A TIME SERIES OF CALIFORNIA SPINY LOBSTER (*PANULIRUS INTERRUPTUS*) PHYLLOSOMA FROM 1951 TO 2008 LINKS ABUNDANCE TO WARM OCEANOGRAPHIC CONDITIONS IN SOUTHERN CALIFORNIA

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ABSTRACT

The California spiny lobster (*Panulirus interruptus*) population is the basis for a valuable commercial and recreational fishery off southern California, yet little is known about its population dynamics. Studies based on CalCOFI sampling in the 1950s indicated that the abundance of phyllosoma larvae may be sensitive to oceanographic conditions such as El Niño events. To further study the potential influence of environmental variability and the fishery on lobster productivity, we developed a 60-year time series of the abundance of lobster phyllosoma from the historical CalCOFI sample collection. Phyllosoma were removed from the midsummer cruises when the early-stage larvae are most abundant in the plankton nearshore. We found that the abundance of the early-stage phyllosoma displayed considerable interannual variability but was significantly positively correlated with El Niño events, mean sea-surface temperature, and the Pacific Decadal Oscillation, which are significantly intercorrelated. Conditions during the warm years (1950s and 1980–present) were the most productive for lobster phyllosoma in the Southern California Bight. Total lobster fishery landings show an increasing trend since 1980 due to increasing commercial landings from 1980–2000 and increased recreational landings since 2005. However, this trend is not observed in the phyllosoma time series or in the Baja California fishery, whose landings are correlated with the U.S. fishery. We suggest that the stage 1 phyllosoma may provide a useful fishery-independent index of spiny lobster spawning stock biomass and stock productivity. Due to the relationship identified here between environmental conditions and phyllosoma abundance, we suggest that this information could be used as an environmental indicator for management.

INTRODUCTION

The California spiny lobster (*Panulirus interruptus*) has been fished commercially off southern California since the late 1800s. Commercial landings peaked around 1949–55, declined in the period 1955–75, and subsequently increased, following the requirement in 1976 that commercial lobster traps be fitted with escape ports to reduce the proportion of "shorts" in the landings (fig. 1) (Neilson 2011). Since 2000, the commercial fishery has landed approximately 300 mt annually, with 319 mt landed in 2010 for an ex-vessel price of $11.13 million. While the commercial landings have been stable since 2000, recreational landings have increased considerably due to the growing popularity of hoopnet fishing, particularly since 2005. The recreational fishery now accounts for 30%–60% of the commercial fishery (fig. 1). However, the fishery was considered sustainable in a recent stock assessment (Neilson 2011), and no regulatory change is currently proposed for California.

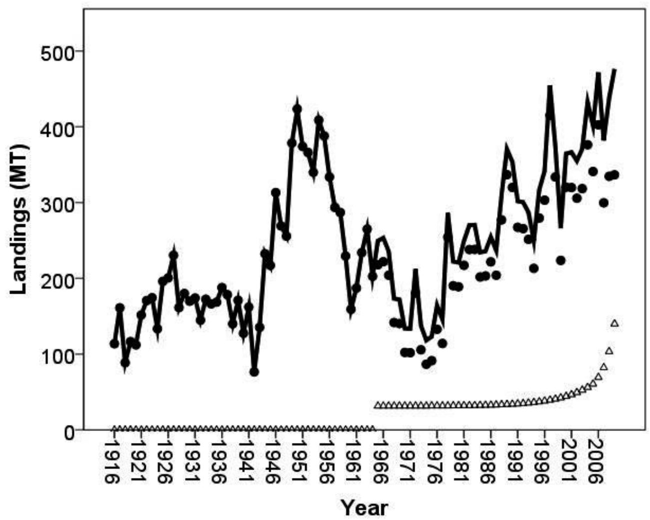

Figure 1. Commercial (solid circles), recreational (open triangles), and total landings (solid line) of spiny lobster off southern California.

Early life-history stages of marine organisms can serve as an indicator of the abundance and productivity of the adult spawning stock (Hsieh et al. 2005). Egg and larval surveys in California Cooperative Oceanic Fisheries Investigations (CalCOFI) are routinely used as indicators of spawning stock biomass for fisheries management (Moser et al. 2001; Lo et al. 2005). We suggest that the early stage phyllosoma may also be suitable as an index for the spawning biomass of spiny lobster: having been in the plankton relatively briefly, their abundance has not been greatly influenced by natural mortality. Because there are no other fishery-independent measures for the

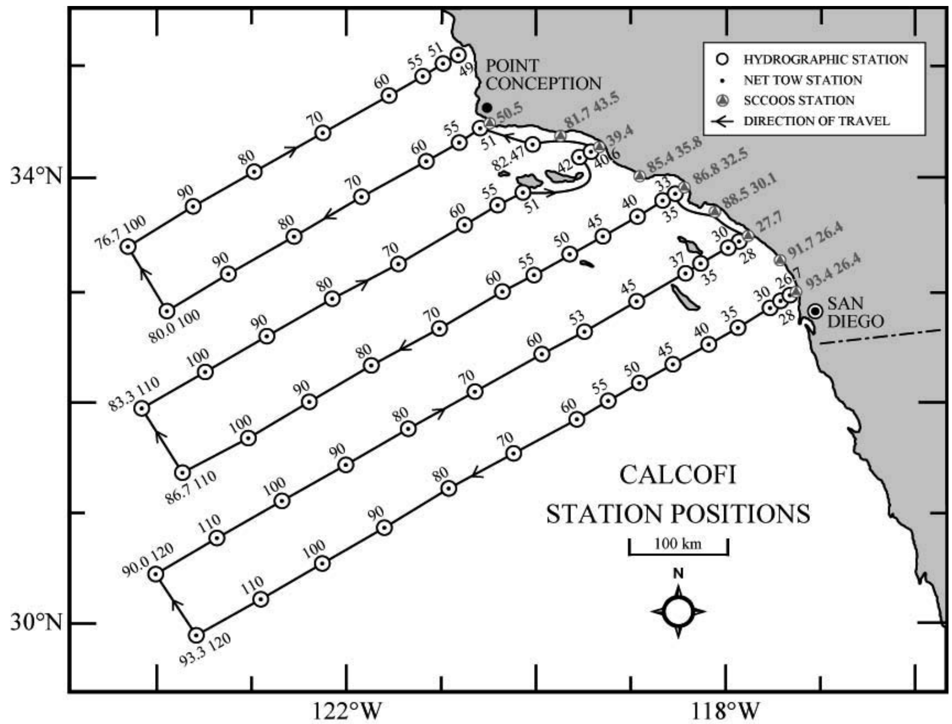

Figure 2. The core CalCOFI sampling area with six transects from the U.S./Mexico border to north of Point Conception. Only stations 60 and inshore were used in the present study because of the coastal distribution of the early-stage phyllosoma.

state of the spiny lobster population, we developed a time series of early-stage lobster from the CalCOFI sampling program, which can potentially provide further input to management of this resource. A phyllosoma time series can also be examined in relation to oceanographic parameters to determine if climate variability has a significant impact on the abundance of larval or adult lobster. Biological indices of ocean condition have provided input to management models for sardine and sablefish fisheries in the California Current (Jacobson and MacCall 1995; King et al. 2001).

The spawning and early life history of the California spiny lobster was examined in the early 1950s using CalCOFI samples (Johnson 1956, 1960a, 1960b). At that time, CalCOFI sampling extended over most of the coast of California, including Baja California (Mexico) and thus encompassed the population's distribution, which extends from Point Conception to Magdalena Bay in Baja California and is centered off central Baja (Johnson 1960a). Spawning occurs in late summer and early autumn, with peak numbers of the early-stage phyllosoma found from July to October. Remarkably, the phyllosoma drift offshore and remain in the plankton for 7–10 months until the following spring, when they metamorphose into the swimming puerulus stage, return to shore, and settle on the bottom as benthic juvenile lobsters (Johnson 1956, 1960b). Pringle 1986 re-examined the CalCOFI time series and showed that the phyllosoma abundance off southern California appeared to be enhanced during El Niño events, when there is increased northerly transport of the Davidson Current from Baja California. The lobster mature at 65–69 mm carapace length at about 5–9 years of age and recruit to the fishery at 82.6 mm, about two years later. Most recruits are removed by the fishery each year.

Our objectives are to utilize the CalCOFI sampling to 1) develop a 60-year time series of phyllosoma and 2) examine potential impacts of ocean conditions and the fishery on phyllosoma abundance.

METHODS

The CalCOFI program has consistently sampled the zooplankton, including invertebrate and fish larvae, over a core area from the U.S./Mexico border to north of Point Conception since 1951, with monthly to quarterly sampling from nearshore to several hundred kilometers offshore (fig. 2). At each station, the physical and chemical properties of the water column to 500 m depth are sampled, and at least one oblique zooplankton tow is undertaken: prior to 1969 to 140 m and subsequently to about 210 m depth. Details of the sampling protocol are found in Kramer et al. 1972 and Ohman and Smith 1995, including the change from a 1-m ring net to the 0.71 m diameter bongo net in 1977. All fish eggs and fish larvae are routinely removed from all zooplankton samples. However, until recently, invertebrate larvae,

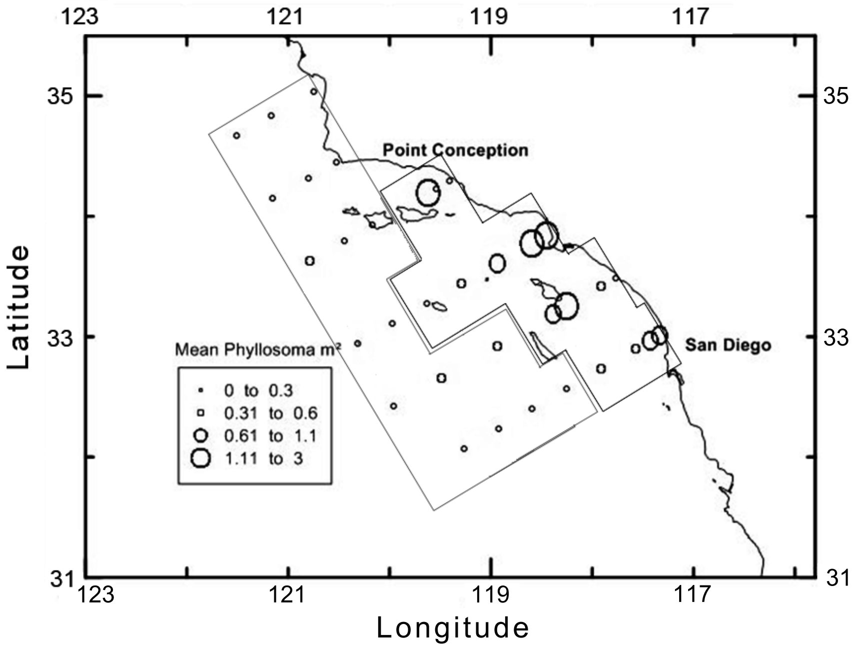

Figure 3. The CalCOFI sampling grid showing the mean abundance of phyllosoma at each station (1951–2008) and the division of the sampling area into high-abundance and low-abundance strata inshore and offshore.

including those of the spiny lobster, were only removed if undertaken by a particular investigator. Spiny lobster phyllosoma larvae are highly distinctive but also a rare component of the plankton. To re-sort all the CalCOFI samples would have been a laborious task. However, Dr. Johnson sorted the samples for the period 1951–57 and 1970–81, and the data were retrieved from the Scripps Library Archive. Since 2008, the CalCOFI program and National Marine Fisheries Service routinely sort for phyllosoma. The early-stage phyllosoma were only found in sufficiently high numbers in July/August, so we focused on the summer CalCOFI cruises from 1958–69 and 1982–2008. Phyllosoma were only rarely obtained seaward of station 60, so we only examined stations on the six core transects (lines 76 to 93) from inshore to station 60 (fig. 2). All samples were sorted under a binocular microscope, and the phyllosoma were staged using the criteria in Johnson 1956. The data are available from the CalCOFI DataZoo data repository: http://oceaninformatics.ucsd.edu/datazoo/data/calcofisio/datasets?action=summary&id=188.

Because of minor changes in station locations over the period of the CalCOFI program, the area was divided into low-abundance offshore and high-abundance coastal strata (fig. 3). Annual mean abundance was first estimated for each stratum and then summed. For statistical analyses, the phyllosoma abundance data were square-root transformed to achieve an approximately normal distribution. Statistical analyses were carried out using standard statistical routines in SPSS®.

We examined relationships between annual mean phyllosoma abundance and environmental variables sampled on CalCOFI cruises and indices for several large-scale environmental features. Sea-surface temperature (SST) was based on the mean annual temperature measured at 10 m from CalCOFI cruises. The Multivariate ENSO (El Niño Southern Oscillation) Index (MEI) (Wolter and Timlin 1998) was obtained from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory MEI Web page: http://www.esrl.noaa.gov/psd/enso/mei; the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) from the University of Washington: http://jisao.washington.edu/pdo/PDO.latest; the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008) from the website of E. Di Lorenzo: http://www.o3d.org/npgo/data/NPGO.txt; and upwelling was based on offshore Ekman transport at 33°N and 119°W (Pacific Fisheries Environmental Laboratory: http://las.pfeg.noaa.gov/las6_5/servlets/dataset).

Commercial lobster landings data from the California Department of Fish and Game (DFG) were obtained from the California Fisheries Information System (CFIS). Landings are recorded by fishers on landing receipts which are input into the CFIS as pounds per landing by DFG block (10 × 10 min blocks). Landings were combined for each year and converted to metric tonnes.

The time series of recreational landings was based on a reconstruction for the years 1965 to the present

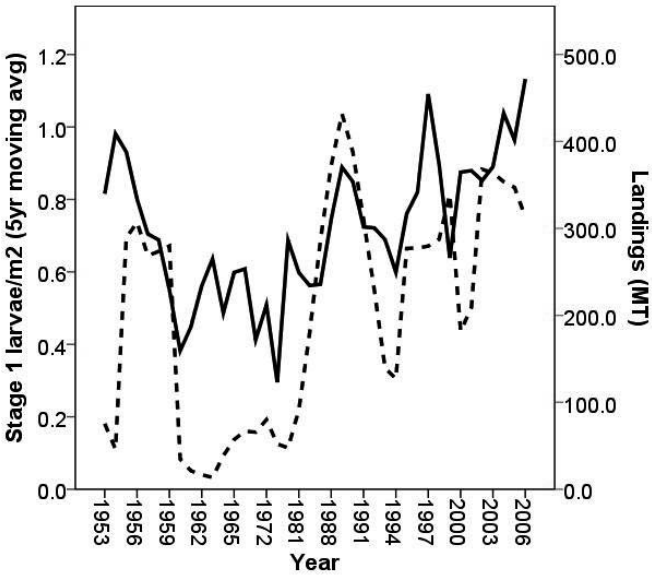

Figure 4. Time series for the abundance of stage 1 phyllosoma of the California spiny lobster (dashed line) and of combined commercial and recreational spiny lobster landings (solid line) off southern California. There is a significant increasing trend in the total landings of lobster since 1981 but not of phyllosoma.

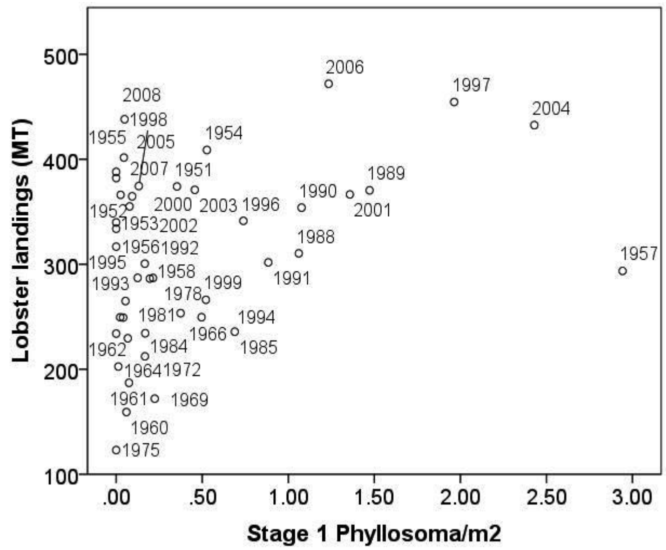

Figure 5. A scatterplot of phyllosoma stage 1 abundance per m^2 and total lobster landings (in metric tonnes).

adopted in the recent stock assessment (Neilson 2011). This reconstruction is based on DFG creel surveys in 1992 and 2007, hoopnet marketing observations for the past decade, spiny lobster report card data from 2008 to the present, and the observation from report card data that the recreational fishery is comprised of separate hoopnet and diving fisheries. Hoopnetting became popular in about 2005 with the majority of the recreational catch prior to that made by diving. Recreational lobster fishing is assumed to have begun in 1965 with constant dive-based catches and gradually increasing hoopnet catches to the value observed in 1992. The interpolation of recreational catch to 2005 again assumes constant dive-based catch but an exponential increase in hoopnet catch to 2005. The rate of exponential increase in hoopnet catch since 2005 was estimated by fitting an exponential relationship from 2005 to the levels observed in the 2008 report cards returns, passing through the levels observed during the 2007 creed survey. Since 2008, the catch has been determined from report card data. This reconstruction assumes that dive catches remained relatively stable over time and that the increase in catch since 2005 was the result of the popularization of fishing with hoopnets.

RESULTS

The phyllosoma stage 1 time series from 1951–2008 is highly variable, but like the landings is characterized by relatively high abundance in the 1950s and from about 1980 to the present, with a period of low abundance in the 1960s and 1970s (fig. 4). There is a significant positive correlation between the two time series ($r = 0.35$, $p < 0.05$). However, the landings time series exhibits a significant positive trend since 1981 ($r = 0.53$, $p < 0.01$), which is not reflected in the stage 1 phyllosoma time series. Examination of the scatterplot between these variables indicates that most years since 2000 appear in the upper left quadrant, indicating relatively high catch relative to the abundance of stage 1 phyllosoma (fig. 5). The plot seems to indicate generally little relationship between landings and phyllosoma abundance at low levels of phyllosoma abundance, but a reasonably linear relationship at moderate to high levels of phyllosoma abundance (≥1 stage-1 phyllosoma m^{-2}), with only one outlier at the far right side of the plot, the 1957 El Niño year, when phyllosoma abundance was very high and landings were only moderate.

We examined the potential stock-recruitment relationship for spiny lobster and whether phyllosoma abundance might be used to predict recruitment to the fishery, using the abundance of stage 1 phyllosoma as an index of spawning stock size. Spiny lobsters are generally caught within a year or two of recruitment to the fishery (Neilson 2011), but the age of maturity and age of recruitment to the fishery are not precisely known. Estimates for the age of maturity range from 3 to 9 years, with 5 years adopted in recent assessments (Serfling and Ford 1975; Engle 1979; Chavez and Gorostieta 2010; Neilson 2011). The age of recruitment to the California fishery is estimated to be approximately 7 years (Neilson 2011). Landings to the California fishery were significantly correlated with the abundance of stage 1 phyllosoma at lags of 7 and 8 years ($r = 0.39$ and $r = 0.37$, respectively, $p < 0.05$) (fig. 6), but not at other lags. A potential stock-recruitment relationship was plotted

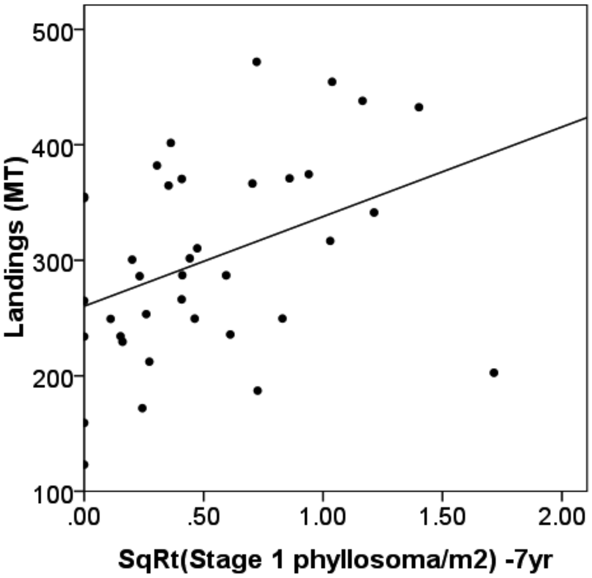

Figure 6. Spiny lobster landings (combined recreational and commercial) plotted against the abundance of stage 1 phyllosoma (numbers per m^2 square-root transformed) lagged by 7 years. The correlation, $r = 0.39$, $p < 0.05$.

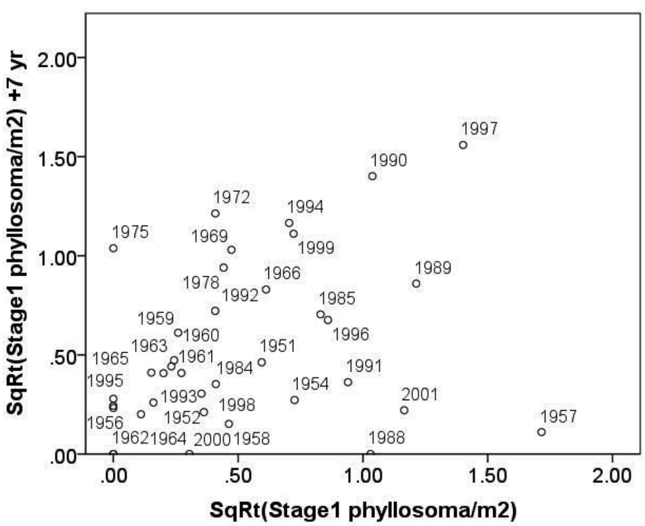

Figure 7. The abundance of stage 1 phyllosoma, an index of spawning stock size, plotted against their abundance 7 years hence, an index of recruitment. Both indices have been square-root transformed.

based on the abundance of stage 1 phyllosoma (a proxy for stock size) and their abundance 7 years hence (a proxy for their recruits) (fig. 7). No clear relationship is seen, although an asymptotic (Beverton-Holt) or dome-shaped (Ricker) relationship could potentially be drawn through the cloud of points. However, the data indicate that while there is considerable variability, good levels of recruitment seem to require at least moderate levels of spawners and initial phyllosoma abundance. There was a comparable correlation between the abundance of stage 1 phyllosoma, an index of stock size, and the abundance of stage 1 phyllosoma 7 years hence (correlation based on square-root transformed variables, $r = 0.31$, $p = 0.06$).

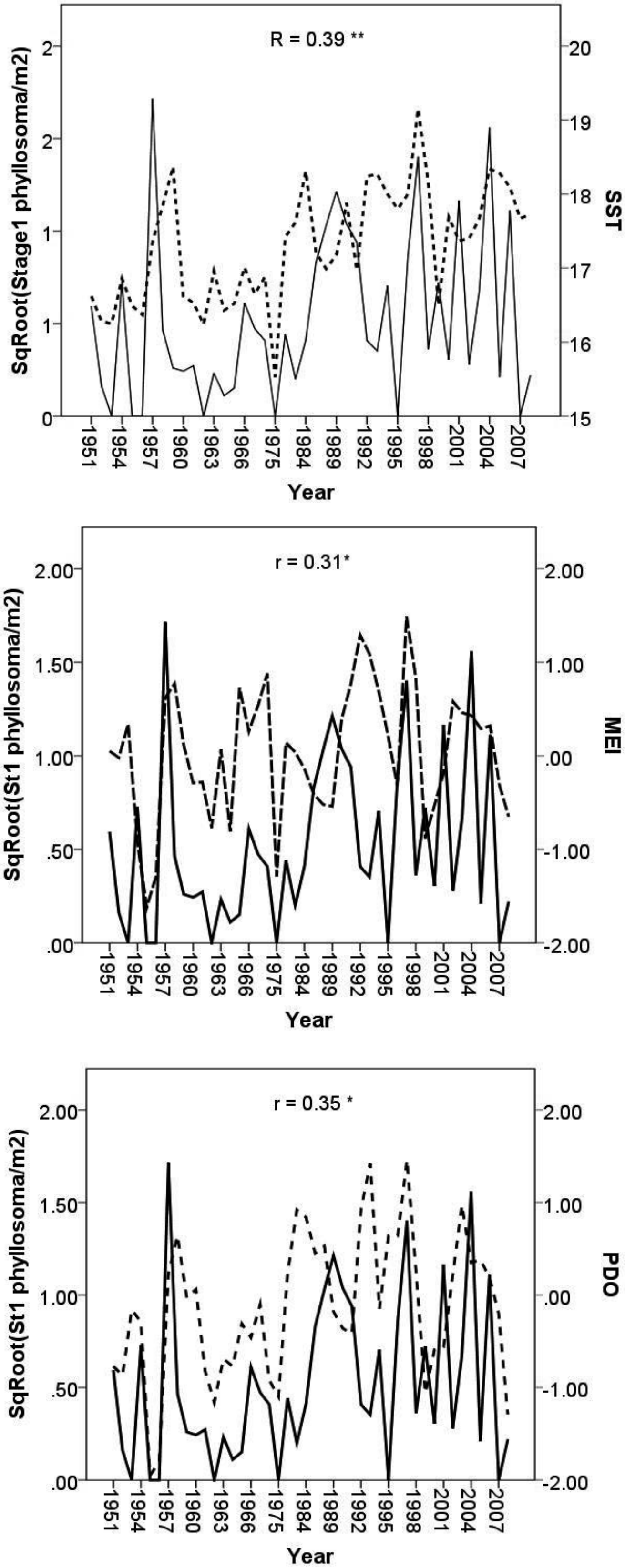

Figure 8. The time series of stage 1 phyllosoma abundance (solid lines) plotted with mean SST, the Multivariate ENSO Index (MEI), and the Pacific Decadal Oscillation (PDO) (dashed lines).

TABLE 1
Pearson correlations of sea-surface temperature (SST), the Multivariate ENSO Index (MEI), and Pacific Decadal Oscillation (PDO) with landings from the California lobster fishery at lags of 0–8 years. *: $p < 0.05$; **: $p < 0.01$; ?: $p < 0.10$; df = 44 at 0 lag.

Correlations	Landings	Landings +1 year	Landings +2 years	Landings +3 years	Landings +4 years	Landings +5 years	Landings +6 years	Landings +7 years	Landings +8 years
SST	.46 **	.19	.23	.37*	.50**	.43**	.35*	.43**	.46**
MEI	.10	–.14	–.04	.17	.26	.37*	.25	.22	.22
PDO	.11	.15	.14	.29?	.44**	.48**	.21	.17	.34*

The stage 1 phyllosoma time series was significantly correlated with several time series related to ocean temperature: the sea-surface temperature (SST) time series averaged from the CalCOFI surveys ($r = 0.39$, $p < 0.01$), the MEI ($r = 0.30$, $p < 0.05$), and the PDO ($r = 0.35$, $p < 0.05$) (fig. 8). All correlations indicate that relatively warm ocean conditions, including El Niño events and the warm phase of the PDO, are positively associated the abundance of phyllosoma. Because of the intercorrelations between SST, the MEI, and the PDO, stepwise regression analysis was carried out. SST was most highly correlated with the abundance of stage 1 phyllosoma, so it entered the regression first, at which point neither the MEI nor the PDO contributed significantly to explaining the remaining variance. The NPGO was not significantly correlated with the abundance of stage 1 phyllosoma.

Correlations of landings were examined with the environmental variables lagged up to eight years. The SST time series was significantly correlated with the total landings 3–8 years hence (table 1). The PDO was significantly correlated with the landings 4, 5, and 8 years later, and the MEI was significantly correlated with landings 5 years later (table 1). Again, the NPGO was not significantly correlated with the landings at any lag.

DISCUSSION

The consistent positive correlation of stage 1 phyllosoma with several indicators of warm ocean conditions such as sea-surface temperature, El Niño events, and the warm phase of the PDO is consistent with earlier studies (Johnson 1960a; Pringle 1986). This relationship led some earlier workers to hypothesize that the relationship was based on the influence of advection, with cool conditions indicative of enhanced southward transport of the California Current and warm conditions (and El Niños, in particular) indicative of enhanced northerly transport by the Davidson Countercurrent. Pringle 1986 and Johnson 1960a noted there were enhanced concentrations of phyllosoma off California and reduced concentrations off Baja during the 1957 El Niño, with the opposite distribution in 1975, when there was strong southward flow of the California Current. Pringle 1986

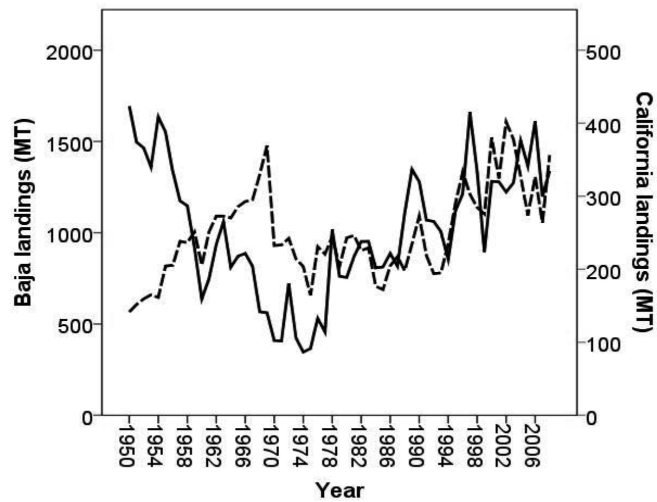

Figure 9. Time series (1956–2008) for landings (in metric tonnes) from the U.S. California (solid line) and Baja California (dashed line) commercial spiny lobster fisheries. Data prior to 1956 are not shown due to limited fishing effort in the Baja fishery. The correlation between the time series is 0.49, $p < 0.01$. (Data for the Baja fishery courtesy of E. Chavez.)

hypothesized that early-stage phyllosoma produced in California waters were mostly advected south to the waters off central Baja, with recruitment to the California fishery dependent on pueruli advected northward by the Davidson Current. However, this implies that recruitment to the Mexican and U.S. fisheries should be inversely correlated, with a negative correlation between El Niños and recruitment to the Mexican fishery, since enhanced northward transport would result in depletion from the more southerly component of the population. However, Phillips et al. 1994 found that the Baja fishery was positively correlated with El Niño events lagged by four years, similar to our finding for the California fishery. More generally, the California and Baja fisheries are significantly positively correlated (fig. 9). These relationships indicate that larval survival and subsequent recruitment throughout the Pacific west coast fishery are positively associated with warm ocean conditions, including the occurrence of El Niño. We observed an anomalously high abundance of phyllosoma relative to the fishery landings off California only during the 1957 El Niño event, suggesting that Pringle's 1986 observation of an inverse relationship in the phyllosoma distribution in U.S. and Mexican waters during that El Niño was anomalous (fig. 5). Thus, the mechanism underlying the correlations between ocean temperature conditions and lobster recruitment remains unclear. However, our findings do not support the hypothesis that enhanced northward or southward transport of the California Current is a primary driver underlying this relationship.

The requirement introduced in 1976 for an escape port in commercial lobster traps closely coincides with the transition in 1978–79 to warm PDO conditions. This raises the possibility that the correlation between phyllosoma abundance and temperature conditions may be spurious, possibly related to coincident changes in the fishery. However, phyllosoma abundance appears to be significantly correlated with SST, the PDO, and ENSO at interannual time scales (fig. 8) and not dependent on a single change in management of the fishery. These correlations are also significant without any lag, indicating that these correlations are based at least in part on enhanced phyllosoma survival.

The correlation between the time series of stage 1 phyllosoma abundance and spiny lobster landings suggests that the landings are correlated with lobster spawning stock biomass. This is consistent with the apparently high levels of exploitation in the fishery, such that most new recruits are removed each year. The fishing season follows the spawning season, so a large proportion of the spawning stock is presumably removed each year. This leads us to speculate why the trend of increasing landings since about 2000 is not reflected in either the phyllosoma time series (fig. 4) or the Baja California fishery, whose landings are significantly correlated with U.S. lobster landings ($r = 0.49$, $p < 0.01$) (fig. 9). This disparity potentially reflects an increasing exploitation rate on spiny lobster. However, we note that the apparent increase in lobster landings is attributable to a substantial increase in recreational landings (fig. 1), whose time series has been reconstructed from only a few years of recreational landings data. There is thus some uncertainty about the recent increasing trend. This merits further attention, given its possible implications for the sustainability of the present fishery.

We suggest that the abundance of stage 1 phyllosoma in the CalCOFI collections may be useful as a fishery-independent index for spiny lobster spawning stock biomass in the waters off California. In addition, SST, the MEI, and the PDO may be used to enhance the index for lobster stock productivity, with warm periods being more productive than cool periods. Stepwise regression analysis and lagged correlation analysis indicated that local SST was most closely related to phyllosoma survival and subsequent recruitment; the broader MEI and PDO climate indices did not significantly contribute to further explaining variance in the time series. There is growing recognition that local and large-scale environmental processes significantly influence the productivity of various exploited populations inhabiting the California Current ecosystem (and elsewhere) and that sustainable management can be enhanced by taking these influences into account, either formally or through the use of more informal "environmental report cards." The sardine, sablefish, and halibut fisheries off the west coast of North America are several fisheries in which exploitation rates are managed with reference to environmental conditions (Jacobson and MacCall 1995; McCaughran 1997; King et al. 2001). Since the phyllosoma time series is now maintained as part of CalCOFI, it represents a low-cost, efficient tool that could help monitor this population, given its susceptibility to variable oceanographic conditions and lack of other fishery-independent measures of its status. The ability to predict lobster recruitment to the fishery would be further enhanced through use of puerulus collectors to monitor juvenile settlement, which has proven an effective means to predict future fishery recruitment in other spiny lobster fisheries (Caputi et al. 1997). A recent trial use of puerulus collectors in the Baja California fishery appears to have been successful (Arteaga-Ríos et al. 2007). The apparent close relationship between landings in the Alta and Baja California lobster fisheries and their similar relationships to environmental conditions suggest that greater data sharing, collaborative research and management between the U.S. and Mexico should be considered to further the sustainable management of this transnational population.

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