitment to the fishery.

Discussion

The research and commercial catch and effort data presented here show that the recruitment of 3-year-old spiny lobster to the fishery has varied considerably at Maro Reef but has remained stable at Necker I., 670 km to the southeast. Fishing effort is not considered sufficiently heavy to explain a decline in recruitment, especially a decline at one bank and not the other. The relationship between recruitment to the fishery at Maro Reef and the FFS–Midway sea level advanced by 4 years suggests that environmental factors impacting the larval stage are responsible for the recruitment variation. The Geosat data suggest that the FFS–Midway sea level measures the SCC. Hence the SCC strength or location dictates recruitment strength to the fishery 4 years later. Consistent with this hypothesis is the mean age of lobsters in the commercial catches as well as the correlation between puerulus settlement at Kure Atoll and FFS–Midway sea level. The lack of correlation between puerulus settlement at FFS and sea level is consistent with the observation that recruitment at the lower end of the NWHI is not linked to the same pattern of variation as Maro Reef. Annual variation in both SCC strength and position has been observed in the western Pacific (White and Hasunuma 1982). In summary, the temporal pattern of spiny lobster recruit-

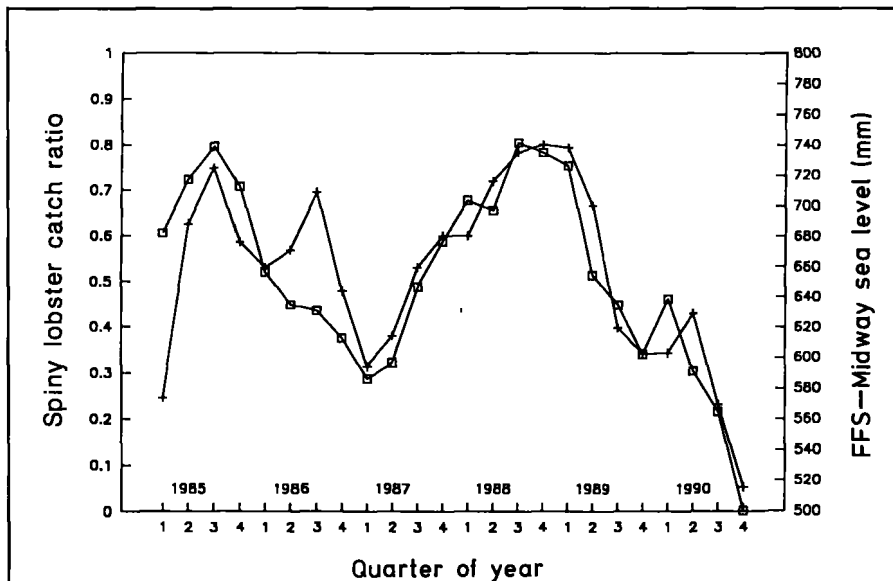


Figure 10
Overlay of 3-quarter moving average of French Frigate Shoals (FFS)–Midway sea level advanced by 4 years (□), with a 3-quarter moving average of the ratio of Maro Reef to Maro Reef plus Necker I., spiny lobster landings (+).

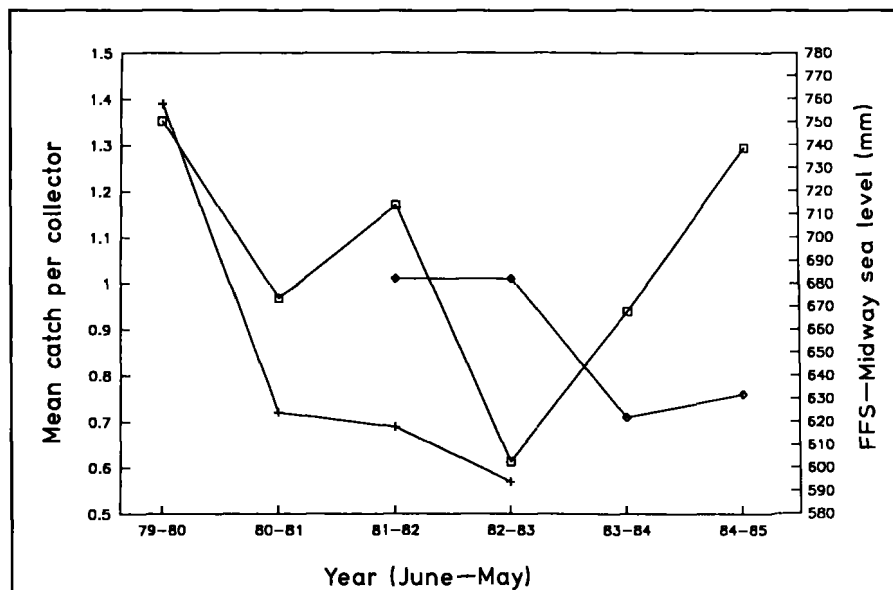


Figure 11
Mean annual puerulus settlement from traps at Kure Atoll (+) and French Frigate Shoals (FFS) (◇) and FFS–Midway sea level (□), all computed on a June–May year.

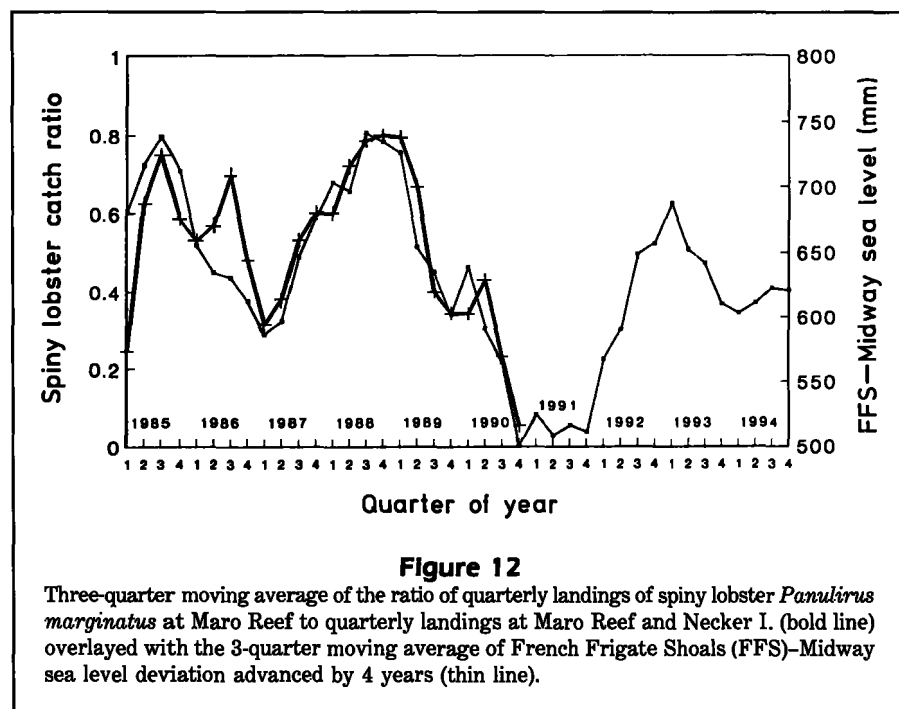
The underlying mechanism linking the correlation between the SCC and subsequent recruitment at Maro Reef is not known. It is possible that the SCC returns larvae, which have been advected west of the archipelago, back to Maro Reef. The SCC has been hypothesized to transport *Acropora* coral from Johnston Atoll (lat. 16°45'N., long. 169°31'W) to FFS (Grigg 1982). In addition, larvae of a spiny lobster species not recorded as an adult in Hawaii have been transported from the Marshall Is. to the Hawaiian Archipelago (Phillips and McWilliam 1989).

However, it may be that the SCC impacts not advection but larval survival. Laboratory studies have shown that spiny lobster larvae suffer a high level of mortality when water temperatures drop below 20°C (T. Kazama, NMFS Honolulu Lab., pers. commun., Sept. 1991). In the years we estimated that the SCC was weak, water temperatures <20°C in the winter have been observed at Maro Reef but not Necker I. If little larval mixing occurs between Maro Reef and Necker I., larval mortality at Maro Reef resulting from low winter temperatures could account for the observed recruitment variation.

A third hypothesis is that when the SCC has a particular speed and location, it produces fronts which retain larvae near Maro Reef. When the SCC is weak or shifts, these fronts are not formed near Maro Reef. Preliminary evidence from the drifter buoys and larval sampling in our study suggests fronts north of Maro Reef and south of Necker I. may be important for lobster larvae (Polovina, pers. observ.)

One potential management application of the lagged relationship between FFS–Midway sea level and recruitment is that it provides up to a 4-year forecast of recruitment to the fishery at Maro Reef. A 3-quarter moving average of the FFS–Midway sea level shifted forward by 4 years forecasts poor recruitment in 1991, followed by an improvement beginning in late 1992 (Fig. 12). During January–May 1991 before the fishery was closed for 6 months, recruitment at Maro Reef clearly had not recovered, as only 1052 spiny lobster were harvested from Maro Reef while 34,746 spiny lobster were harvested from Necker I. Recall that the relative catches between banks provide an index of relative abundance, since the fleet moves to maximize the CPUE. The FFS–Midway sea level data forecast that catches at Maro Reef will improve beginning in late 1992 (Fig. 12). Data from larval tows are consistent with this forecast. Standardized larval tows, taken in June and November 1989 over a grid of stations from the 200 m isobath out to 56 km around both Necker I. and Maro Reef, caught 3802 and 3342 late-stage phyllosomes, respectively (J. Polovina, unpubl. data). A *t*-test, based on a lognormal distribution, finds no significant difference in the mean abundance of larvae between Maro Reef and Necker I. If we assume that larval abundance was high around Necker I. in 1989, then good larval recruitment apparently has returned to Maro Reef. This is consistent with the observed higher sea-level values in 1989 (shown as 1993 values in Fig. 12, since the sea level has been advanced by 4 years) and suggests that catches will be high at Maro Reef in 1993.

The FFS–Midway sea level time-series from 1976 to 1990 (Fig. 3) shows that ENSO events may result in poor recruitment to the fishery 4 years later, but the series also shows a long-term decline. Reasons for the low FFS–Midway sea level during ENSO events are not known, but may be related to a decrease in surface water supplied to the SCC in the western Pacific. Such a change could be associated with the circulation disruptions observed in the tropical Pacific during ENSO events (Meyers and Donguy 1984). The long-term decline in sea level from 1976 to 1990 suggests there is a low-frequency component in the variation in SCC strength and, hence, lobster recruitment. Thus, it may be some time before recruitment to the fishery is at the early 1980s' level.



Acknowledgments

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