An immunochemical approach to quantifying predation by euphausiids on the early stages of anchovy

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ABSTRACT: Off southern California (USA), euphausiid crustaceans appear to be significant predators on the early stages of northern anchovy *Engraulis mordax*. Between 47 and 78 % of the natural mortality of northern anchovy eggs and yolk-sac larvae can be explained by euphausiid predation. The incidence of predation was determined from direct evidence provided by an immunochemical technique that detects anchovy remains in individual euphausiids. Rates of predation were determined from euphausiid feeding rates and digestion rates. The impact on the anchovy population was estimated by quantifying predator abundance by species, estimating predator and prey co-occurrence considering the diel migratory patterns of the predator, determining the number of prey removed d^{-1}, and generating natural mortality rates for the anchovy. Euphausiids ate 2.8 % of the anchovy population d^{-1} in the nearshore area and 1.7 % d^{-1} in the offshore area.

INTRODUCTION

Predation may be a major cause of larval fish mortality in the sea, yet the evidence is not conclusive because methods to assess mortality due to predation have been difficult to develop (Hunter 1984, Sissenwine 1984, Bailey & Houde 1989). Clearly, to discern predator-prey relationships, the predators need to be identified. Direct observation of stomach contents identified planktivorous fish as important predators of fish eggs and larvae (Hunter 1984, Brownell 1985, Dann et al. 1985, Alheit 1987). Likewise, visual analyses of the gastric cavities of gelatinous zooplankters revealed that they can be significant predators on the early stages of fishes (Moller 1984, Purcell 1985, 1989, 1990). Yet predator-prey relationships remain obscure in many situations where predator gut contents cannot be identified through visual analyses.

Direct evidence of predation by carnivorous crustaceans that macerate their prey is limited. In the field, only a few studies report larval fish remains in crustacean guts (Bailey & Yen 1983, Alvariño 1985, Yamashita et al. 1985, Yen 1987) despite the array of crustacean predators identified in the laboratory (Hunter 1984, Bailey & Houde 1989).

Crustacean predators of fish eggs and larvae in the sea need to be identified, and their predation rates need to be quantified. Serological methods that raise antibodies against the target prey successfully detected predation by invertebrates (Boreham & Ohiagu 1978, Feller et al. 1979, Theilacker et al. 1986), and these methods, which yield information on incidence only, can be quantified with additional information (Calver 1984, Sunderland 1988, Theilacker 1988). Recently, Theilacker et al. (1986) developed antibodies to the yolk protein of the northern anchovy *Engraulis mordax*, detected the yolk protein in the gut of a euphausiid crustacean *Euphausia pacifica*, and estimated predation rates at a limited field site (Theilacker 1988).

Here we evaluate, spatially and temporally, northern anchovy egg and larval mortality due to predation by the euphausiid assemblage commonly found in the California Current. We collected anchovy eggs and larvae and euphausiids during 2 California Cooperative Oceanic Fisheries Investigations (CalCOFI) sur-

veys. CalCOFI has been making seasonal measurements of the physical, chemical and biological characteristics of the California Current for more than 40 yr. CalCOFI cruises encompass the entire anchovy population during the peak of spawning. We analyzed the standardized plankton collections to estimate prey and predator abundance and applied an immunoassay, ELISPOT enzyme-linked immunospot assay, to identify the predators. We used this information to quantify predation rates. The predator net collected adult euphausiids only for the immunoassay. But because it is common for abundance of juvenile (6 to 11 mm) euphausiids to be an order of magnitude higher than adults (>11 mm) (Brinton & Wyllie 1976), we included both size classes to estimate the impact of the euphausiid assemblage on the anchovy population. Ignoring the smaller size class would have underestimated the predation impact.

METHODS

Field collections. Field collections were made on 2 CalCOFI cruises: one in November 1986, prior to peak spawning of northern anchovy, aboard the RV 'New Horizon' and one in March 1987, during peak anchovy spawning, aboard the NOAA vessel 'David Starr Jordan'. We considered the November collections to be a control set. At each station (Fig. 1), euphausiids and anchovy eggs and larvae were collected with standard double oblique plankton tows to 210 m using a Bongo net. Additionally, for the mortality estimates, anchovy eggs and larvae were collected with a CalVET (or PAIROVET) net lowered to a depth of 70 m. Both Bongo and CalVET nets are paired cylindrical-conical nets. The Bongo net frame has 505 µm mesh nets on both sides and the CalVET has 150 and 333 µm mesh nets (Smith & Richardson 1977, Smith et al. 1985). It was shown that there was no extrusion of eggs or larvae through the 150 µm mesh (Lo 1983). The samples were preserved in 5 % buffered formaldehyde.

Non-quantitative, oblique hauls to 50 m were taken to collect euphausiids intended for immunoassays whenever the ship was on station (Fig. 1) between 22:00 and 02:00 h. The depth and time of haul were chosen because many euphausiids migrate toward the sea surface at night (Brinton 1967) where they co-occur with eggs and yolk-sac larvae of northern anchovy which inhabit the upper 50 m of the sea (Ahlstrom 1959). Additionally, feeding activity for *Euphausia pacifica* is maximal after sunset and during most of the night when they have moved into the surface layers (Willason & Cox 1987). Euphausiids were collected using a black, 2 mm mesh Bongo net fitted with a plastic cod end. The dark net color should have decreased predator avoidance, and the large mesh should have allowed the prey to pass through the net, precluding potential biases caused by euphausiids feeding in the net (Nicol 1984). The plastic cod end was used to assure the retrieval of euphausiids in good condition. The large-mesh net selected for larger individuals.

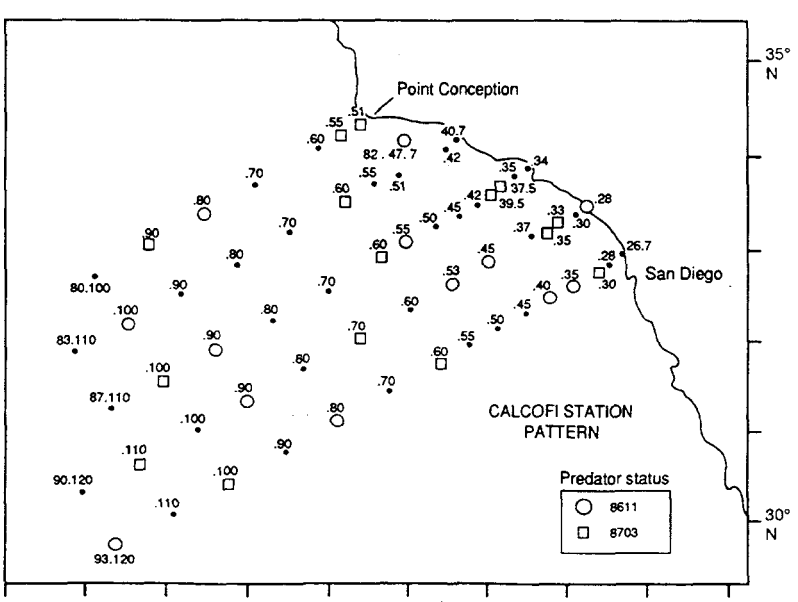


Fig. 1. Station pattern sampled by California Cooperative Oceanic Fisheries Investigations. Stations where separate collections were made for predators are indicated for November 1986 (CalCOFI Cruise 8611) and March 1987 (CalCOFI Cruise 8703)

Euphausiids were carefully transferred into buckets of surface seawater, 14 to 15 °C. (Ship's seawater was avoided, as it is often contaminated with metal ions.) Actively swimming euphausiids were selected, blotted quickly to remove excess seawater, and placed individually into 1.5 ml plastic tubes that were set in crushed ice. The sort-

ing process took about 1 min ind^{-1} from bucket to cooled tube; after 10 min, groups of tubes were frozen at −80 °C.

Euphausiid abundance. In the laboratory, all preserved euphausiids were identified to the species level. These included the 6 most common species which were used in the immunological analyses and 10 additional species which were present and also considered to be possible predators. Subsampling and counting procedures are described in Brinton (1976). All specimens ≥6 mm were enumerated in 2 size groups, (6 to 11 mm, >11 mm), then their abundance was standardized to numbers under 10 m^2 of water using the standard haul factor (Smith & Richardson 1977). Earlier laboratory experiments with *Euphausia pacifica* showed that feeding rates differed between these 2 size groups (Theilacker & Lasker 1974); euphausiids <11 mm preyed on anchovy eggs and larvae at about one-third the rate of the larger size group.

The stations were divided into 2 categories for analysis. Category 1 included stations with a high euphausiid predation incidence, as determined by the immunoassay, and the other category included stations with a low predation incidence. Any station with predation incidence equal to or greater than the overall average was considered Category 1. Eleven stations from the March cruise were used in the analysis. Offshore stations (Stn numbers greater than 70) were excluded because they are beyond the geographic distribution of anchovy eggs and few yolk-sac larvae were found offshore in past surveys. An analysis of variance procedure was used to compare abundance data of euphausiids >11 mm between the November and March cruises after the total abundance >11 mm from each station was logarithm transformed.

Prey abundance and mortality rates. Anchovy eggs were counted, staged, and ages were assigned according to developmental rates (Lo 1985, Moser & Ahlstrom 1985). Then eggs were grouped by half-day categories. Anchovy larvae were counted and measured. Stations used to determine prey abundance were the same stations used in euphausiid collections. Both eggs and yolk-sac larvae were used in the calculation of prey abundance. Standard length of net-collected and preserved yolk-sac larvae is ≤2.5 mm.

Age-specific abundance of anchovy eggs collected from CalVET net tows and size-specific abundance of larvae <9 mm from Bongo net tows were used in computing mortality rates. All stations occupied during the March 1987 cruise were used in this analysis. Preserved larval standard length was converted to live size (Theilacker 1980) and the age was estimated from a temperature-dependent Gompertz age-length growth curve (Methot & Hewitt 1980, Lo 1983). The larval abundance data were adjusted to conform to the following standard conditions: no extrusion (Lo 1983) and a constant water volume filtered per unit depth (Smith & Richardson 1977).

The abundance of larvae in each 1 mm length group was converted to daily production according to the following equation, assuming a steady state. For each station:

$$P_L = \frac{x\,(SHF/10)\,(0.05)}{(R_L)\,(\%\ sort)\,(dr_L)\,(av_L)} \quad (1)$$

where P_L = daily yolk-sac larval production per 0.05 m^2 at average age 5 d from fertilization (<2.75mm); x = no. of 2.5 mm larvae; SHF = standard haul factor, a factor used to convert catch of larvae to the no. of larvae under 10 m^2 water (Smith & Richardson 1977); 0.05 (m^2) = sea surface area covered by the CalVET net; R_L = retention rate for length L (mm) anchovy larvae (Lo 1983); $\%\ sort$ = percent of sample sorted by tow; dr_L (d) = average duration for each 1 mm length interval from 2.5 to 8.75 mm; and av_L = the proportion of larvae that did not avoid the net.

Larval length was converted to age according to the procedures described in Lo (1985, 1986). The decrease in the daily abundance of eggs and larvae with age was considered to be their morality. A single-equation model was chosen to describe anchovy egg and larval mortality (Lo 1986):

$$P_t = P_0 e^{-z x_1}\,(x_2/U)^{-\beta}, \quad (2)$$

where P_t = daily egg or larval production per 0.05 m^2 at age t (d); P_0 = daily egg production at age 0; z = daily instantaneous mortality rate for eggs and yolk-sac larvae; x_1 indexes eggs and larvae younger than age U days, $x_1 = t$ for $t < U$, $x_1 = U$ for $t > U$; x_2 indexes larvae older than age U days, $x_2 = U$ for $t < U$, $x_2 = t$ for $t > U$; U = age when the form of instantaneous mortality rate changes; β = coefficient for the instantaneous mortality rate for larvae where the daily instantaneous mortality rate = β/t, $t > U$; and t = age (d).

Mortality rates of anchovy eggs and yolk-sac larvae were initially computed for the 2 high- and low-predation categories. Because of the few stations in each category (6 and 5 stations respectively), we could not detect a difference in total mortality between these 2 categories. In order to obtain a more precise and accurate overall mortality estimate, we used the abundance data for anchovy eggs and larvae (<10 mm) from the entire March cruise.

Immunoassay. Aboard ship, a subsample (usually 6 to 10) of each night's euphausiid collection stored at −80 °C was assayed the following day. After the cruise, additional euphausiids were assayed at the Southwest Fisheries Science Center (SWFSC). Details of the immunoassay, a solid-phase enzyme-linked immunospot assay (ELISPOT) are given in Theilacker et al. (1986).

Rabbits were immunized with anchovy yolk protein (the antigen) to prepare the primary, polyclonal antibody. Polyclonal antibodies were used to increase the likelihood of antibody binding to prey proteins that are partially degraded due to euphausiid proteolytic activity.

Only euphausiids >11 mm were used in the assay. The stomach, hepatopancreas and hindgut were dissected out from the body and placed into 10 µl of extraction buffer. Tissues were teased apart, and the extract was dotted onto 0.45 µm pore nitrocellulose paper. The euphausiid gut contents on the nitrocellulose paper was reacted with the primary antibody. If the unknown gut contents contained anchovy yolk protein, it formed a complex with the primary antibody. The resulting antigen-antibody complex was treated with a secondary antibody which had been tagged with the enzyme alkaline phosphatase. The immobilized complex of antigen, primary antibody and secondary antibody on the nitrocellulose paper was visualized with a histochemical phosphatase stain; positive phosphatase activity produced a blue-black color (Theilacker et al. 1986).

In the ELISPOT, the color intensity of the reaction is directly related to the concentration of antigen (Ohman et al. 1991). However, in this situation, the concentration of antigen (yolk) did not correspond to the number of eggs or yolk-sac larvae eaten by the predator. The concentration of yolk ind.$^{-1}$ is not a constant because as eggs and larvae develop, they utilize yolk and the quantity of yolk ind.$^{-1}$ decreases. Thus, in our application, the immunoassay determines only the presence of yolk protein and not the number of eggs or larvae in the predator's gut.

Gut residence time and detection time. To estimate daily consumption by the euphausiid assemblage, information on the persistence of yolk protein in the guts of actively feeding individuals at *in situ* temperatures is required. The length of time a meal can be detected in a predator's gut using an immunoassay was designated the 'detection time' (Calver 1984, Sunderland 1988). In the SWFSC aquarium, we fed anchovy eggs to live *Euphausia pacifica* >11 mm collected on the March cruise. In our tests, 20 eggs were fed to individual euphausiids in 500 ml filtered seawater at 14°C. Because earlier experiments showed that *E. pacifica* ate an average of 1 egg in 2 h, the feeding treatment lasted 2 h. The actual time of ingestion was unknown. After 1 or 2 eggs were eaten (determined by counting the remaining eggs), we either immediately froze the euphausiid for the 0-time sample or subsequently fed it algae (non-antibody reactive) and sampled at 30 or 60 min intervals for 6 h. Algae was fed because earlier experiments showed that euphausiids retain their gut contents when feeding is interrupted (Lasker 1966, Willason & Cox 1987).

The percent of tested euphausiids exhibiting a positive reaction to anchovy yolk protein was expected to decrease with time. The difference in % positives between 2 points (t_1 and t_2) provides an estimate of the proportion of euphausiids whose detection time = t_2. If the decrease in % positive is linear, the loss rate per unit time is a constant (slope of the line), and the time corresponding to the 50 % positive is the average detection time. We assayed individual euphausiids using the ELISPOT procedure to determine the average detection time for actively foraging *Euphausia pacifica* >11 mm. We ascribed the average detection time to the >11 mm size category of all species analyzed in this study to compute hourly predation rates.

We have no data on detection time for 6 to 11 mm euphausiids. Ross (1982) found that allometric equations best described the relation between *Euphausia pacifica* body weight and rates of ingestion, respiration, excretion, growth and molting, thus revealing that all weight-specific physiological rates decreased with the increasing weight of the euphausiid. Because we could find no values in the literature to allow for a better assumption, we assumed that the fractional difference in the rate of digestion between 6 to 11 mm euphausiids and >11 mm euphausiids was similar to the fractional difference in feeding rate. Thus, we inferred that the loss rate for yolk protein in 6 to 11 mm euphausiid guts was one-third the loss rate for >11 mm individuals, and we divided the slope of the equation describing *E. pacifica* gut residence time by 3 to estimate the average detection time for the 6 to 11 mm euphausiid assemblage.

Predation rate. Daily euphausiid predation was estimated by considering the fraction of the euphausiid population by species that migrate into the depths inhabited by anchovy and the duration that they co-occur in the upper waters. Then the abundance of each euphausiid species by size was multiplied by the species-specific daily ingestion.

Among the euphausiids we sampled, vertical distribution is best known for *Euphausia pacifica*. *E. pacifica* has a daily depth range of 0 to 600 m. Juveniles and adults occupy a daytime depth of 300 to 600 m (Brinton & Wyllie 1976), but reach the upper 50 m at night (Brinton 1967). Brinton (1976) determined that 87 % of *E. pacifica* >6 mm reached the upper 50 m at night. Night was considered 1 h after sunset to 1 h before sunrise; total duration was ca 10 h in March. Thus to calculate predation rate we multiplied the total number of *E. pacifica* under 10 m^2 by 0.87. Abundances of the other euphausiids present in the study were similarly adjusted (Table 1).

Species-specific daily ingestion was determined by considering the results of the immunoassay. Because the immunoassay only determined the presence or

Table 1. Day and night vertical range of euphausiid species[a]

Species	Vertical range	% Population reaching upper 50 m at night 6–11 mm	>11.5 mm
Euphausia pacifica	0–600 m	87	87
E. gibboides[b]	0–600 m	87	87
E. eximia	0–600 m	87	87
E. recurva	0–600 m	87	87
E. mutica	0–600 m	87	87
E. hemigibba	0–600 m	87	87
Nematoscelis difficilis	Thermocline to ca 300–600 m	70	40
N. atlantica	Thermocline to ca 300–600 m	70	40
N. tenella	Thermocline to ca 300–600 m	70	40
Thysanoessa gregaria	0–150 m[c]	60	60
T. spinifera	0–100 m[c]	87	87
Thysanopoda astylata	0–600 m	87	87
Stylocheiron carinatum	0–150 m	87	87
S. affine	0–200 m[c]	87	87
Nictiphanes simplex	0–150 m	87	87

[a] Data taken from Brinton (1962, 1967)
[b] Adults are >15 mm; they do not usually reach the upper 50 m at night
[c] Day and night depth

absence of yolk protein in euphausiid guts, a Poisson distribution was used to describe the mean no. of prey ingested over an interval of time defined by the duration of gut passage, or the detection time. This distribution assumes that ingestion events were independent and randomly distributed over each time interval. Accordingly, the frequency of negative assays can be related to the number of ingestion events by

$$P(x=0) = e^{-\mu} \quad (3)$$

where $P(x=0)$ = the probability of no anchovy being eaten (negative immunoassays) and μ = mean no. of prey ingested per time interval. That is, we equated the relative frequency of zero predation to the exp(−mean) and solved for the mean no. of eggs and yolk-sac larvae eaten by 1 euphausiid. The mean number eaten h^{-1} was estimated by dividing by the laboratory-determined detection time. Ingestion by 6 to 11 mm euphausiids was assumed to be the same as *Euphausia pacifica* of that size and was multiplied by 0.3 to account for their slower feeding rate (Theilacker & Lasker 1974, Ross 1982). Detection time for the 6 to 11 mm group was adjusted as discussed above.

Here a negative assay provides more information than a positive one. A negative assay indicates that the euphausiid predator has not eaten during the measured detection time. A positive assay indicates that the euphausiid has eaten 1 or more prey; there is no temporal information.

To estimate the impact of the euphausiid population preying on the anchovy population, we compared the loss of anchovy with the total natural egg and larval mortality that was determined independently.

RESULTS

Field collections

On the November cruise in 1986, plankton collections were taken at 58 stations. At 13 stations, tows for invertebrate predators were also made (Fig. 1). Only 1 of the predator collections was taken inshore where some anchovy spawning had occurred (Fig. 2a).

On the March cruise in 1987, plankton collections were taken at 57 stations. Fifteen invertebrate tows were taken (Fig. 1), and 10 of them corresponded to areas where anchovy eggs and yolk-sac larvae were collected. In 1987, anchovy spawning was moderate in the Southern California Bight (Fig. 2b).

Euphausiid abundance

The mean abundance of adult euphausiids >11.0 mm, all species combined, was similar between the November (346.5 ind. per 10 m^2) and March (287.9 ind. per 10 m^2) cruises ($F = 0.33$; df = 1,23; $p = 0.57$; F-test computed on log-transformed data). The abundance under 10 m^2 at 12 stations in November ($n = 12$) ranged from 18 to 1074 adults, and in March (n = 13) abundance ranged from 41 to 1352 adults. The high-abundance, nearshore (<60 mile) stations were dominated by *Euphausia pacifica* and *Nematoscelis difficilis* in November and March (Tables 2 & 3).

Five euphausiid species dominated the assemblage in March; these species were analyzed for evidence of predation and their abundance is detailed here together with information on depth distribution (Table 1) and relative abundance (Brinton 1967, Brinton & Wyllie 1976). A sixth euphausiid species, *Nyctiphanes simplex*, was analyzed for 1 station only (87.39.5; Table 3).

Euphausia pacifica, usually the most common species in the southern California area, was present at 9 of the 10 stations used in the predation analysis for the March cruise and was dominant at 5 of the 10 stations.

Nematoscelis difficilis is usually second in abundance among the euphausiids in the southern California area. It migrates through a vertical range of about 300 m. The 2 size groups of *N. difficilis* were

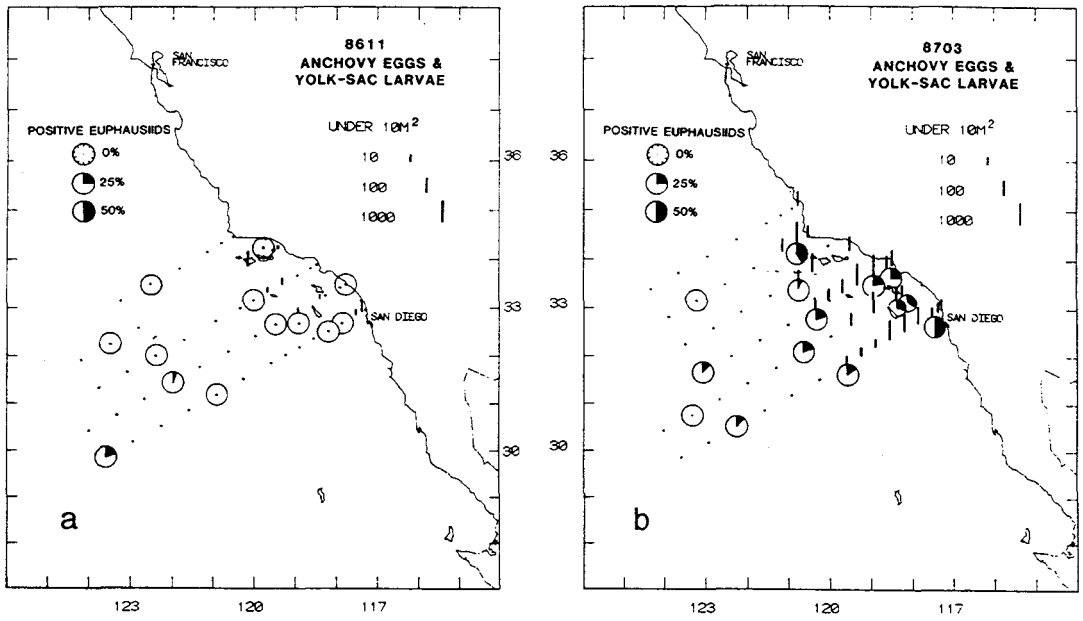


Fig. 2. *Engraulis mordax*. Distribution of positive euphausiid predators, expressed as % positive, superimposed on northern anchovy egg and yolk-sac larval abundance for (a) November 1986 and (b) March 1987. Anchovy numbers adjusted to equal the average abundance under 10 m^2 of sea surface

dominant at Stns 87.35 and 93.30 and present at all 10 stations.

Euphausia gibboides migrates from a depth of 300 to 500 m in the daytime to the thermocline at night. It was present at 9 of the 10 stations in the study area. Like *Euphausia recurva*, it occurred more offshore than *E. pacifica*, but their distribution overlapped. The highest abundance was at Stn 93.60 with both size groups equal in number. *E. gibboides* adults would not be expected to reach the upper 50 m at night unless the thermocline was particularly shallow, therefore individuals >15.5 mm were not used in the predation estimate.

Euphausia eximia was present in 5 of the 10 stations in this study, with its highest abundance at Stn 83.60. All developmental stages of *E. eximia* are concentrated in the surface layer at night.

Euphausia recurva migrates from 300-600 m to 0-100 m at night. It was present at 6 of the 10 stations in this study, reaching its highest abundance at Stn 93.60 with a total of 425 ind. per 10 m^2 for the >11.5 mm group.

Nyctiphanes simplex migrates from 150 m to the surface at night. It was present at 8 of the 10 study stations, and its highest abundances were at Stns 93.30 and 87.39.5.

Prey abundance and mortality rate

The presence of anchovy prey was minimal in November and abundant in March, with most of the spawning occurring in the Southern California Bight (Fig. 2a, b). In November, anchovy eggs were found at only 1 predator station (36 eggs per 10 m^2 at Stn 90.45), whereas in March, abundant eggs and yolk-sac larvae were collected at the nearshore predator stations (Table 4).

Mortality rates for the March cruise were determined using Eq. 2, assuming that eggs and yolk-sac larvae (younger than 5 d) follow an exponential decay (z = 0.036, SE = 0.036) and older larvae follow a Peratotype of instantaneous mortality (β = 1.989, SE = 0.213) (Table 5). P_0 = 4.13 eggs per 0.05 m^2 (SE = 0.67) for the entire survey area. The z-value of 0.036 was later used as the daily mortality rate for both high- and low-predation categories described in the 'Methods' section.

Euphausiid predation

On the November cruise, only 1 euphausiid collection station (90.45) was taken near shore where there was some anchovy spawning (Fig. 2a). In all, 119 eu-

Table 2. Mean abundance of the dominant euphausiid species under 10 m^2 of sea surface taken at stations where predator collections were made in November 1986. 95 % confidence intervals obtained from $\log_{10}$ transformation are in parentheses

Cruise 8611 Stn	Size (mm)	Species[a] Ep	Er	Eg	Ex	Nd	Other	Total
80. 80	6–11	1201	120	0	0	529	415	2265
	>11	10	71	30	0	30	0	141
83. 100	6–11	3278	41	20	0	902	798	5039
	>11	20	20	20	0	102	0	162
87. 55	6–11	1227	0	21	0	1355	297	2900
	>11	0	0	22	22	171	0	215
90	6–11	292	136	49	0	970	342	1789
	>11	0	10	0	0	49	49	108
90. 28	6–11	0	0	0	0	0	198	198
	>11	0	0	0	0	0	18	18
45	6–11	1033	0	32	0	506	295	1866
	>11	32	0	11	11	118	0	172
53	6–11	944	22	0	22	630	538	2156
	>11	245	0	22	66	741	0	1074
90	6–11	30	80	10	0	490	712	1272
	>11	0	30	10	0	50	0	90
93. 35	6–11	280	0	0	0	992	520	1792
	>11	20	0	10	50	682	0	762
40	6–11	902	50	0	40	409	970	2371
	>11	122	10	51	10	336	20	549
80	6–11	538	33	22	22	314	707	1636
	>11	33	0	11	11	201	0	256
120	6–11	0	83	0	0	0	478	561
	>11	0	20	10	0	0	581	611
Mean:	6–11 mm	1987.1 (929–2671)						
	>11 mm	346.5 (106–441)						

[a] *Ep = Euphausia pacifica; Er = E. recurva; Eg = E. gibboides; Ex = E. eximia; Nd = Nematoscelis difficilis;* Other = *E. hemigibba, E. mutica, N. atlantica, N. tenella, Nyctiphanes simplex (Ns), Thysanoessa gregaria, T. spinifera, Stylocherion affine, S. carinatum, S. suhmi, Thysanopoda astylata*

phausiids were assayed and 2 individuals tested positive for anchovy remains. The 2 positive-reactive euphausiids, both *Euphausia gibboides*, were collected at 2 stations 250 to 350 mile offshore where no eggs or larvae were collected (Fig. 2a).

On the March cruise, predator samples were taken at 10 stations where anchovy eggs and yolk-sac larvae were collected. Between 9 and 50 % of the predatory euphausiids at these stations tested positive (Table 6). In all, 67 or 24 % of the 283 euphausiids assayed tested positive for anchovy yolk protein. Although the relation between percent positive euphausiids and prey abundance was variable at low prey levels, the number of euphausiids eating anchovy seemed to increase rapidly with a small increase in prey abundance (Fig. 3). Maximum percent feeding appeared to be above 1000 prey under 10 m^2. Again, as in the November cruise, a few positive-reactive euphausiids (*Euphausia recurva*) were taken from offshore stations outside the anchovy spawning area (Table 6, Fig. 2b).

Gut residence time and detection time

Results from the digestion experiments showed that yolk protein, consumed by eating 1 or 2 anchovy eggs, could not be detected in the guts of actively foraging euphausiids after 6 h (Fig. 4). The decrease in the percentage of positive euphausiids appeared to be linear with time; an exponential description of the data was

Table 3. Abundance of the dominant euphausiid species under 10 m^2 of sea surface taken at stations where predator collections were made in March 1987. 95 % confidence intervals obtained from log_{10} transformation are in parentheses. Species abbreviations as in Table 2

Cruise 8703 Stn	Size (mm)	Species *Ep*	*Er*	*Eg*	*Ex*	*Nd*	Other	Total
80. 55	6-11	997	62	10	0	0	82	1151
	>11	1248	0	0	0	104	0	1352
90	6-11	55	93	0	0	185	485	818
	>11	0	61	0	0	20	20	101
83. 60	6-11	2367	216	20	157	512	855	4127
	>11	124	0	10	10	59	0	203
87. 37.5	6-11	234	0	11	0	87	43	375
	>11	266	0	11	0	535	0	812
39.5	6-11	146	10	10	10	252	817	1245
	>11	0	0	0	0	31	10[a]	41
60	6-11	351	33	11	11	154	308	868
	>11	111	11	11	0	187	0	320
100	6-11	119	30	0	0	10	590	749
	>11	0	0	0	0	108	30	138
90. 33				Non-quantitative				
35	6-11	85	0	11	0	227	65	388
	>11	202	0	0	0	0	11	213
70	6-11	32	39	19	0	10	108	208
	>11	11	29	0	0	0	19	59
110	6-11	0	91	0	0	0	280	371
	>11	0	20	0	0	0	61	81
93. 30	6-11	102	0	0	11	362	498	973
	>11	152	0	0	0	34	11	197
60	6-11	0	425	42	74	212	509	1262
	>11	0	53	21	11	32	22	139
100	6-11	0	304	0	0	0	497	801
	>11	0	0	0	0	0	86	86
Mean:	6-11 mm	1025.9 (378-1576)						
	>11 mm	287.9 (93-309)						

[a]The >11 mm size class at this station was mainly *Nyctiphanes simplex*

poor. The weighted linear regression predicted a loss rate of about 13 % h^{-1} (slope), a detection time of 7.2 h, and a 50 % probability of complete digestion of the yolk protein after 3.5 h.

Euphausiid predation rate

To set up a comparative analysis of prey mortality due to euphausiid predation, we used the computed predation incidence (0.237; Table 6) as a guide for grouping the stations into 2 categories: an area of high predation (≥0.24) and an area of low predation (<0.24). Our hypothesis was that more prey will be eaten in the high-predation area. The high-predation category included the following 6 stations: 93.28, 93.30, 90.33, 90.35, 87.37.5, and 80.55. To have a sufficient number of eggs and larvae for the analysis of prey abundance in the high-predation area, we included Stn 93.28, which was very close to Stn 93.30. The low-predation category contained 5 stations: 93.60, 90.70, 87.39.5, 87.60, and 83.60. Stations in the high-predation category were closer to shore than those in the low-predation category (Fig. 1, Tables 4 & 6).

The potential predation impact by the euphausiid population was estimated by considering the abundance and feeding rate of each predatory species quantified in this study. The nearshore euphausiid spe-

Table 4. *Engraulis mordax*. Abundance of northern anchovy eggs and yolk-sac larvae under 10 m^2 of sea surface taken in Bongo net tows at stations where predator collections were made in March 1987

Cruise 8703 Stn	Anchovy eggs	Anchovy yolk-sac larvae
80. 51	580	32
55	39244	793
90	0	0
83. 60	0	256
87. 37.5	1259	13833
39.5	24220	15487
60	0	1568
100	0	0
90. 33	877	7787
35	1576	7200
70	0	0
110	0	0
93. 28	559	7835
30	525	145
60	0	389
100	0	0
Total	68840	55325

Table 5. Daily production under 0.05 m^2 (P_t) of anchovy eggs (E) and larvae at age t from the March 1987 cruise. Eggs are from 40 stations and larvae are from 46 stations. See 'Methods' for x_1 and x_2. P_t were computed for the entire survey area in Fig. 1. The inverse of *MSE* was used as case weight for a weighted nonlinear regression

Egg or larvae (mm)	t (d)	Pt	x_1	x_2	*MSE*
E	0.38	3.945	0.38	5	1.1394
E	0.83	3.262	0.83	5	1.1394
E	1.39	3.909	1.39	5	1.1394
E	1.85	4.320	1.85	5	1.1394
E	2.40	5.590	2.40	5	1.1394
E	2.80	2.800	2.80	5	1.1394
2.0–3.0	4.87	3.570	5	4.87	0.049
3.5–4.0	8.54	1.595	5	8.54	0.049
4.5–5.0	11.27	0.502	5	11.27	0.049
5.5–6.0	13.65	0.311	5	13.65	0.049
6.5–7.0	15.88	0.236	5	15.88	0.049
7.5–8.0	18.14	0.147	5	18.14	0.049
8.5–9.0	20.34	0.153	5	20.34	0.049

cies ate 2291 anchovy eggs and yolk-sac larvae d^{-1} per 10 m^2, roughly 3 times the number of prey eaten daily by the offshore euphausiids (Table 7). No variances for these estimates were obtained. At these feeding rates, the euphausiid assemblage ate ca 2.8 % of the anchovy population d^{-1} in the nearshore area and 1.7 % d^{-1} in the offshore area (Table 7). This rate of predation accounts for between 47 and 78 % (0.017/0.036 = 0.47; 0.028/0.036 = 0.78) of the anchovy natural mortality (Table 7).

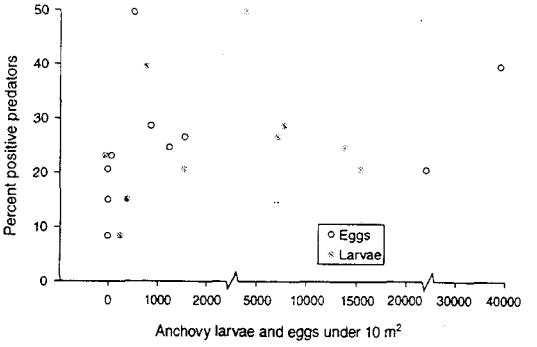
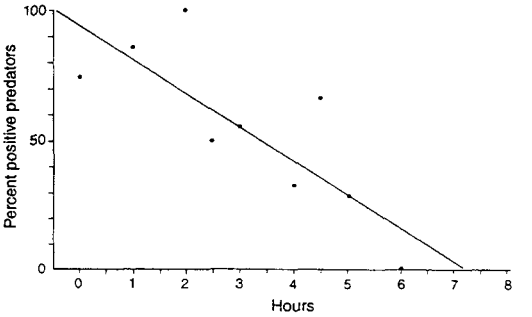


Fig. 3. *Engraulis mordax*. Scatter diagram of abundance of northern anchovy eggs and yolk-sac larvae and the positive-reactive euphausiid predators at concurrent stations in March 1987



HOURS FED ALGAE	ELISPOT (fraction+)	ELISPOT (percent+)
0	6/8	75
1	6/7	86
2	7/7	100
2.5	1/2	50
3	5/9	56
4	2/6	33
4.5	2/3	66
5	2/7	29
6	0/6	0

Fig. 4. *Euphausia pacifica, Engraulis mordax*. Percent of actively foraging *E. pacifica* that have anchovy yolk protein in their guts (p, percent positive; no. positive/no. tested) as a function of hours since feeding (t, in hours): $p = 94.6 - 12.7\ t$

DISCUSSION

The ELISPOT immunoassay confirmed that predation by euphausiids was a significant source of mortality for the young stages of northern anchovy off California. Anchovy prey may be extremely vulnerable to euphausiids, for the pelagic eggs are spawned

Table 6. Predator stations in March 1987 and frequencies of positive immunoassay reactions (no. positive/no. examined) by species. Species abbreviations as in Table 2

Cruise 8703 Stn	Species *Ep*	*Er*	*Eg*	*Ex*	*Nd*	*Ns*	Other	Positive fraction	Total % positive
81. 55	8/19	-	-	-	0/1	-	-	8/20	40.0
90	0/1	0/2	-	0/3	-	-	-	0/6	0
83. 60	2/20	-	-	0/1	0/2	-	-	2/23	8.7
87. 37.5	4/17	-	1/2	-	0/1	-	-	5/20	25.0
39.5	-	-	-	-	0/1	4/18	-	4/19	21.1
60	1/7	0/1	2/4	0/1	1/5	-	0/1	4/19	21.1
100	-	3/9	0/4	-	0/7	-	-	3/20	15.0
90. 33	6/19	-	-	-	0/1	-	1/4	7/24	29.2
35	7/25	-	-	-	-	-	0/1	7/26	26.9
70	-	4/15	0/2	-	-	-	-	4/17	23.5
110	-	0/15	0/1	-	-	-	-	0/16	0
93. 30	17/34	-	-	-	1/2	-	-	18/36	50.0
60	-	0/9	1/2	1/1	0/1	-	-	2/13	15.4
100	-	3/24	-	-	-	-	-	3/24	12.5
Total	45/142	10/75	4/15	1/6	2/21	4/18	1/6	67/283	23.7
% Positive	31.7	13.3	26.7	16.7	9.5	22.2	16.7		

in a large patch and in an area of high euphausiid concentration at night when the euphausiids rise to the surface. McGurk (1986) has suggested that the patchy distribution of fish eggs and larvae may result in high mortality rates due to predation. During this study between 47 and 78 % of the natural mortality could be ascribed to euphausiid predation. It is reasonable to suggest that predation, and not starvation, was the main source of early mortality since eggs and early larvae are not dependent on exogenous foods.

To analyze our data, we stratified the stations according to predation rate. The population abundance of euphausiids was quantified over the area of co-occurrence with anchovy. Our hypothesis was that more prey will be eaten in areas where the incidence of predation was high. Calculated predation rates that relied on direct evidence of predator gut contents, prey and predator co-occurrence, prey and predator abundance estimates, and predator digestive capacities indicated that the fraction of the anchovy population removed by the euphausiid population was greater nearshore (0.028) than offshore (0.017). Thus euphausiid feeding rate seemed to depend on encounter rate resulting in higher predation nearshore where prey were more abundant. *Euphausia pacifica* dominated the nearshore stations and had the highest (37 %) incidence of predation. An earlier feasibility study had a similar outcome (Theilacker 1988). The incidence of predation by *E. pacifica* detected using ELISPOT was greater (79 %) at a single nearshore station where anchovy densities were higher than at an offshore station (8 %) where anchovy densities were low.

A more meaningful, physiological approach to establishing differences between stations would be to stratify by prey abundance using the prey levels above and below the critical prey level for maximum feeding rate as portrayed by a functional response curve (Peterman & Gatto 1987). Although we do not have sufficient data to determine this level, the general shape of the relation described in Fig. 3 suggests that the maximum percent feeding by euphausiids occurred at prey concentrations of ca 1000 prey per 10 m^2. The relation between euphausiid predation and prey abundance appeared to increase rapidly with a small increase in prey level (Fig. 3). In our study, the cutoff used for the high and low predation areas (24 % positive predators) corresponded to what appears to be the critical prey concentration (Fig. 3), lending additional credence to the areas selected for comparison. Additionally, little predation was observed in November 1986 (Fig. 2a) when the maximum prey concentration was 100 per 10 m^2.

Although laboratory data on the predatory behavior of some of the assemblage euphausiids is not available, it is clear on grounds of functional morphology as well as experimental evidence and gut content studies, that the relative importance of plant and animal prey differs in euphausiid species (Mauchline 1967). Most euphausiids are omnivorous (Ohman 1984, McClatchie 1985). Stuart (1986) found in the laboratory that adult (≥11 mm) *Euphausia lucens* were able to consume large numbers of anchovy larvae. *E. lucens* also consumes phytoplankton and copepods (Stuart & Pillar 1990). Theilacker & Lasker (1974) showed in laboratory experiments that the median number of yolk-sac anchovy larvae eaten ind.$^{-1}$ d^{-1} by *E. pacifica* ranged from 2 to 17: larval (<6 mm) *E. pacifica* ate 2, juveniles (6 to 11 mm) ate 6, and adults (>11 mm) ate

17. In this study, 6 species tested from the field had eaten anchovy. In the laboratory, euphausiids were capable of consuming enough anchovy prey to meet their daily metabolic requirements (*E. pacifica*, Theilacker & Lasker 1974; *E. lucens*, Stuart 1986). But for *E. pacifica* <11 mm, there appears to be a point of satiation. Offered abundant prey, juvenile *E. pacifica* seldom ate more than 6 larvae d^{-1} (Theilacker & Lasker 1974). Therefore our estimates of 0.1 to 2 anchovy consumed d^{-1} $ind.^{-1}$ seem reasonable considering that they would also be consuming other prey. Likewise, measured phytoplankton ingestion rates of *E. pacifica* studied in the field were low, probably because they were consuming other foods in addition to phytoplankton (Willason & Cox 1987).

Euphausiids are numerically one of the major plank-

Table 7. Comparison between the high- and low-predation stations of euphausiid species-specific feeding rates, the impact of euphausiid predation on the anchovy population, and total anchovy natural mortality rates

Predator		Ind. per 10 m^2	No. analyzed	No. not feeding	Freq. of zeros	No. eaten $ind.^{-1}$ h^{-1}[a]	Fraction co-occurring	No. of anchovy eaten d^{-1} per 10 m^2
High predation stations 'inshore'								
Euphausia pacifica	6–11 mm	1269				0.0125	0.87	138.05
	>11 mm	1804	114	72	0.6316	0.1313	0.87	2 060.65
E. recurva	6–11 mm	62						
	>11 mm	0	0					
E. giboides	6–11 mm	32				0.0189	0.87	5.25
	11.5–15 mm	0	2	1	0.5000	0.1980	0.87	0.00
E. eximia	6–11 mm	11						
	>11 mm	0	0					
Nematoscelis difficilis	6–11 mm	816				0.0061	0.70	34.68
	>11 mm	138	5	4	0.8000	0.0638	0.40	35.19
Nyctiphanes simplex	6–11 mm	508						
	>11 mm	11	0					
Other	6–11 mm	202				0.0061	0.87	10.67
	>11 mm	22	5	4	0.8000	0.0638	0.87	12.20
Total	6–11 mm	2900						
	>11 mm	1975	126					
Total no. of anchovy eaten								2 291.45
No. of anchovy eggs & larvae per 10 m^2								81 633.18
Fraction of anchovy population eaten d^{-1}								0.028
Total mortality, *Z* (SE)								0.036 (0.036)
Low predation stations 'offshore'								
E. pacifica	6–11 mm	3130				0.0032	0.87	87.27
	>11 mm	512	27	24	0.8889	0.0337	0.87	149.90
E. recurva	6–11 mm	723				0.0178	0.87	111.93
	>11 mm	93	25	13	0.5200	0.1868	0.87	151.17
E. giboides	6–11 mm	113				0.0128	0.87	12.57
	11.5–15 mm	53	8	5	0.6250	0.1343	0.87	61.92
E. eximia	6–11 mm	252				0.0110	1.00	27.80
	>11 mm	21	3	2	0.6667	0.1158	1.00	24.33
N. difficilis	6–11 mm	1675				0.0032	0.70	37.58
	>11 mm	396	9	8	0.8889	0.0337	0.40	53.31
N. simplex	6–11 mm	836				0.0068	0.87	49.74
	>11 mm	10	18	14	0.7778	0.0718	0.87	6.25
Other	6–11 mm	1814				0.0000	0.87	0.00
	>11 mm	41	1	1	1.0000	0.0000	0.87	0.00
Total	6–11 mm	8543						
	>11 mm	1126	91					
Total no. of anchovy eaten								717.78
No. of anchovy eggs & larvae per 10 m^2								41 920.53
Fraction of anchovy population eaten d^{-1}								0.017
Total mortality, *Z* (SE)								0.036 (0.036)

[a] Poisson distribution was assumed

tonic organisms in the eastern north Pacific (Boden et al. 1955). They co-occur with the eggs and larvae of pelagic spawning fishes. The euphausiid abundances that we calculated are averages. At times, abundances of euphausiids are extremely high. Surface swarms of *Thysanoessa spinifera* are common events off California during spring and summer (Smith & Adams 1988). There are numerous theories, including congregating to feed, about the mechanisms that cause swarming, but Smith & Adams (1988) argue that it is mainly related to reproduction. Likewise, Endo et al. (1985) concluded that *E. pacifica* in Sendai Bay, Japan, swarmed for reasons other than feeding (e.g. possibly mating). On the other hand, Brown et al. (1979, in McClatchie 1985) note that swarms of *Meganyctiphanes norvegica* in the Bay of Fundy preyed on copepods. Stimuli for swarming are complex and probably vary (Komaki 1967, Antezana et al. 1972). However, the tendency for euphausiids to concentrate near the surface during swarming could contribute importantly to variability in predation mortality of anchovy larvae.

In addition to euphausiids preying on the young stages of fish, other carnivorous invertebrates in the California Current also may eat fish eggs and larvae. The biomass of calanoid copepods appears to be about 3 times that of euphausiids (Isaacs et al. 1969). In laboratory experiments, some predatory copepods can consume as many fish larvae d^{-1} as euphausiids (Hunter 1984, Bailey & Houde 1989); however, unlike euphausiids (Theilacker & Lasker 1974), copepod feeding rate is reduced in the presence of an alternate prey (Lillelund & Lasker 1971, Bailey & Yen 1983). Thus, it is reasonable to expect euphausiids to continue to feed on larvae when they are available.

In the field, gelatinous invertebrates are considered significant predators on both eggs and larvae (Moller 1984, Purcell 1985, 1989, 1990). De Lafontaine & Leggett (1988) consider jellyfish predation to be the primary cause of mortality of larval capelin *Mallotus villosus*. In the California Current, jellyfish are not a significant portion of the plankton assemblage during the anchovy spawning season (Alvariño 1980). Planktivorous fish are abundant in upwelling systems, and they are significant predators of fish eggs (MacCall 1980, Dann et al. 1985, Alheit 1987). Hunter & Kimbrell (1980) estimated that 17.2 % of the population of northern anchovy eggs was removed by cannibalism; the impact on fish larvae is more difficult to assess due to the rapid digestion of the larvae by the fish. In the laboratory, it seems that predatory fishes mainly consume eggs and older, more visible fish larvae, whereas the yolk-sac stages are less vulnerable (Folkvord & Hunter 1986, Pepin 1987, Margulies 1989).

Identifying the major predators of the young stages of fish and measuring and quantifying their impact is a massive undertaking. The immunochemical method offers a powerful approach for identifying potential crustacean predators and elevating the status of a potential predator to a positive one. Currently the ELISPOT immunoassay is being used to study predation by amphipods, mysiids, and euphausiids on the young stages of walleye pollock *Theragra chalcogramma* in the Gulf of Alaska (Bailey et al. in press).

Immunoassay surveys provide an important method to identify factors affecting recruitment processes. Thus, we feel it is essential to comment on the inherent limitations of the immunoassay and on the assumptions we made, and to make recommendations for future studies.

One limitation of our antiserum is that it does not differentiate between predators feeding on eggs or on yolk-sac larvae. Laboratory experiments show that euphausiids and copepods mostly consume yolk-sac larvae, and that they appear to be ineffective predators on eggs (Hunter 1984). A possible reason for this result is that most pelagic eggs float on the surface in static laboratory containers and are unavailable to the predators. In the sea, where mixing occurs above the thermocline, Ahlstrom (1959) has shown that pelagic eggs are well distributed. Additionally in the field, Bailey et al. (unpubl.) have detected walleye pollock egg yolk protein in the guts of predatory invertebrates prior to the period of hatching.

Another limitation that complicates the quantification process is that the immunoassay, as applied in this study, yielded information only on the presence or absence of yolk protein in the predator's gut. Thus, in addition to not differentiating between egg and yolk-sac larvae, it did not distinguish between 1 or more prey having been eaten. Consequently, this approach is appropriate to study predators that have low daily consumption rates. Daily consumption rates measured in the laboratory for copepods, euphausiids, and amphipods range from 1 to 24, albeit at prey densities higher than those that occur in the field (Hunter 1984, Bailey & Houde 1989).

Spurious reactions could occur if the antisera cross-reacts with yolk protein from other fish. Using our antibody preparation, we have obtained cross-reactions with dot blots of yolk from single eggs (ca 60 µg yolk protein dry wt egg^{-1}) of sardine *Sardinops sagax* Pacific mackerel *Scomber japonicus* and Pacific herring *Clupea pallasi*. However, we have additional experimental evidence that suggests yolk protein from other fish could not be detected *in vivo*.

We compared equivalent amounts of Pacific mackerel and anchovy yolk protein in an ELISPOT titre test. Side-by-side testing revealed a much reduced reaction for mackerel protein at all protein concentrations and

no visible reaction at protein concentrations less than 0.3 µg. Thus, it appears Pacific mackerel yolk proteins have few antigenic sites in common with anchovy protein. Since we rarely find more than 0.3 µg of anchovy yolk protein in euphausiid stomachs, presumably due to the degradation of the yolk protein by euphausiid proteolytic activity (an anchovy yolk-sac larvae contains about 6 µg yolk protein; Theilacker et al. 1986), we assume that mackerel and other fish yolk proteins will behave similarly and that after digestion by euphausiids too few sites will be retained to elicit a visible reaction.

To determine whether cross-reactions occurred in the field samples, we collected and tested predators off California in November before peak anchovy spawning when other fish eggs and larvae were present (Fig. 5). Because most of the euphausiids (117/119, 98.3 %) tested negative, we did not consider cross-reactions to be a problem.

We obtained a few spurious reactions outside the anchovy spawning area. Two *Euphausia gibboides* in November and 6 *E. recurva* in March, collected west of Stn 90 on lines 87 and 93 (Figs. 1, 2a, b), tested positive for anchovy yolk protein. We cannot explain these spurious reactions, but it is in the realm of possibilities that anchovy eggs from the western boundary of the spawning area could be entrained in eddys or filaments and relocated offshore. Fiedler (1986) deduced from satellite imagery and field information that in March of 1985 an eddy entrained and transported anchovy larvae to the same offshore area between lines 87 and 93. This was a recurrent eddy, found in an anomalous location in March 1985. The total time for transport to carry water offshore is not well known, although filament speeds of up to 0.7 m s^{-1} have been documented off central California (Strub et al. 1991). Speeds this strong could transport anchovy embryos offshore where the predators were collected within 6 d, the period that yolk is retained in developing anchovy. Yet the collecting nets sampled no anchovy products in this offshore area. Perhaps euphausiids, which encounter larger spheres and integrate over longer time periods than nets do, are better samplers than nets. In any event, these few curious, positive-reactive euphausiids contributed little to the overall estimate of the predation impact.

We made several assumptions which, if wrong, could modify the outcome. The calculation of the predatory impact of the euphausiid assemblage is sensitive to the functions describing ingestion and gut residence time. Here we used the measured rate for *Euphausia pacifica* gut residence time, and because little was known about this rate for the 5 other species studied, we ascribed the *E. pacifica* rate to them as well. Fifty percent of the euphausiids examined in this study were *E. pacifica*. The assumptions we made were: (1) the 6 to 11 mm size class of the investigated species feeds at the same rate as *E. pacifica* of that size; (2) gut residence time of anchovy yolk protein for the investigated euphausiids >11 mm is the same as for *E. pacifica* >11 mm; and (3) gut residence time for the 6 to 11 mm group is 3 times that of euphausiids >11 mm.

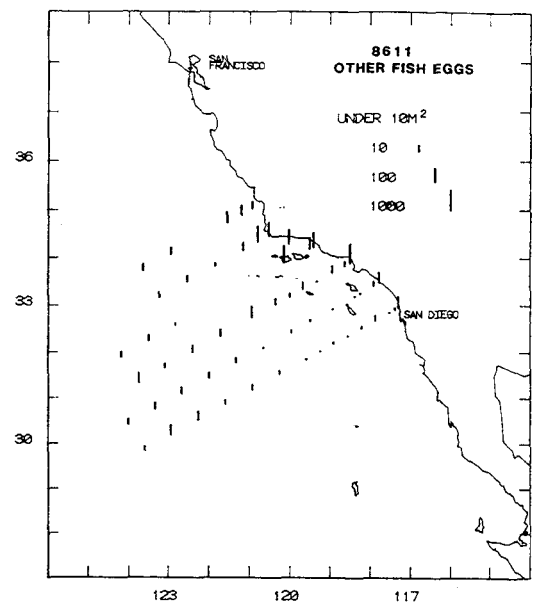


Fig. 5. Abundance of other fish eggs in November 1986. Egg numbers adjusted to equal the average abundance under 10 m^2 of sea surface

Willason & Cox (1987) determined the residence time for phytoplankton pigment in the guts of *Euphausia pacifica* >11 mm after feeding them on charcoal particles. They used an exponential model to describe gut clearance. Using their model, we calculated that 3 to 5 % of the initial pigment remained in the euphausiid guts after 3.5 h, the average detection time determined for our experiments. Although they found that some plant pigment still could be measured in the guts for 10 h, we found no detectable yolk protein after 6 h. Thus, their measurements for gut residence time of phytoplankton prey for euphausiids >11 mm differ somewhat from our gut clearance measurements for ichthyoplankton prey. Willason & Cox (1987) did not study the smaller size class, and we could find no values in the literature for euphausiids <11 mm.

Clearly, further studies are needed to substantiate size-specific functions for ingestion and detection time for the primary predator species. An accurate measure

of predation for the 6 to 11 mm size group is important. In our study area, the total number of 6 to 11 mm euphausiids at the low-predation stations was about 8 times the number of >11 mm euphausiids. It is common for abundance of 6 to 11 mm euphausiids to be an order of magnitude higher than the >11 mm size class (Brinton & Wyllie 1976).

We believe our results are conservative. Predator abundance may be underestimated due to euphausiids avoiding the collecting net and to their contagious distributions that we discussed earlier. Additionally, we may have overestimated average detection time because 25 % of the individuals tested in the laboratory had completely digested the protein within the 2 h feeding trial (see euphausiids at Hour 0, Fig. 4).

In the future, to resolve the potential cross-reaction dilemma, we suggest testing the gut contents of euphausiids fed in the laboratory on the eggs or larvae of other, co-occurring fishes. Ideally it would be best to dedicate a cruise to this study and to take sufficient samples to confidently estimate mortality rates using only eggs and yolk-sac larvae.

Our study showed that euphausiids are important predators on the early life history stages of anchovy. The impact of the euphausiid population was substantial. Euphausiid crustaceans are ubiquitous in the sea and numerically one of the major planktonic organisms in the eastern north Pacific (Boden et al. 1955) having a great potential to impact all fish populations that spawn pelagic eggs.

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