

CAN WE RELATE LARVAL FISH ABUNDANCE TO RECRUITMENT OR POPULATION STABILITY? A PRELIMINARY ANALYSIS OF RECRUITMENT TO A TEMPERATE ROCKY REEF

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ABSTRACT

The fish assemblage at King Harbor, California, has been studied since 1974 by means of diver transect and ichthyoplankton collection. This preliminary report is an attempt to relate abundance data sets (larvae, juveniles, subadults, and adults, by species) to fluctuations in the fish assemblage. The significant changes that have occurred are probably associated with the El Niño events of 1978-79 and 1982-84. These warming trends have reduced the abundance of cool-temperate species while increasing the proportion of warm-temperate ones. These changes could result from adult emigration or reproductive and recruitment failure. The decrease in viviparous embiotocids seems to correlate with fewer juveniles since 1976. For oviparous species, changes in adult abundance may be reflected in larval abundance, but in most cases recruitment and larval abundance do not appear closely correlated. This situation may result from a sampling bias toward early (post-yolk-sac, preflexion) larval stages. The relationship between larval abundance and recruitment has been experimentally examined on a predator-cleared reef. Assuming that a gauntlet of resident predators is responsible for removing a large percentage of settling recruits, we have removed all fish monthly from an isolated reef and compared rates of settling to observed planktonic abundances. Two species, *Lythrypnus dalli* and *Arteidius creaseri*, have shown correspondence between larval abundance and recruitment, and this method appears to provide a way of relating the two data sets. Future expanded recruitment sampling and increased knowledge of larval longevity should increase the utility of these data.

RESUMEN

Los peces de King Harbor, California, han sido estudiados por medio de buzos y de colecta de ictioplancton. Este estudio preliminar intenta relacionar datos de abundancia (larvas, juveniles, subadultos y adultos, por especie) con fluctuaciones en el conjunto de peces. Los cambios significativos que han ocurrido están probablemente relacionados con los eventos El Niño de 1978-79 y 1982-84. Estos calentamientos han reducido la abundancia de las especies

frío-temperadas y aumentado la proporción de aquellas cálido-temperadas. Estos cambios pueden ser el resultado de una emigración de adultos, o un fracaso en la reproducción y en el reclutamiento. Desde 1976, la disminución de embiotócidos vivíparos parece estar relacionada con una escasez de juveniles. Los cambios en la abundancia de adultos de especies ovíparas pueden estar reflejados en la abundancia larval; sin embargo, en la mayoría de los casos, el reclutamiento y la abundancia larval no parecen estar relacionados. Esta situación puede ser el resultado de un sesgo en el muestreo hacia estadios larvales tempranos (post-saco vitelino, preflexión). La relación entre abundancia larval y reclutamiento ha sido examinada experimentalmente en un arrecife sin depredadores. Suponiendo que un conjunto de depredadores residentes elimina un alto porcentaje de los nuevos reclutas, se sacaron mensualmente todos los peces de un arrecife aislado. Se compararon las tasas de asentamiento en el arrecife con las abundancias observadas en el plancton. Dos especies, *Lythrypnus dalli* y *Arteidius creaseri*, mostraron cierta relación entre la abundancia larval y el reclutamiento; este método permitiría relacionar estos dos conjuntos de observaciones. A futuro, un muestreo más extenso del reclutamiento y un aumento en el conocimiento de la longevidad larval deberían aumentar la utilidad de esta información.

INTRODUCTION

The assemblage of fishes at King Harbor, California, has been studied since 1974 (Terry and Stephens 1976; Ellison et al. 1979; Stephens and Zerba 1981; Stephens et al. 1984). During this 12-year period, major environmental perturbations have occurred (Cayan 1979; Smith and Eppley 1982; McLain 1984). At the origin of this study, temperatures were anomalously cold, but in 1978-79 a small El Niño event occurred, followed in 1982-84 by a major El Niño. These thermal events produced concomitant changes in the fish assemblage at King Harbor (Stephens and Zerba 1981; Stephens et al. 1984). The alterations probably resulted from a combination of adult emigration and changes in spawning or recruitment success. We have monitored the egg and larval abundance at

King Harbor stations monthly during this study and have recorded juveniles of 63 of the 105 species observed in the harbor. Presently, we have data on about 30 species represented by all three stages (larvae, juveniles, and adults).

Most of the literature on population dynamics of marine fishes has been concerned with migratory pelagic or demersal stocks. These stocks may follow controlled patterns, including timed spawning periods coordinated with oceanographic events—a highly evolved condition (Cushing 1975). Long-term records from selected fisheries have allowed a few time series to be developed from these data. For reef fish assemblages, few such records exist. Further, we know of no data relating larval abundance to recruitment for these fishes, and few studies are available describing larval drift patterns (Ahlstrom 1971, 1972; Leis and Miller 1976). Recently, Brothers et al. (1983) and Victor (1985) have documented larval longevity in some tropical and a few temperate species, but these data are unknown for most species. Because estimates of larval longevity are often long (20-60 days) for reef fishes, it seems probable that no relationship exists between the resident spawning assemblage and recruiting larvae.

A number of recent studies have focused on reef recruitment. The majority of these have dealt with tropical reef assemblages (Sale 1977, 1978, 1980, 1984; Talbot et al. 1978; Williams 1980; Victor 1982, 1983, 1984). These recruitment studies have not simultaneously monitored pelagic larval availability; they report primarily on juvenile success, habitat specificity, etc. We have monitored pelagic larvae as well as juvenile success and adult population fluctuations. Our study also includes two years of experimental data designed to determine the effect of resident fishes on larval settlement. This preliminary report will attempt to integrate these data sources and suggest their roles in reef fish population dynamics.

MATERIALS AND METHODS

Since 1974, regular 5-minute isobathic diver transects have been swum at 3-m depth intervals between 1.5 and 15 m (Terry and Stephens 1976). Species abundance by observable life-history stage has been enumerated at eight stations in King Harbor (Redondo Beach, California). Initially, transects were taken monthly; they became quarterly in 1976. The mean number of transects per year = 147.7 (SD = 56.7), maximum = 314 (1975), minimum = 102 (1978). Ichthyoplankton collections are taken with a standard conical plankton net (333 μ) fitted with a TSK flowmeter. All samples are preserved using a formaldehyde and sodium borate solution. Monthly nighttime surface collections were taken at station DS

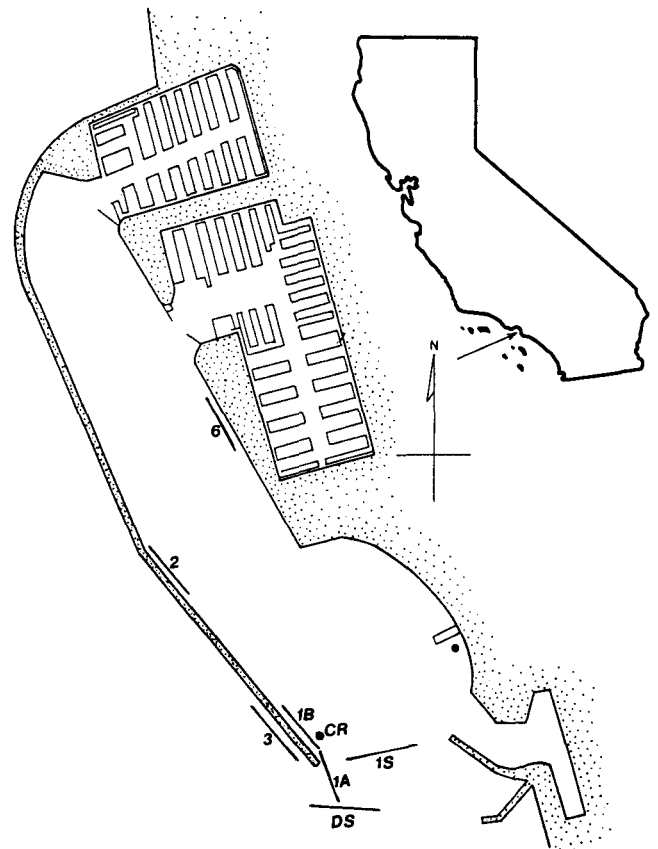


Figure 1. King Harbor study site. 1A, 1B, 2, 3, 6 = diver isobathic transect stations; 1S, DS = plankton stations; CR = cable reef.

(Figure 1) from January 1974 to February 1978 and from February 1982 to the present. Station 1S, in close proximity, has been sampled monthly since April 1978; additionally, mid-depth and epibenthic collections have been made at this station since August 1980. The epibenthic collections are diver-assisted and were taken during the day until night benthic sampling began in June 1985. Data from surface stations DS and 1S taken on the same dates were tested for concordance (Kendall's tau) and found to be significantly associated ($P < .05$). We have therefore combined surface data from these two stations (1974-85). Since 1974, 2,173 samples have been taken, and 1,186 have been completely sorted and identified, including all surface samples from stations DS and 1S.

Resident fishes were first removed from Cable Reef in July 1984. This small rock isolate, 5 m in circumference and 1.5 m high, is located at a depth of 11 m just inside the harbor entrance and 20 m from the breakwater. Since 1984 the reef has been sampled monthly by anesthetizing the fish with quinaldine and vacuuming the surface with an air lift fitted with 333- μ mesh bags. Samples are preserved in Formalin except where otolith data are to be analyzed: these samples are preserved in 95% ethanol. Temperature profile data are

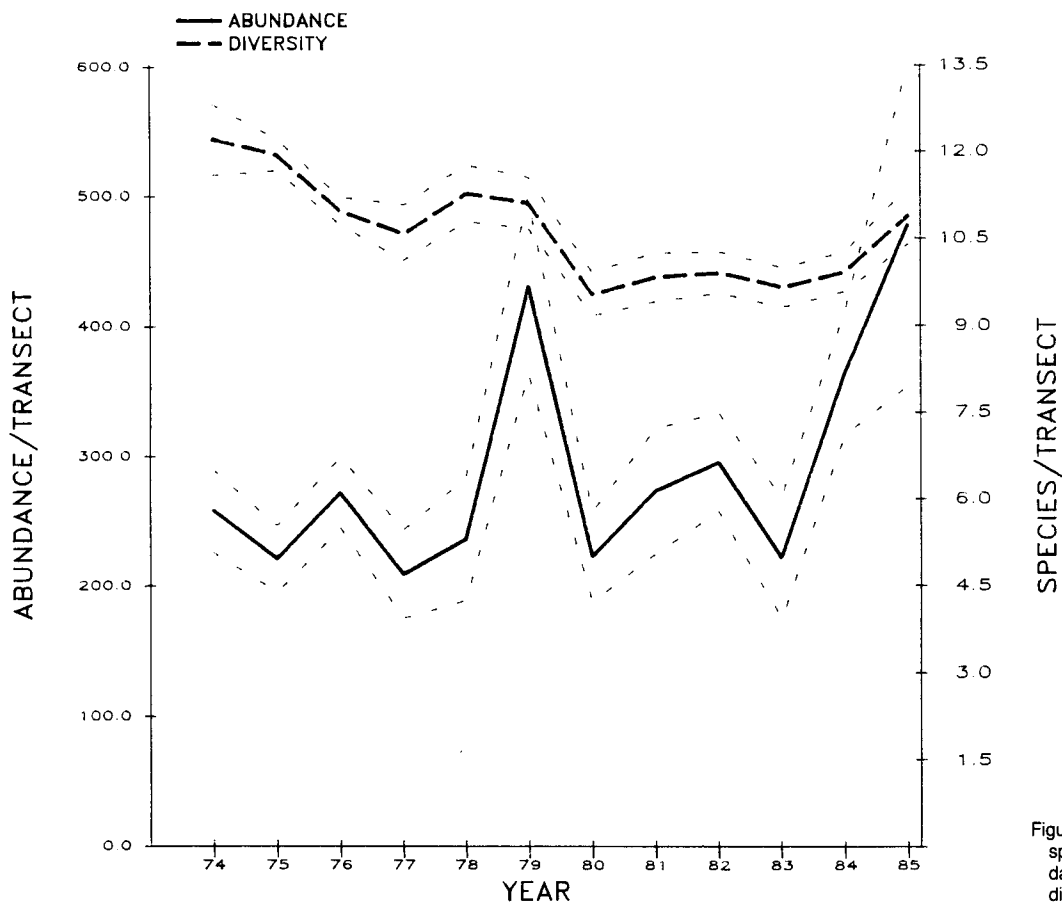


Figure 2. Yearly mean number of species transect⁻¹ and mean abundance of fish transect⁻¹ (dashes indicate 95% confidence limits).

taken during all field sampling with diver thermometers and YSI telethermometers. Data are entered and stored in Occidental's Prime 550 computer.

CHANGES IN KING HARBOR FISH POPULATIONS (1974-85)

Generally during this study period, the fish assemblage as described by annual abundance of fishes and by annual mean number of species has remained relatively stable (Figure 2). The highest mean number of species per transect was recorded in 1974 (13.1), the lowest in 1980 (9.7), and the mean for this 12-year period was 11.1 (SD = 1.22). The highest mean number of fish per transect was recorded in 1985 (450), the lowest in 1980 (117.4), with a 12-year mean of 154.8 (SD = 126.0). The numbers of individuals have fluctuated considerably but suggest a nonsignificant increasing trend ($y = 214.8 + 10.95x$, $r = 0.5$). The number of species has decreased slightly but significantly ($y = 11.87 - .19x$, $r = .75$, $.01 < P < .05$). Individually, a number of species have disappeared from the study site, and new ones have replaced them. In fact, the existing assemblage is significantly different today from the one originally present in 1974 (Stephens and Zerba 1981).

When the annual abundance is broken down by adults, juveniles, and larvae, and these categories are compared over the 12-year period (Figure 3), the abundance of larvae decreases ($r = .64$, $.01 < P < .05$), while the abundance of adults increases ($r = .71$, $.01 < P < .05$). Juvenile abundance shows no significant correlation ($r = .39$). The larval diversity data (Figure 4) agree closely with the pattern of larval abundance. These latter data suggest that increases or decreases in abundance reflect addition or subtraction of species.

We have related adult abundance to changes in thermal conditions (Stephens and Zerba 1981; Stephens et al. 1984) and have attempted to relate changes in larval abundance to the major temperature shifts. Overall larval abundance was greater during cooler years, as indicated by comparison to annual minimal monthly temperatures (Figure 4). The decline of some species during the study period may be related to decreased larval or spawning success with increased water temperatures, though adult emigration may have occurred. The species that have increased are those favoring warmer conditions. These changes in abundance of dominant King Harbor species are presented in Figures 5-10. Table 1 presents linear

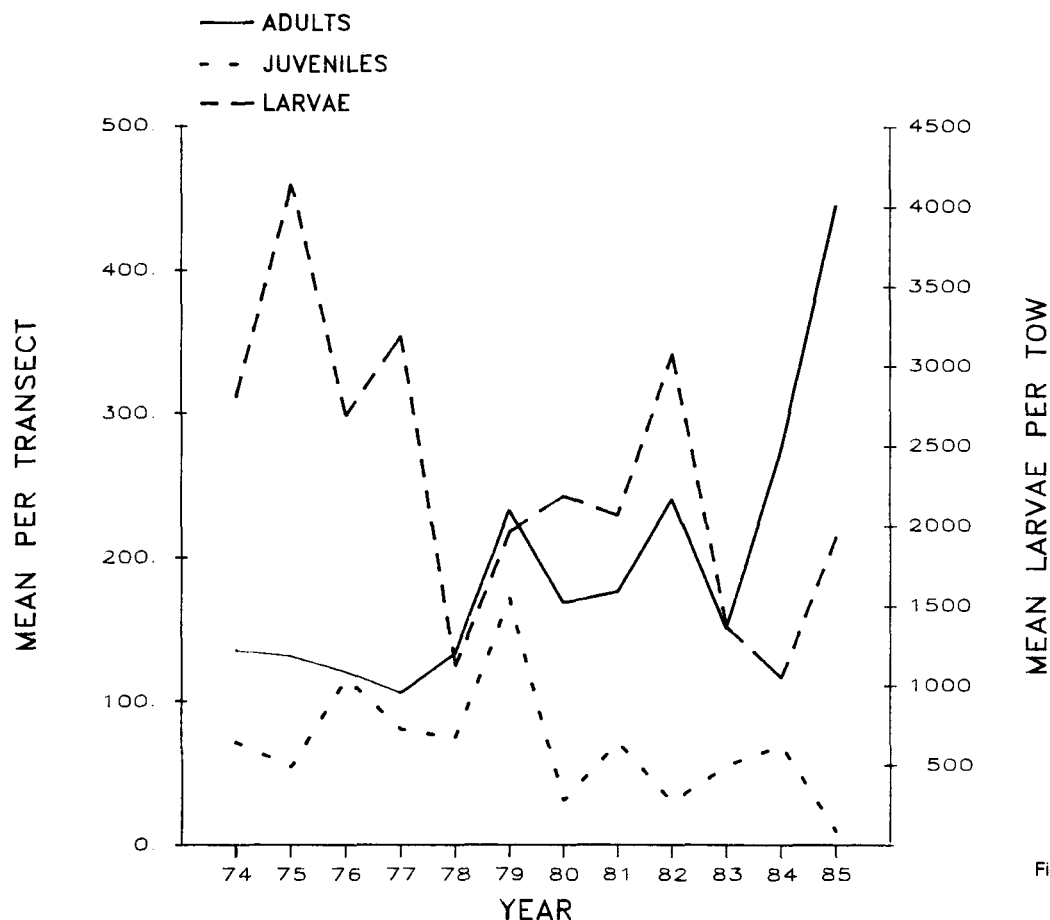


Figure 3. Annual abundance of adults-subadults, juveniles, and larvae at King Harbor.

regression data and Pearson's correlation coefficients for these species. *Chromis punctipinnis*, *Girella nigricans*, *Halichoeres semicinctus*, *Lythrypnus dalli*, and *Paralabrax nebulifer* show significant positive correlations (1974-85), whereas *Cymatogaster aggregata*, *Embiotoca jacksoni*, *Hypsurus caryi*, *Oxylebius picta*, *Phanerodon furcatus*, *Rhacochilus vacca*, *Sebastes mystinus*, and *S. serranoides* show significant negative correlations during this period. These data generally agree with the species' thermal characteristics as tested in laboratory gradient experiments (Ehrlich et al. 1979; Shrode et al. 1982, 1983; Hose et al., in prep.).

Some of the above-cited species are represented by adequate larval and/or juvenile data for preliminary recruitment analysis (Table 2). The viviparous embiotocids lack larval stages and the concomitant vagaries of planktonic existence. Parturition occurs at the study site. All five species that were abundant at King Harbor in 1974—*C. aggregata* (Figure 6), *E. jacksoni* (Figure 6), *H. caryi* (Figure 7), *P. furcatus* (Figure 9), and *R. vacca* (Figure 9)—have declined in abundance, and all have shown reduced juvenile abundance since the last cold anomaly (1975-76). The maximum abundance of embiotocid juveniles was in

1974-75 (Table 2). A linear decline in abundance for more than ten years would result from lack of adequate recruitment and adult attrition in resident long-lived species like *E. jacksoni* (Hough 1981). The other species are more often wanderers or have seasonal migration patterns (e.g., *Cymatogaster* [Wiebe 1968]) and may not fit this scenario.

The ovoviparous rockfishes (*Sebastes*) show a similar pattern. The blue *S. mystinus* (Figure 10) and olive *S. serranoides* (Figure 10) were extremely abundant as juveniles and yearlings in King Harbor during the pre-El Niño period but declined precipitously in warm-water years, with juveniles being absent or very rare since 1980. The calico *S. dalli* (Figure 9) recruited well in 1975 and 1979. Following the initial recruitment, the population declined about 25% per year, and this small, relatively short-lived species appears to survive four to five years from a single recruitment event. Following 1979, however, adults disappeared, apparently in response to warm water. Rockfishes in general have not recruited well to shallow water since the onset of the 1978-79 El Niño (Mearns et al. 1980). Both recruitment failure and emigration may have occurred.

TABLE 1
 Linear Regressions and Correlation Coefficients for 1974-1986 Data

	Linear regression	r	Significance
<i>Anisotremus davidsonii</i>	$y = 0.30 + 0.13x$	0.41	NS
<i>Atherinops affinis</i>	$y = 43.90 - 2.28x$	-0.42	NS
<i>Chromis punctipinnis</i>	$y = 2.33 + 14.20x$	0.85	.001
<i>Citharichthys stigmatæus</i>	$y = 0.72 - 0.08x$	-0.57	NS
<i>Coryphopterus nicholsii</i>	$y = 0.44 - 0.18x$	-0.28	NS
<i>Cymatogaster aggregata</i>	$y = 47.00 - 4.81x$	-0.73	.01
<i>Embiotoca jacksoni</i>	$y = 16.10 - 0.46x$	-0.58	.05
<i>Girella nigricans</i>	$y = 5.38 + 1.37x$	0.85	.001
<i>Halichoeres semicinctus</i>	$y = -2.25 + 0.82x$	0.82	.01
<i>Heterostichus rostratus</i>	$y = 0.32 + 0.05x$	0.55	NS
<i>Hyperprosopon argenteum</i>	$y = 7.81 - 0.60x$	-0.33	NS
<i>Hypsurus caryi</i>	$y = 8.60 - 0.66x$	-0.80	.01
<i>Hypsypops rubicundus</i>	$y = 3.49 + 0.03x$	-0.41	NS
<i>Lythrypnus dalli</i>	$y = -4.82 + 1.29x$	0.77	.01
<i>Medialuna californiensis</i>	$y = 1.28 - 0.06x$	-0.31	NS
<i>Oxyjulis californica</i>	$y = 20.56 + 0.44x$	0.14	NS
<i>Oxylebius pictus</i>	$y = 0.58 - 0.04x$	-0.65	.05
<i>Paralabrax clathratus</i>	$y = 6.37 + 0.47x$	0.40	NS
<i>Paralabrax nebulifer</i>	$y = -1.28 + 0.75x$	0.86	.001
<i>Phanerodon furcatus</i>	$y = 5.81 + 0.31x$	-0.68	.05
<i>Rhacochilus toxotes</i>	$y = 0.72 + 0.39x$	0.32	NS
<i>Rhacochilus vacca</i>	$y = 9.44 - 0.59x$	-0.82	.01
<i>Sebastes dallii</i>	$y = 1.51 - 0.13x$	-0.42	NS
<i>Sebastes mystinus</i>	$y = 14.59 - 1.58x$	-0.78	.01
<i>Sebastes serranoides</i>	$y = 6.09 - 0.58x$	-0.74	.01
<i>Semicossyphus pulcher</i>	$y = 0.60 - 0.00x$	-0.03	NS
<i>Trachurus symmetricus</i>	$y = 6.43 + 3.10x$	0.33	NS

TABLE 2
 Mean Abundance by Year: Larvae per Thousand Cubic Meters and Juveniles per Transect

Species	Stage	Years											
		1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
<i>Cymatogaster aggregata</i>	J	16.7	28.6	20.6	1.1	12.3	5.5	0.3	0.4	0.6	0.1	0	0
<i>Embiotoca jacksoni</i>	J	2.1	4.3	2.7	0.5	0.7	1.0	0.7	1.5	1.9	0.2	1.1	1.2
<i>Hypsurus caryi</i>	J	1.1	0.7	0.2	0.2	0.2	0.1	0.1	0	0	0	0.1	0
<i>Phanerodon furcatus</i>	J	0.8	0.6	0.1	0	0	0.1	0.1	0	0*	0	0.1	0.2
<i>Rhacochilus toxotes</i>	J	0.1	0.2	0*	0	0	0	0*	0*	0	0	0	0
<i>Rhacochilus vacca</i>	J	2.4	2.6	0.3	0.2	0.1	0.2	0.5	0.4	0.7	0.1	0.4	0.1
<i>Chromis punctipinnis</i>	L	176.9	0	10.8	0	0	236.2	242.6	0	100.8	12.3	10.4	0
	J	14.3	9.8	56.3	27.5	36.5	81.0	23.7	35.4	20.2	46.0	58.1	29.9
<i>Hypsypops rubicundus</i>	L	0	0	0	91.4	245.7	190.9	384.4	57.2	149.9	80.2	37.1	111.4
	J	0.4	0.7	0.9	1.3	0.9	0.3	0*	0.1	0*	0*	0.1	0.1
<i>Halichoeres semicinctus</i>	L	1.2	0	0	0	0.4	4.4	0.5	0	1.	155	0.9	1.2
	J	0.1	0*	0.1	0.1	0.1	0.9	0.5	0.1	0.2	0.9	3.0	0.4
<i>Oxyjulis californica</i>	L	21.1	130.3	72.8	97.0	0	0	185.6	358.4	151.1	214.9	22.5	32.2
	J	2.4	3.8	7.6	17.6	11.0	17.1	2.4	3.8	0.7	1.6	0.8	1.0
<i>Semicossyphus pulcher</i>	L	10.4	0	0	12.2	0	44.8	0	0	70.1	35.6	10.4	0
	J	0.1	0*	0	0.9	0.5	0.5	0	0	0.1	0	0.1	0*
<i>Cheilotrema saturnum</i>	L	68.8	38.7	279.8	79.4	20.9	45.8	0	71.6	116.5	48.4	45.3	42.7
	J	1.7	0.5	0.7	0.8	2.3	1.5	0.6	1.8	0	0*	1.0	0.3
<i>Anisotremus davidsonii</i>	L	11.6	0	0	0	0	0	0	0	0	21.6	10.4	22.1
	J	0	0.2	0	0.2	0.9	0*	0.3	0.1	0.1	0.2	1.0	0.5
<i>Girella nigricans</i>	L	0	0	11.1	10.6	0	0	0	0	0	0	0	0
	J	2.1	0.7	3.4	0.9	0.4	4.1	0.6	3.6	1.8	1.5	1.2	0.6
<i>Sebastes mystinus</i>	J	21.8	6.9	2.7	4.8	0.6	0.2	0	0	0	0	0	0
<i>Sebastes serranoides</i>	J	5.2	1.9	3.1	7.9	0.1	0.2	0	0	0	0	0.2	0.2
<i>Paralabrax clathratus</i>	J	0.5	0.6	7.1	1.4	5.6	7.0	1.4	3.3	2.0	0.2	1.4	0.9
<i>Paralabrax nebulifer</i>	J	0*	0*	0.8	0*	1.4	1.0	0*	0.1	0.1	0.1	0.7	0.1

* 0 < abundance < .05 J = juveniles L = larvae

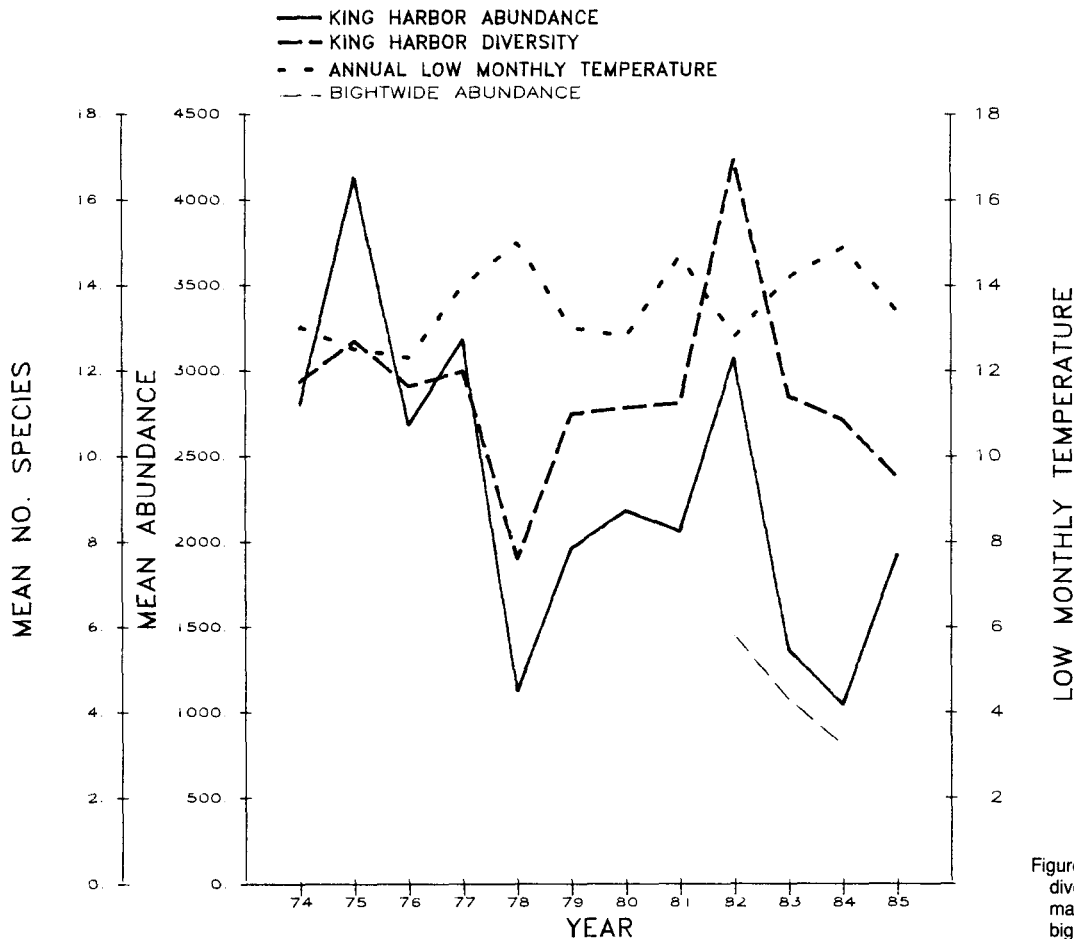


Figure 4. Annual larval abundance and diversity at King Harbor, annual minimal monthly mean temperature, and bightwide larval abundance.

The genus *Paralabrax* includes three species at King Harbor: *P. clathratus*, *P. maculatofasciatus*, and *P. nebulifer*. Their larvae cannot presently be separated. These resident serranids produce pelagic eggs and larvae. Both *P. nebulifer* and *P. clathratus* (Figure 8) have increased with the warm water, but this increase relates only marginally to juvenile abundance and not at all to available larvae (Figure 11). The immigrant stage of *P. nebulifer* may be the subadult, because schools of first-year fish have been observed entering the harbor.

The oviparous wrasses (resident or wandering) have generally increased in El Niño years. As an example, the data for *Halichoeres semicinctus* (Figure 12) may show a direct relationship between larval availability, juvenile recruitment, and adult abundance. Victor (1985) lists 29.9 days as the mean larval life of *H. semicinctus*, certainly long enough for considerable larval transport. Our data suggest a three-year lag between larval abundance and that of adults.

The resident, territorial, nest-guarding pomacentrid *Hypsypops rubicundus* (Figure 13) shows statistically significant correlation between adult and larval abundance ($r = .84, P < .01$), and the decrease in larval

numbers (1982-84) was directly correlated with the number of nest failures in these years (Singer and Stephens, in prep.). In this long-lived, territorial species (Clarke 1970) successful recruitment may be regulated by adult abundance (Beverton and Holt-type recruitment, Eberhardt 1977).

Finally, the annual or semiannual nest-guarding oviparous goby *Lythrypnus dalli* (Figure 14) shows a significant correlation ($r = .81, .01 < P < .05$) between abundance of adults and larvae. In this case, the fact that adults are short-lived with low fecundity makes the relationship between adults and larvae quite precise.

The above examples indicate that though in some cases there may be a relationship between adult abundance and larval abundance (a fact recognized by fishery egg and larval surveys), larval abundance may, but does not predictably, translate into recruitment (Smith 1981).

LARVAL ABUNDANCE AND JUVENILE RECRUITMENT

The relationship between larval abundance and recruitment should be more intimate if the larvae

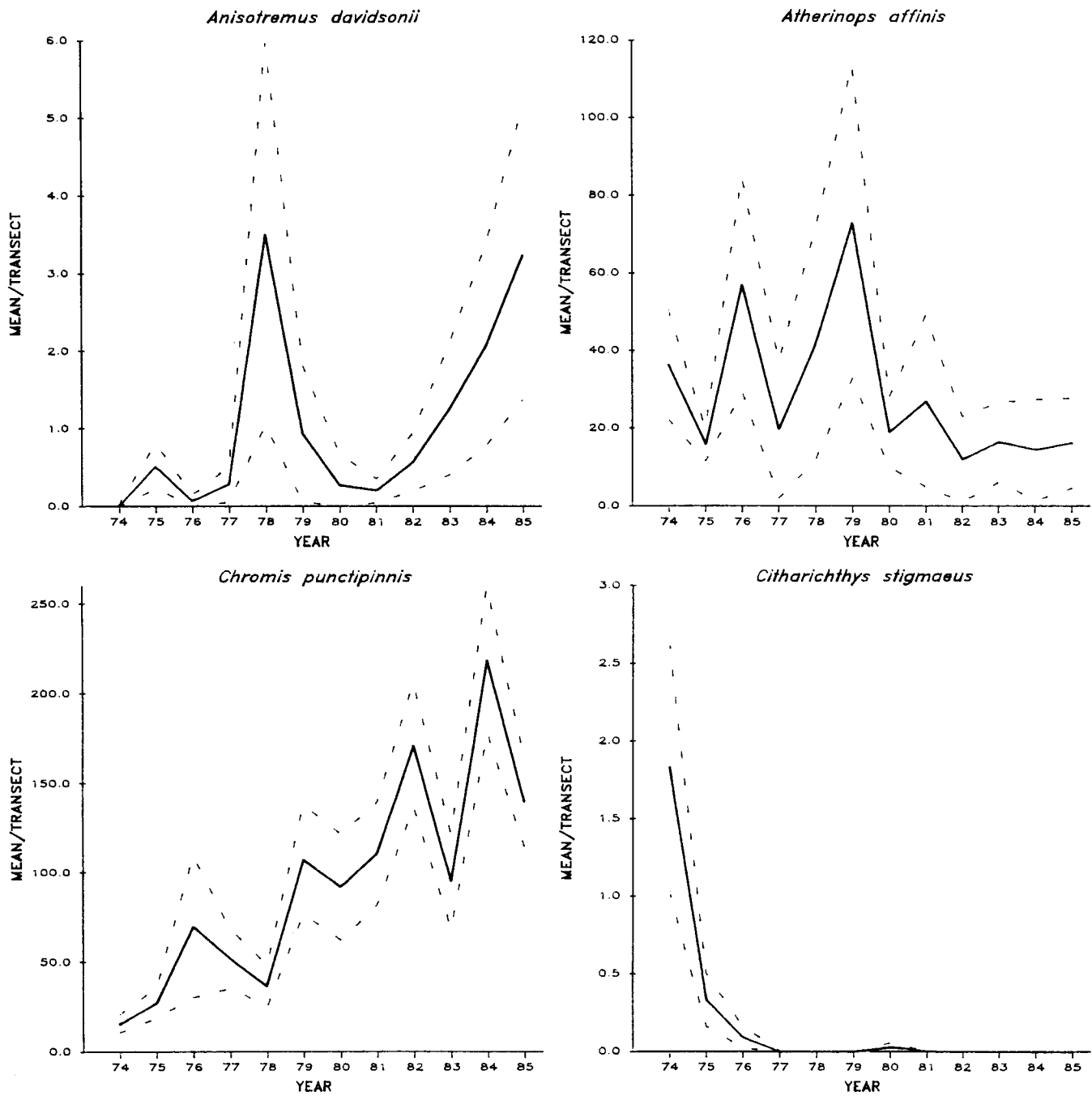


Figure 5. Annual abundance transect⁻¹ by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

sampled represent later stages of development (flexion or late preflexion). Though these stages are sampled, the majority of the identifiable larvae taken are post-yolk-sac, preflexion stages. Later larvae are not only less numerous (depleted by starvation, predation) but are probably more adept at avoiding nets. More late larvae have been captured in our epibenthic, nocturnal samples, which we began taking in 1985. Table 3 presents the percentage of "returning" late larval stages in the stratified plankton samples. A relatively high

TABLE 3
 Percent Late Larval Stages by Depth,
 June-September 1985

Genus	Surface	Mid-depth	Epibenthic
<i>Hypsoblennius</i>	0.12	0	0.38
<i>Gibbonsia</i>	0	34.5	30.6
<i>Paraclinus</i>	10.5	17.6	15.6
<i>Lythrypnus</i>	0	1.3	0.9
<i>Gobiesox</i>	0	0	22.3
<i>Paralabrax</i>	0	-	2.9

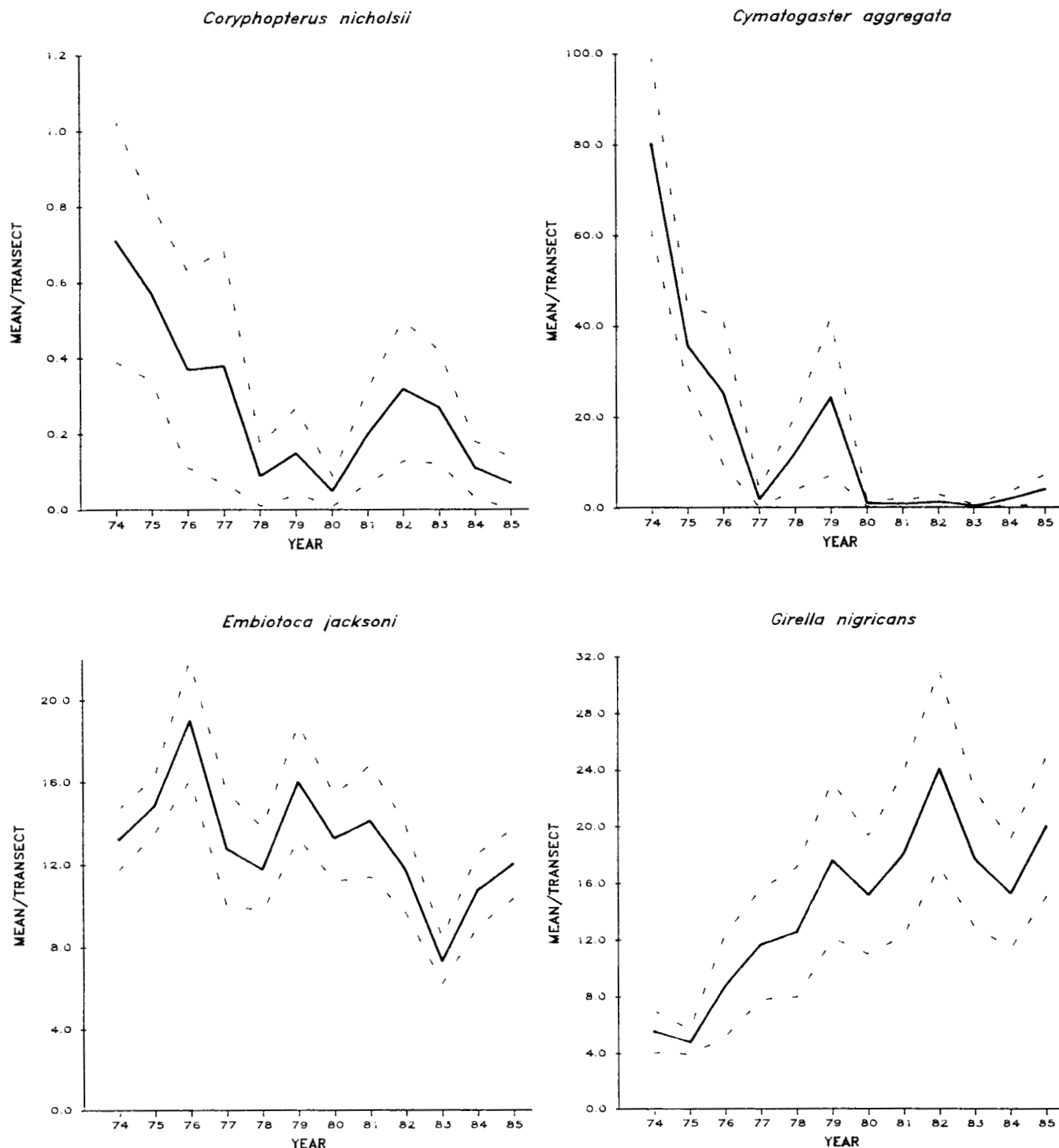


Figure 6. Annual abundance transect⁻¹ by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

number of these late larvae are sampled for a few species.

Even if we are able to adequately sample "returning" larvae as they enter the reef environment, they will be subject to increasing numbers of predators as they approach the substrate (Johannes 1978). Only those that survive this "predator gauntlet" will be available

for settlement. The correlation between available returning larvae and the abundance of settlers should be affected by the abundance of predators. We feel that small, cryptic resident fishes such as blennies and gobies are important elements of this predator community, and we have begun laboratory experiments to document their removal of settling larvae (Stephens, in

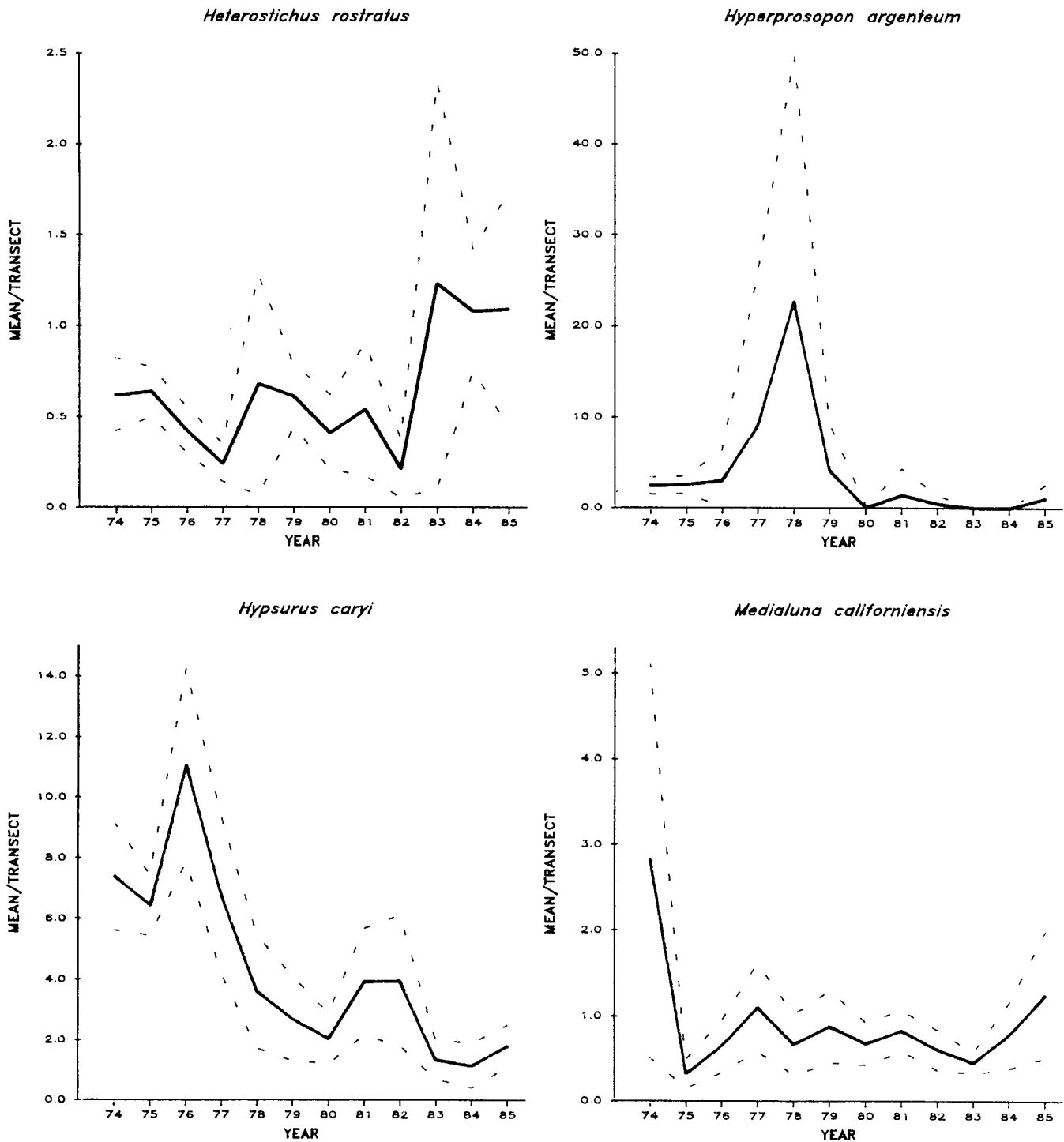


Figure 7. Annual abundance transect⁻¹ by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

prep.). Our removal of resident fishes from Cable Reef was designed to test the relationship between larval abundance and the abundance of settlers in the absence of predators.

In the first year's study (July 1984-July 1985) we collected 445 newly settled larvae of 6 species, and 559 immigrants of 21 species on the predator-free reef. The

total (1,035) is about ten times the original population (Table 4). After the initial fish removal (July 24, 1984), a high percentage of immigration to the reef occurred from the surrounding shell and some adjacent rocks. From July 1984 to March 1985, larval settling only accounted for an average of 25% of the recruitment. From April 1985 to November 1985, 78% of the re-

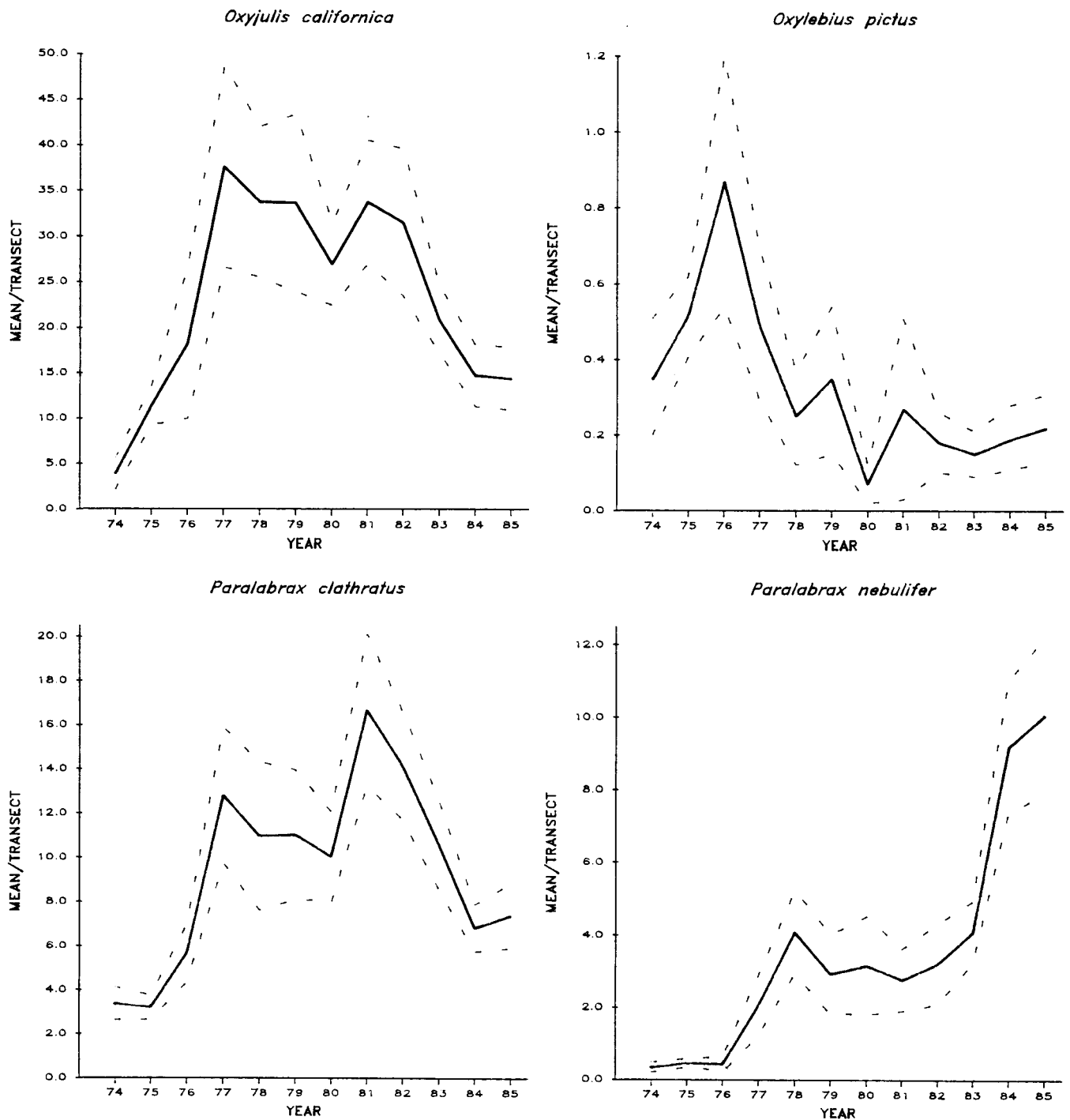


Figure 8. Annual abundance transect⁻¹ by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

recruitment was via larval settling. Only two species, the cottid *Artedius creaseri* (winter-spring) and the goby *Lythrypnus dalli* (summer) had obvious settling pulses and showed some tentative correlation to the pelagic larval abundance. A number of species abundant in the plankton and originally present in the habitat (e.g., *Hypsoblennius jenkinsi* and *Paraclinus integripinnis*) were taken only occasionally during this study.

Table 5 presents annual larval abundance data for Cable Reef residents (1974-85). Settling activity was reduced during the summer of 1985. Even *L. dalli*, which had been dominant in the plankton since March 1985, did not recruit to the reef until mid-September, which may reflect later recruitment caused by the breakdown of El Niño. This lack of recruitment was also observed in two samples taken from control reefs

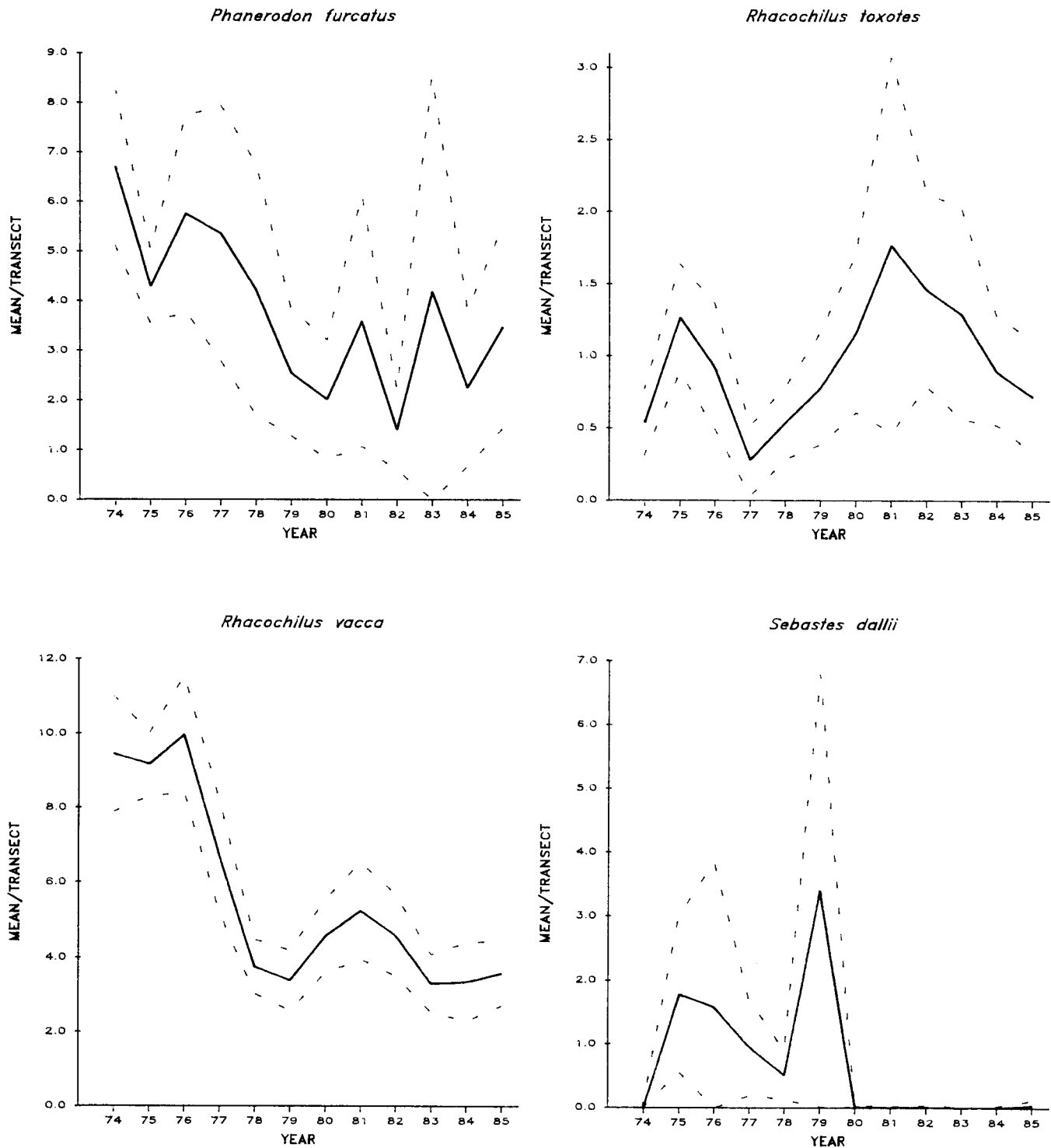


Figure 9. Annual abundance transect⁻¹ by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

at similar depths in July-August. Both control reefs showed only spring recruitment of *A. creaseri*, suggesting that the recruitment pattern observed during our study reflected that of unmodified reefs at the same depth. For the species that did settle, the level of settling was much higher at the predator-free reef, which

we conclude resulted from the absence of the predator gauntlet. Our data suggest that this high level of settling might not correlate with the observed planktonic abundance. The number of *A. creaseri* in the plankton during 1985 was not high; the mean annual abundance of 5.3 larvae/1000 m³ was insignificantly lower

TABLE 4
 Fish Removed from Cable Reef

	Original assemblage		1984												1985					Total
	July	Aug	Sept	Ocr	Nov	Dec	Jan	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov				
<i>Alloclinus holderi</i>	1	—	—	—	1	—	—	—	—	—	—	—	1	1	—	—	4			
<i>Artedius creaseri</i>	4	4	4	6	1	—	—	5	36	119	14	3	12	2	—	—	210			
<i>Chromis punctipinnis</i>	—	2	29	4	2	9	—	—	—	—	—	—	—	—	—	—	46			
<i>Coryphopterus nicholsii</i>	—	1	—	—	—	—	—	—	—	—	—	—	2	1	—	—	4			
<i>Gibbonsia elegans</i>	4	3	1	1	—	1	—	—	—	—	—	—	1	—	—	—	11			
<i>Gobiesox rhessodon</i>	1	2	—	—	—	—	—	1	1	—	—	—	—	1	—	—	6			
<i>Hypsoblennius gentilis</i>	—	—	—	1	—	—	—	—	—	—	1	1	2	—	—	—	5			
<i>Hypsoblennius jenkinsi</i>	12	11	7	15	5	6	4	1	—	—	—	—	—	2	1	—	64			
<i>Lythrypnus dalli</i>	63	111	199	126	75	60	28	14	2	3	—	1	8	67	32	75	864			
<i>Neoclinus stephensae</i>	12	8	2	8	1	—	3	2	1	—	—	5	1	—	1	1	45			
<i>Odontopyxis trispinosa</i>	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1			
<i>Orthonopias triacis</i>	5	—	1	1	1	—	—	—	—	6	1	1	2	1	—	1	20			
<i>Oxylebius pictus</i>	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1			
<i>Paraclinus integripinnis</i>	6	1	1	—	2	—	—	—	—	—	—	—	—	—	—	—	10			
<i>Paralabrax maculatofasciatus</i>	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	1			
<i>Paralabrax nebulifer</i>	—	—	—	—	—	2	1	—	1	—	—	—	—	—	—	—	4			
<i>Rathbunella</i> sp.	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	1	3			
<i>Scorpaena guttata</i>	4	—	—	—	—	1	—	—	—	—	2	—	—	—	—	—	7			
<i>Scorpaenichthys marmoratus</i>	4	—	—	—	—	—	—	—	1	2	—	—	2	—	1	—	10			
<i>Sebastes auriculatus</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1			
<i>Sebastes miniatus</i>	—	—	—	—	—	—	1	2	1	3	—	—	—	—	—	—	7			
<i>Syngnathus</i> sp.	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1			
Total individuals	117	143	245	164	88	79	37	25	43	134	18	12	32	75	35	78	1325			
Total species	12	9	9	10	8	6	5	6	7	6	4	6	8	7	4	4	—			

(Kruskal-Wallis) than the 11-year mean for 1974-85 (10.1/1000 m³). The maximum annual larval abundance for this species was 20.6/1000 m³ in 1982.

Because the number of settled recruits on the predator-free reef was higher than previously observed for this species on unmodified reefs, it appears that removal of resident fish allowed enhanced recruitment. Recruit abundance at the predator-free reef may be more strongly correlated with larval availability than it is at unmodified habitats, a fact that again would appear to support our premise. The temporal relationship between monthly larval abundance and settling for *A. creaseri* is shown in Figure 15. Only with additional

paired planktonic and recruitment samples can we determine the concordance between larval abundance and recruitment in the absence of the predator gauntlet.

Lythrypnus dalli recruited very successfully to the predator-free reef in 1984. In this case, the planktonic larvae were quite abundant ($x = 171.6/1000 \text{ m}^3$) versus the maximum recorded mean (1985) of 232.1/1000 m³, whereas the mean for the 11 completely sampled years was 78.4/1000 m³. The abundance of *L. dalli* as a plankter and a reef inhabitant at King Harbor has been significantly higher since the onset of El Niño in 1978 (Kruskal-Wallis, $P < .05$). This semiannual species maintains its population only with continual recruit-

TABLE 5
 Annual Abundance of Larvae per Thousand Cubic Meters for Species Inhabiting Cable Reef

	Years													
	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	12-yr	
Number of tows	19	18	22	26	26	30	21	10	23	24	24	24	\bar{x}	
<i>Artedius creaseri</i>	\bar{x}	6.3	19.5	18.6	0.8	2.7	1.3	16.9	9.0	20.6	11.9	7.3	5.3	10.1
	SD	14.5	38.5	60.2	2.8	5.2	5.2	21.3	18.0	47.0	18.4	14.7	12.6	7.3
<i>Lythrypnus dalli</i>	\bar{x}	6.0	4.9	2.4	6.2	18.5	63.9	50.6	35.6	167.6	187.1	171.6	232.1	78.4
	SD	15.2	10.0	8.0	11.6	32.7	140.6	84.7	64.8	235.5	405.0	225.8	491.4	84.7
<i>Gibbonsia elegans</i>	\bar{x}	6.7	1.2	1.8	1.1	20.0	17.1	21.0	6.7	4.5	1.4	5.4	2.9	7.5
	SD	11.4	5.2	4.0	5.8	43.6	24.6	41.1	9.5	10.4	5.0	11.0	8.5	7.5
<i>Paraclinus integripinnis</i>	\bar{x}	33.1	20.3	5.2	26.3	32.9	271.7	32.4	235.7	68.7	25.6	49.9	20.2	68.5
	SD	66.4	57.4	12.5	69.8	55.4	558.7	55.1	466.4	179.7	54.6	122.8	56.0	88.3
<i>Hypsoblennius</i> sp.	\bar{x}	1751.9	946.4	529.8	984.6	320.9	548.9	1009.8	633.8	761.6	410.1	262.4	705.1	738.7
	SD	3261.9	1372.8	705.2	1659.4	562.4	571.2	1353.0	1050.8	1055.0	575.3	459.3	1348.1	405.1
<i>Neoclinus</i> sp.	\bar{x}	4.3	7.1	5.7	13.0	4.0	5.7	12.5	1.2	11.2	1.4	0	0.4	5.5
	SD	7.2	20.0	14.5	28.7	9.4	11.6	15.8	3.6	20.2	4.9	0	2.0	4.6

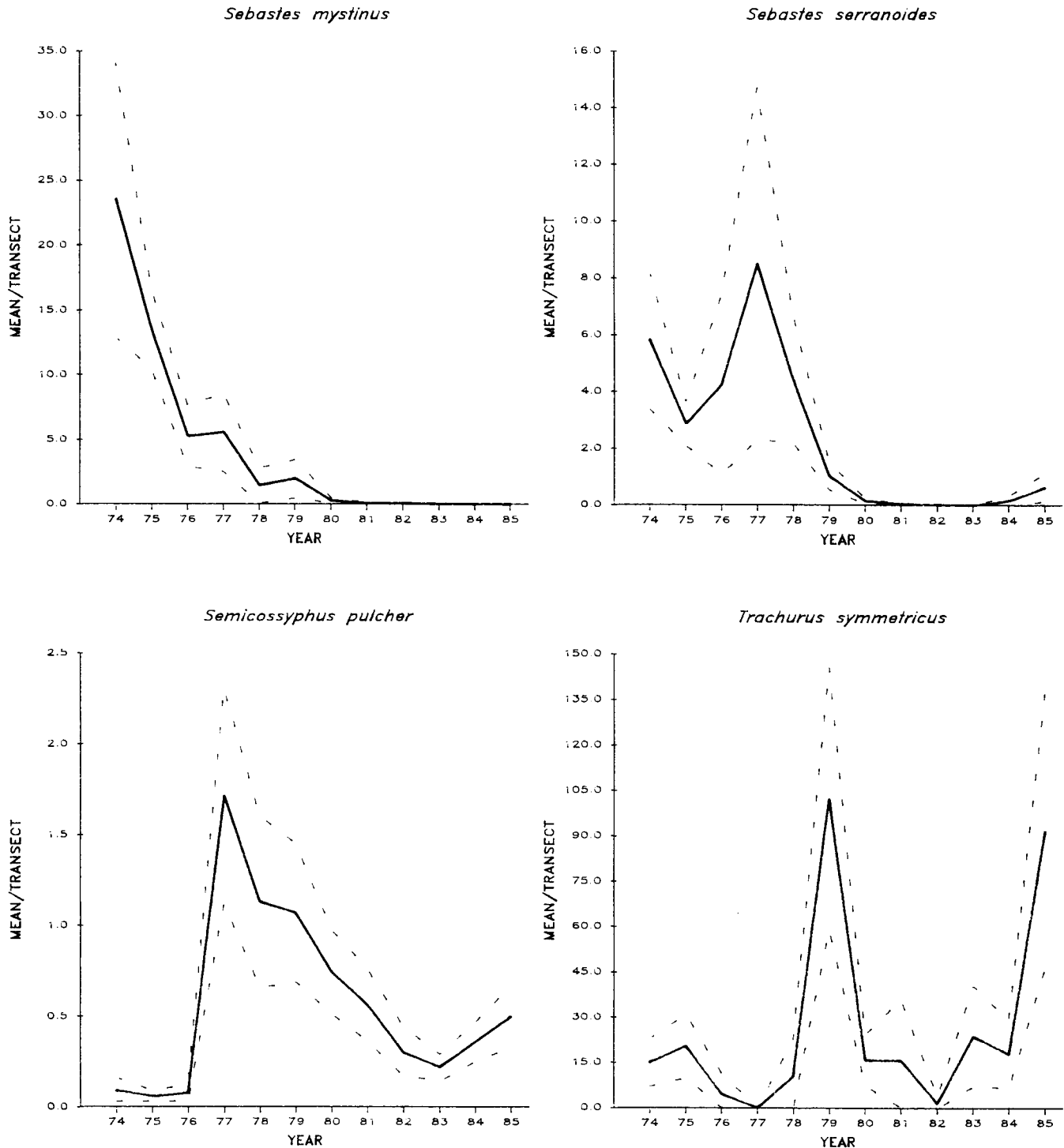


Figure 10. Annual abundance transect⁻¹ by species: adults, subadults, and juveniles combined (dashes indicate 95% confidence limits).

ment and has been extremely abundant since 1981 (Figure 14). The larval abundance (summer 1985) suggested another very strong recruitment year, but the settling of 234 recruits (September 1985-February 1986) did not quite match the success of 1984 ($n = 263$), though larval abundance was higher. The

temporal relationship between larval abundance and settlement for *Lythrypnus* is presented in Figure 16.

When the experimental reef was first sampled, the blennies *H. jenkinsi*, *Neoclinus stephensae*, *P. integripinnis*, *Gibbonsia elegans*, and *Alloclinus holderi* made up 30% of the assemblage (Table 4). During

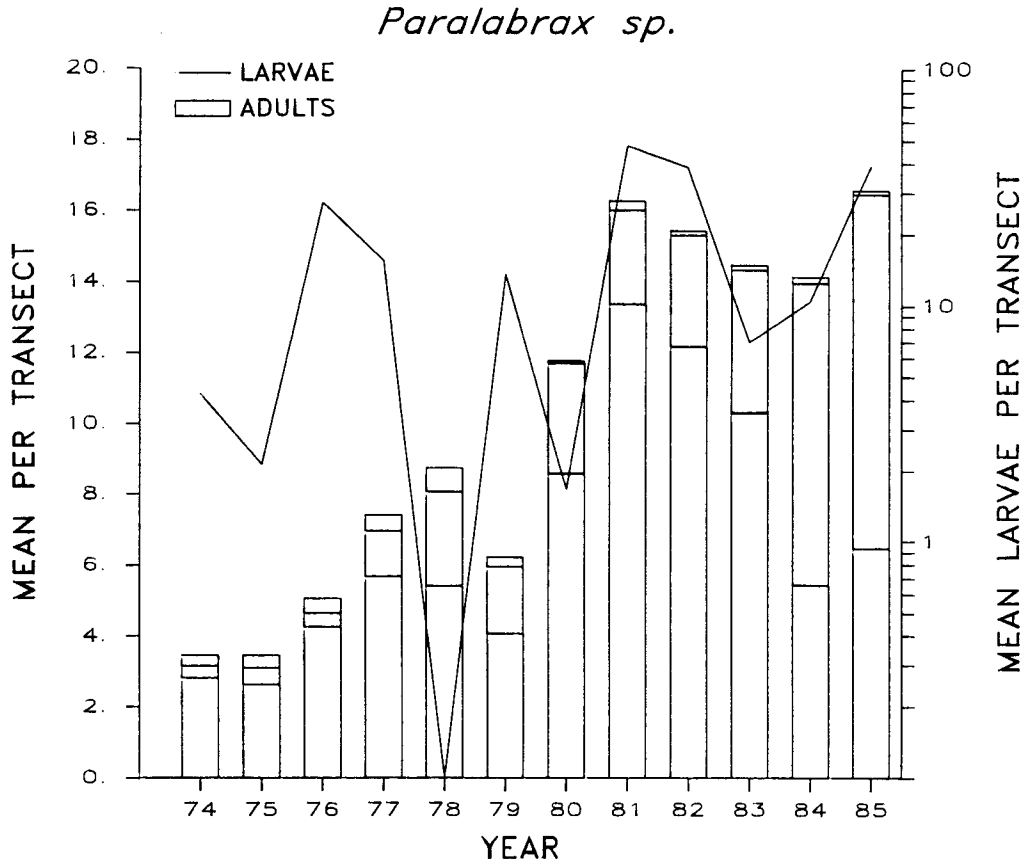


Figure 11. Abundance of larvae, juveniles, and adults of *Paralabrax*. Each bar represents the adults of three species: *P. clathratus* is the base, *P. nebulifer* the center, and *P. maculatofasciatus* the top.

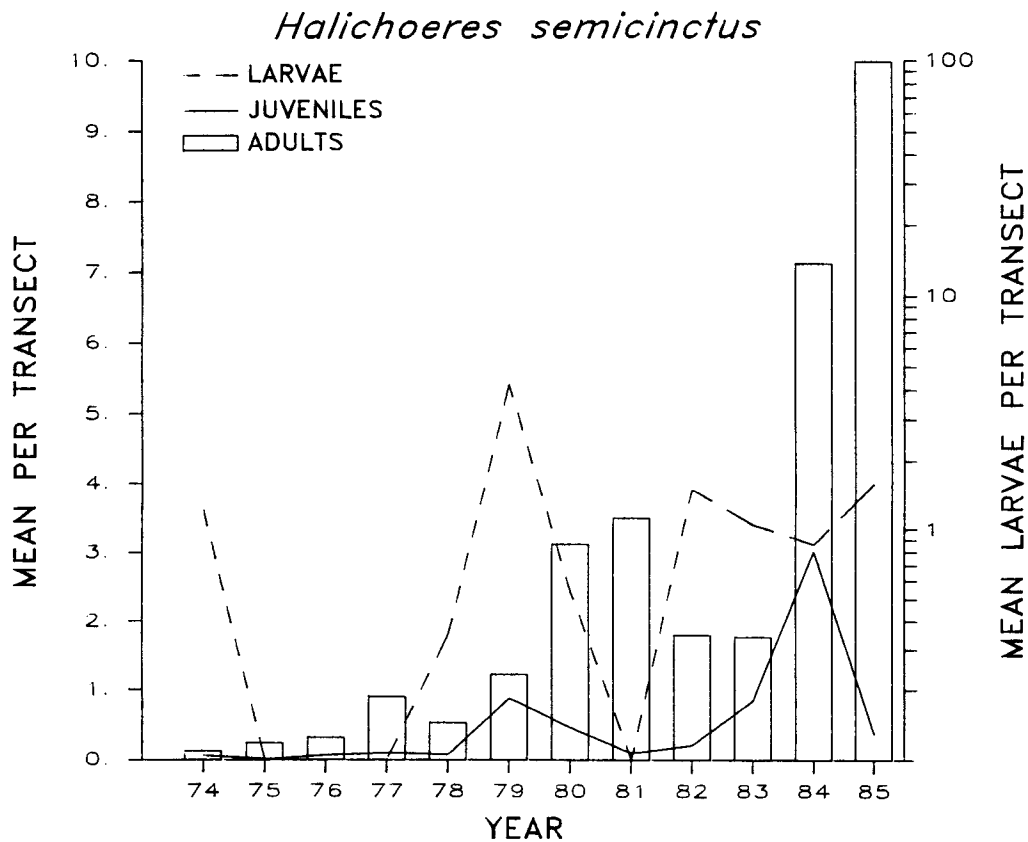


Figure 12. Abundance of adults, juveniles, and larvae of *Halichoeres semicinctus*.

Hypsypops rubicundus

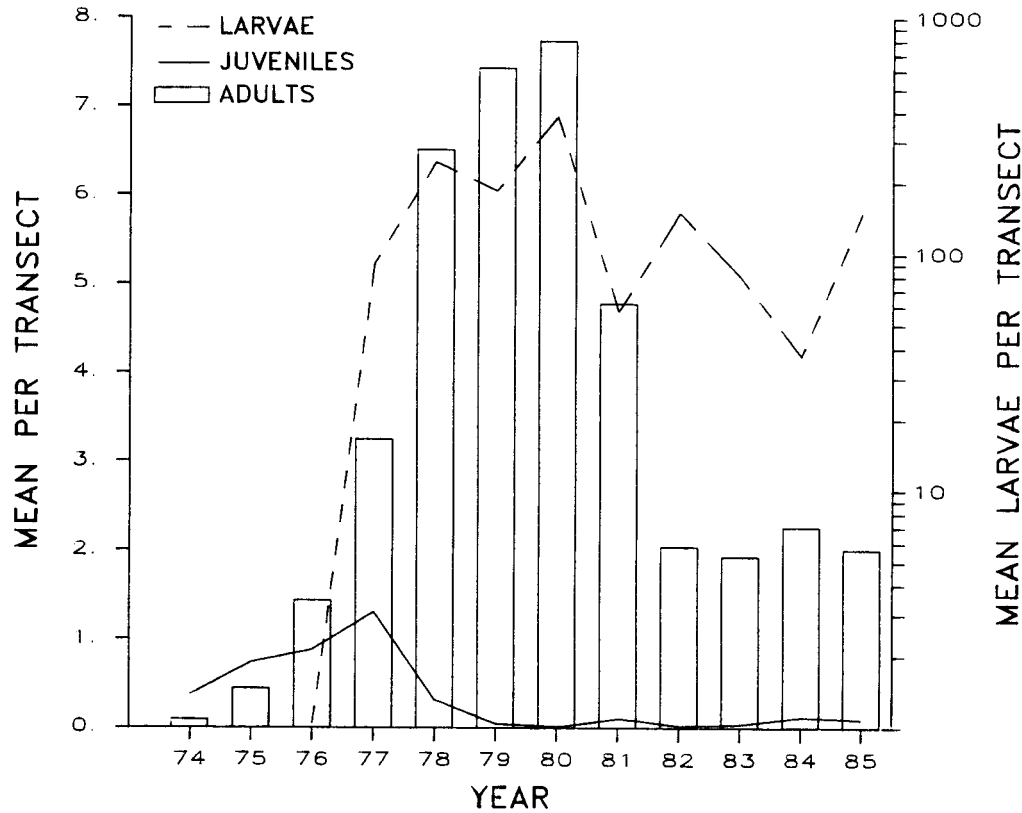


Figure 13. Abundance of adults, juveniles, and larvae of *Hypsypops rubicundus*.

Lythrypnus dalli

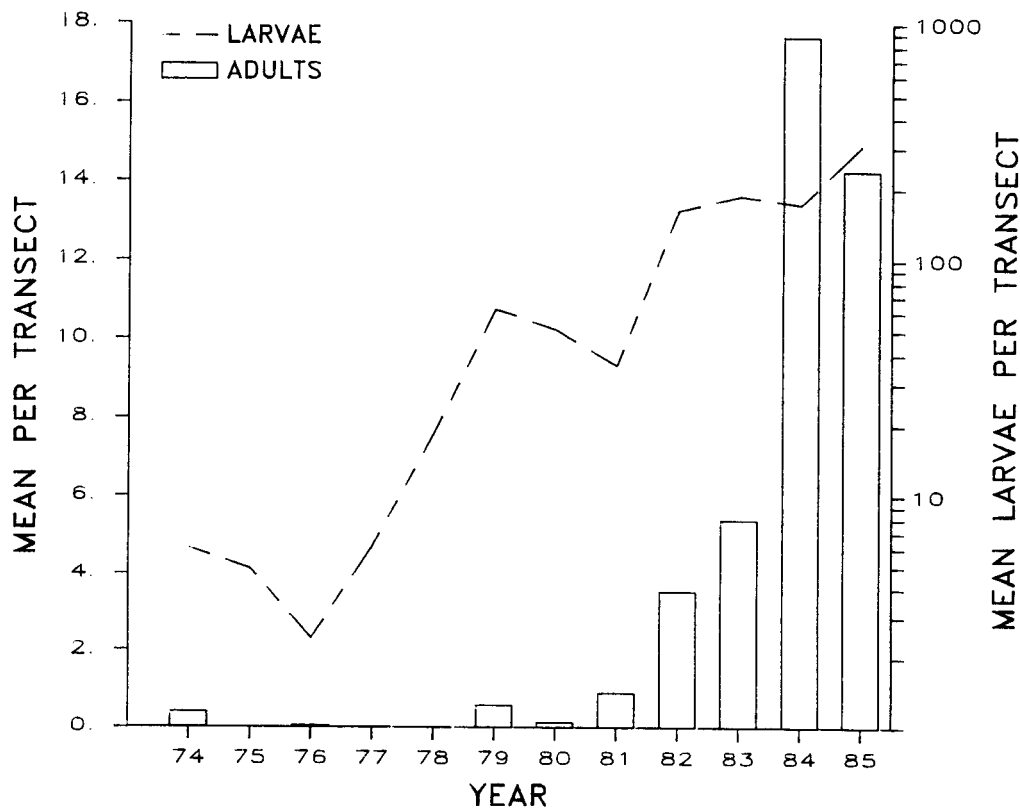


Figure 14. Abundance of larvae and adults of *Lythrypnus dalli*.

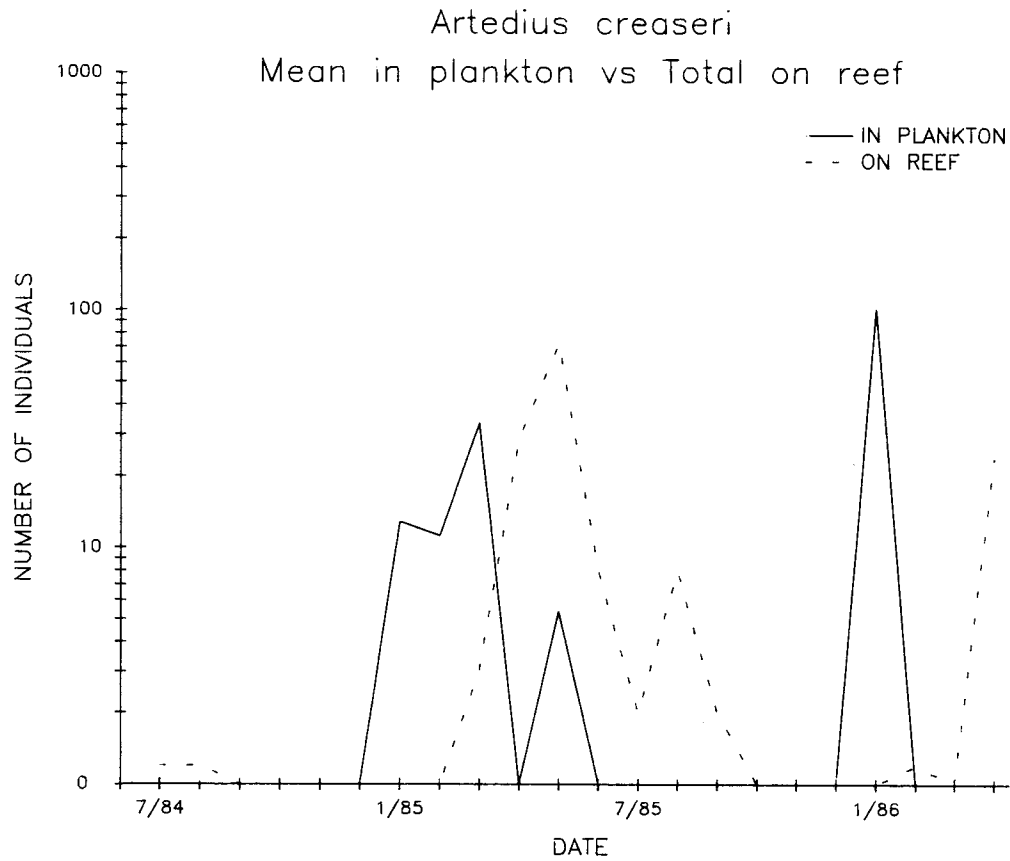


Figure 15. Temporal relationship between larval and recruit abundance, *Arteidius creaseri*.

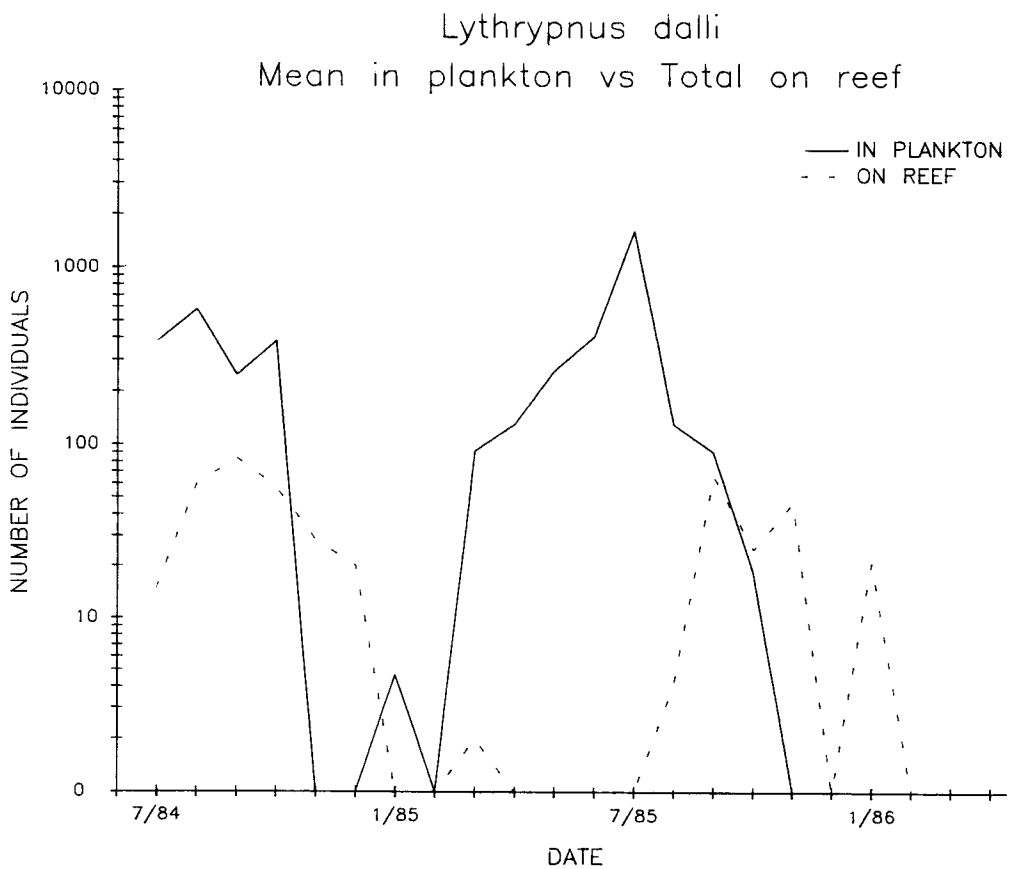


Figure 16. Temporal relationship between larval and recruit abundance, *Lythrypnus dalli*.

summer 1984, both *H. jenkinsi* and *N. stephensae* recruited to the reef at close to replacement levels, while the remaining three species did not recruit. During 1985 only two *H. jenkinsi* and two *A. holderi* settled on the reef, while *N. stephensae* again recruited at about replacement level. Again, *P. integripinnis* and *G. elegans* did not recruit. When these recruitment data are compared to the annual larval abundance for each species (Table 5), all species—with the exception of *Hypsoblennius* (1985)—showed relatively low (below mean) levels of availability (*A. holderi* larvae have not yet been described). The absence of recruitment to the predator-free reef may reflect this lowered larval availability.

By contrast, the almost complete absence of settling of *H. jenkinsi* in 1985 does not appear to correlate to larval density. There are a number of untested possibilities that could explain this situation. Some evidence (La Belle and Nursall 1985) suggests that blenny larvae settle preferentially to reefs occupied by conspecifics. Removal of adults would then cause lower settling. It is also possible that *H. jenkinsi* settles primarily in shallower water: the larvae are surface-orienting, and the center of distribution of adults is <10 m (Stephens et al. 1970). If this is true, the predator-free reef would be a marginal habitat. We have sampled a series of very shallow reefs this last year, and *H. jenkinsi* settlement

did occur in these habitats. Our studies now include reefs at 3 and 15 m, bracketing by depth the original study site. A third possibility is that the *Hypsoblennius* larvae that increased in 1985 were not *H. jenkinsi* but congeners which cannot, at present, be distinguished at preflexion stages.

Finally, a phenomenon of possible interest is suggested from *P. integripinnis* and *A. creaseri* data, which suggest that larval settlement may occur to soft (sandy) substrate. Movement of the cottid *A. creaseri* onto our reef suggests such a phenomenon, and Marliave's (1977) data for a congeneric species, though inconclusive, did show a settling preference for coarse gravel. Our data (Table 6) and that recently published by Barnett et al. (1984) appear to suggest that *Paraclinus*, which is taken abundantly in the epibenthic and midwater plankton at night, drops to low levels in these samples during the day ($x^2 < .01$). Some of this difference could be related to diurnal net avoidance, but we suggest that *Paraclinus* may presettle to the soft substrate during the day. Nocturnal excursions by these settlers into the water column to feed would allow drift to transport the metamorphosing juveniles onto available rock substrate. Compared to planktonic larvae, these presettled individuals might be better developed and more able to avoid the predator gauntlet present in a reef habitat. Further, immigration

TABLE 6
 Day/Night Distribution of Selected Larvae/1000 m³, Summer 1985 (Surface Samples Excluded)

	June		July		August	
	Mid-depth	Bottom	Mid-depth	Bottom	Mid-depth	Bottom
Day						
<i>Hypsoblennius</i> sp.	1,353.9	386.8	389.8	329.4	550.4	206.8
Clinid "A"	20.8	143.7	21.1	270.6/11.8	33.0	82.7/10.3
<i>Paraclinus integripinnis</i>	541.6/62.5 ^a	99.5	198.7/10.5	0	539.4/22.0	1,251.3/51.7
Goby "A/C"	166.6	22.1	21.1	235.5	22.0	62.0
<i>Lythrypnus dalli</i>	41.7	33.2	0	11.8	44.0	20.7
<i>Gobiesox rhessodon</i>	41.7	66.2	63.2	270.6	11.0	62.0
<i>Paralabrax</i> sp.	0	44.2	10.5/52.7	47.1	0	10.3
<i>Pleuronichthys verticalis</i>	41.7	11.1	10.5/10.5	188.2/35.3	0	20.7
<i>Heterostichus rostratus</i>	0	0	10.5	0	0	31.0
<i>Hypsypops rubicundus</i>	0	0	0	0	0	0
Night						
<i>Hypsoblennius</i> sp.	776.5	316.1	1,876.3	242.5	2,037.8	1,849.7
Clinid "A"	0/11.8	189.7/115.9	12.1	88.2/22.0	9.8/9.8	74.4/21.3
<i>Paraclinus integripinnis</i>	483.0/82.0	653.3/21.1	2,324.2/363.0	3,681.3/407.8	1,273.6/407.8	435.8/276.4
Goby "A/C"	0	073.8	411.6	407.8	313.5	414.6
<i>Lythrypnus dalli</i>	0	243.3	1,222.6	826.6	215.5/19.6	255.1/10.6
<i>Gobiesox rhessodon</i>	11.8	73.8/21.1	96.8	143.3/44.1	9.8	10.6
<i>Paralabrax</i> sp.	0	10.5	447.9	330.7/11.0	0	21.3
<i>Pleuronichthys verticalis</i>	11.8	21.1	12.1	0	0	0
<i>Heterostichus rostratus</i>	0	21.2	12.1	22.0	0	0
<i>Hypsypops rubicundus</i>	70.8	126.4	254.2	11.0	9.8	10.6

^aDenominator when present = number of late-stage larvae

would occur at night, which would reduce initial predation, because most discrete plankton feeders are visually orienting (Zaret 1980). Though we have thus far concentrated our epibenthic sampling to above-reef habitats, we are presently building an epibenthic sled to intensively sample the soft substrate (Madenjian and Jude 1985) in order to test this hypothesis.

SOME TENTATIVE CONCLUSIONS FROM THESE PRELIMINARY DATA

The present analysis suffers from a number of shortcomings that we hope to eliminate in the future; primarily, we lack detailed and specific juvenile fish surveys, and have had difficulty in sampling returning larvae. The available data, however, show some interesting relationships. Because we sample predominantly young larval stages before their offshore dilution with the coastal larval pool, there is a reasonable concordance between larval production and local population levels. The relationship between these early larval stages and incipient settlers will depend on a series of factors: the relationship between larval production in the local assemblage to that in the rest of the Southern California Bight, and the distributional pattern of the local larvae.

Little or no data are presently available regarding distributional patterns, but newly available data on larval age at least give us an estimate of the length of planktonic life. Preliminary bightwide data (Figure 4) appear to show the same pattern of total larval abundance for the bight as for King Harbor (1982-84), but the species data are not as clear. If there is annual agreement between larval production on local reefs and throughout the bight, there should be some level of agreement between larval production and incipient settlers. The same situation would obtain if larvae were not dispersed to the coastal pool. The relationship between incipient settlers and recruits depends upon the hazards of settling. Our predator-free experimental reef has demonstrated a close relationship between available larvae and recruitment in *Lythrypnus dalli* and *Artedius creaseri*, but other species have not recruited when expected. Better knowledge of settlement stimuli and wider latitude in available depths and types of predator-free habitats will enhance our continuing studies. We feel that our approach of combining a time series of samples with experimental analysis of recruitment may yield insight into the phenomena regulating fish stability on a temperate reef.

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