

Dispersion and development patterns in larvae of *Nyctiphanes simplex* (Euphausiacea) in the upwelling region off Baja California

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ABSTRACT: Distribution of *Nyctiphanes simplex* larvae in relation to development stage and presence of fecund females is described for January–February, April, July and October 1966 in the area between Point Baja and Point Abreojos, off Baja California, Mexico. Recruitment was observed to be year round, but most intensive in fall and winter. Largest aggregations of fecund females ($>10 \text{ ind. m}^{-2}$) occurred off Point Baja-Point Canoas in all months except July. Vizcaino Bay seems to be a feeding site in winter and a very important reproduction site in fall. Heating of waters offshore and the presence of a clockwise eddy inside Vizcaino Bay at the end of the most intensive months of upwelling constrained the distribution of females. Although fewer spawning females (carrying external eggs or spent) were present during winter, spring and summer, females in those seasons had greater body lengths (11.3, 12.4 and 11.6 mm on average respectively) than those during fall (10.1 mm on average). The largest spawning female (15.8 mm) was found in July off Point Eugenia. Proportions of particular furcilia forms in stages F_1 to F_2 (distinguished by the degree of development of pleopods) were more similar along the north-south axis than onshore-offshore, following the generally along-shore orientation of isotherms. Dominance of short developmental pathways in F_1 and F_2 stages (single instar in each stage) was most often observed near the shore, associated with isotherms of 17°C in winter and summer and with low temperatures in spring. Elsewhere the dominant pathway for this species was 1 instar in F_1 and 2 instars in F_2 . However, even the longest pathways were sometimes associated with stations near the coast. Greatest body lengths, especially in late furcilia stages, were found at stations where developmental pathways were generally short, while smaller larvae (in equivalent stages) were associated with longer pathways.

KEY WORDS: Euphausiid · Upwelling · Instar

INTRODUCTION

Coastal upwelling occurring in the California Current System has been the subject of many studies (Wooster & Reid 1963, Bakun 1973, 1975, Walsh et al. 1974, 1977, Bakun & Nelson 1977, Nelson 1977, Barton & Argote 1980, CODE Group 1983, Huyer 1983). Large-scale upwelling of cool subsurface waters along the coast is evident in charts of surface temperature

produced by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program since 1949. Off western Baja California strong upwelling usually occurs from March to June, driven by prevailing northerly winds (Bakun & Nelson 1977). A cell of upwelling-downwelling has been suggested to explain the negative wind-stress curl from Point Baja to Point Eugenia (30 to 28°N). In southern Baja California the influence of upwelling seems to be particularly restricted to the coast, based on sea surface temperatures. There, however, the temperature effects of offshore Ekman transport could be masked by strong incident radiation, since Point Eugenia (28°N) sepa-

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rates areas of maximum and minimum cloud cover (Bakun & Nelson 1977).

Use of satellite images has shown that the upwelling is more complex than the simple model of an upwelling-downwelling cell. Other structures, such as eddies and plumes, have been observed (e.g. Traganza et al. 1983). Biological consequences of upwelling remain unclear. Short-term studies at Point San Hipolito (27° N) during 2 successive springs revealed differences in community structure of plankton and in primary production values, though in both years water with characteristics of the California Current upwelled from a depth of 50 to 60 m (Walsh et al. 1974, 1977). Studies of the life histories of dominant zooplankton species occupying these unstable ecosystems are required in order to gain understanding of species adaptations associated with them. One of the species of the upwelling zone in the eastern subtropical Pacific is the coastal euphausiid *Nyctiphanes simplex* (Brinton 1962). Total and larval abundance of *N. simplex* through its range in the northern hemisphere (20 to 35° N) has been documented for a number of CalCOFI surveys from 1939 to 1963 (Brinton 1967a, 1973, Brinton & Townsend 1980). In coastal sta-

tions off southern Baja California, Longhurst (1967) estimated euphausiid dry weight at 6.8 mg m^{-3} (33% of the total zooplankton) during June 1964; *N. simplex* was the third most abundant zooplankton species after the copepods *Calanus pacificus* (then called *C. helgolandicus*) and *Acartia tonsa*.

Nyctiphanes simplex, like certain other coastal euphausiids, protects its eggs in external ovisacs. Emergence of larvae occurs in the pseudometanauplius stage (Boden 1951). The larvae start to feed actively in the calyptopsis phase. In the furcilia phase eyes project beyond the sides of carapace, and pleopods develop in sequence from anterior to posterior abdominal segments, appearing first as nonsetose rudiments which become setose and functional at the next moult (Mauchline & Fisher 1969). The number of moults needed to complete 5 pairs of setose pleopods and the subsequent reduction in number of terminal telson spines from 7 to 1 is variable in this species (Boden 1951, Lavaniegos 1992). The presence of many different furcilia forms indicates diversity in developmental pathways.

Ontogenic variability observed in many coastal euphausiid species has been interpreted as an adaptation to the changing coastal zone (Mauchline & Fisher 1969). The role of variation in exogenous factors such as food and temperature in inducing variable forms has been tested in the laboratory (Le Roux 1973, Pillar 1985, Lavaniegos 1992). However, ecological studies relating larval variability of *Nyctiphanes simplex* to the upwelling regime and circulation of water do not yet exist. This is the objective of the present study.

METHODS

Zooplankton samples were used from CalCOFI (California Cooperative Oceanic Fisheries Investigations) cruises 6601, 6604, 6607 and 6610 (January–February, April, July and October 1966) in the area between Point Baja and Point Abreojos (27 to 30° N, Fig. 1), from the coast to 300 km offshore. These cruises provided the best available coverage of the mid-Baja California coastal region through 4 seasons of the year. The net employed was conical with a ring 1 m in diameter and 2.35 m long made of 0.55 mm mesh with 0.25 mm mesh in the cod end bag and in a 40 cm long section immediately in

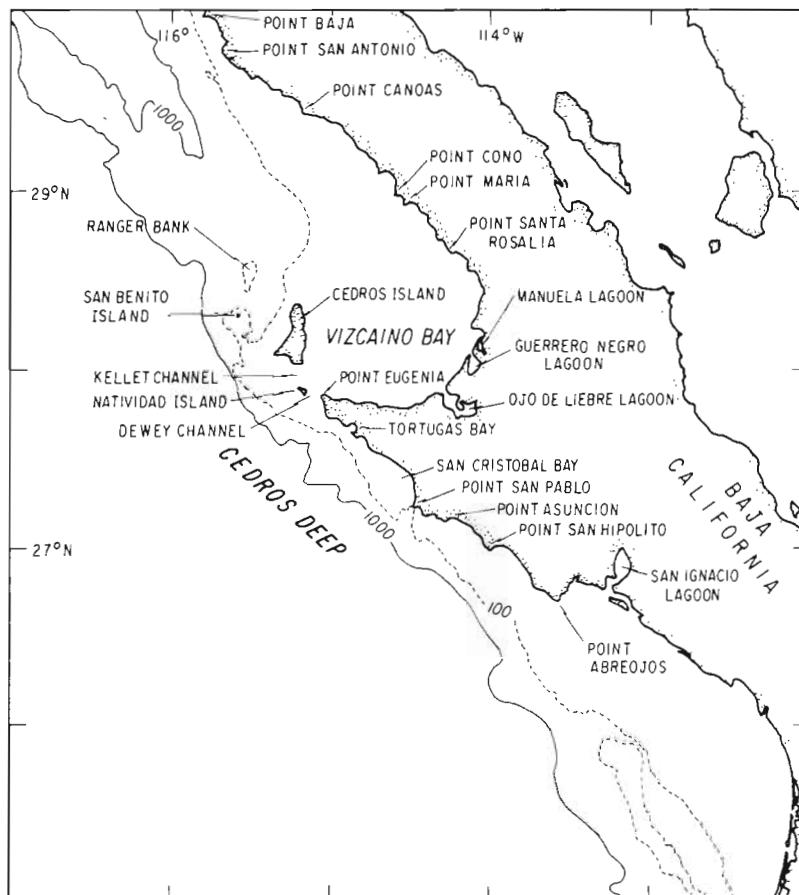


Fig. 1 Study area off western Baja California, Mexico. Isobaths are in fathoms

front of it. It was towed obliquely from 140 m to the surface. A flowmeter in front of the net was used to measure the volume of water strained (Ahlstrom 1948).

Zooplankton volume was measured by displacement in a graduated cylinder (Ahlstrom & Thraillkill 1963). Samples were subsampled with a Folsom splitter for counting of *Nyctiphanes simplex* larvae. Most aliquots were $\frac{1}{4}$ or $\frac{1}{8}$ of the sample. In some cases smaller aliquots ($\frac{1}{16}$ or $\frac{1}{32}$) were required. A total of 200 to 400 larvae were counted per sample. Adults were sorted from the entire sample.

Volume and abundance per tow were converted to volume (or abundance) per square meter of sea surface by means of:

$$y = \frac{x (\text{tow depth})}{\text{filtered water}}$$

where y = volume or abundance per m^2 ; x = volume or abundance in the sample; and filtered water = the volume of water filtered during the haul, as measured by the flowmeter. Samples obtained between sunset and sunrise, according to Pacific standard time, are considered night-time samples.

Larval developmental stage, number of pleopods and number of terminal telson spines were recorded. Adults were sexed and maturation state recorded. Males were identified by the presence of petasma, but only those bearing an internal (pigmented and visible through the cuticle) or protruded spermatophore were considered mature. Females were identified by dissecting the ovaries. Immature females had small and translucent oocytes. The group of mature females included those with swollen and opaque oocytes, those carrying external eggs and those appearing spent (with a hollow space between the last thoracopods and the first pleopods). Body length (to nearest 0.1 mm) of all specimens was measured with a micrometer from the point of the rostrum to the end of the telson.

RESULTS

Physical environment

The area between Point Baja and Point Abrejos (Fig. 1) was selected for study since it is the middle part of the North Pacific distributional range of *Nyctiphanes simplex*, which usually extends from southern California to near the tip of Baja California (Brinton 1962). The coastal shelf is narrow and the slope is steep from the western side of Cedros Island southward to Point Abrejos. Vizcaíno Bay is the most extended portion of the shelf, delimited at the south by Point Eugenia and at the west by Cedros Island. The Bay

describes a semicircle 110 km in diameter, exposed to the sea at the northwest. The topography inside Vizcaíno Bay and the restriction on circulation imposed by sill depths of Kellet (40 to 45 m) and Dewey (25 to 30 m) Channels allow a clockwise eddy to develop (Dawson 1952, Wyllie 1960, Crowe & Schwartzlose 1972, Mancilla-Peraza et al. 1993).

There is little rainfall during winter throughout the area. Wind blows from the northwest throughout the year, with seasonal changes in intensity. Upwellings during spring and early summer are the most intensive, cooling the water along the coast. But, near coastal prominences, these processes are often persistent year round (Bakun & Nelson 1977). Mean upwelled water during May–June was estimated to be $200 \text{ m}^3 \text{ s}^{-1}$ per 100 m of coast for the period 1946 to 1971, at 2 locations (30° N , 119° W and 27° N , 116° W) near the study area (Bakun 1973). During 1966 upwelling indices were low throughout the year in relation to the long-term mean, peaking in July off Point Baja and in June off Point Eugenia (132 and $95 \text{ m}^3 \text{ s}^{-1}$ per 100 m of coast respectively). These indices are based on calculations of offshore Ekman surface wind transport, inferred from monthly mean surface atmospheric pressure data. There are limitations to Bakun's upwelling indices, since they are derived from a 3° latitude-longitude grid and a simplified boundary layer is assumed (Bakun 1973, Bakun & Nelson 1977, Huyer 1983). However, they are used here as broad scale indications of upwelling intensity.

In 1966, the distribution of water temperature at 10 m depth (Fig. 2) during January–February showed an offshore plume of warm water ($> 18^\circ \text{ C}$) extending from the south and a pocket of water warmer than 17° C inside Vizcaíno Bay. This was the only cruise without clear evidence of upwelling, based on the structure of isotherms perpendicular to the coastline. In April relatively homogeneous cold water (16 to 17° C) was present offshore with parallel isotherms of 14 to 15° C along the shore. In July a strong latitudinal gradient from 17 to 21° C developed offshore and the most intense upwelling was north of Vizcaíno Bay and near Point San Hipolito as indicated by parallel isotherms of 13 to 17° C . There was weakening of upwelling in fall, becoming more restricted to the prominences of Point Baja and Point Eugenia. Warming was then at a maximum offshore.

Vertical profiles of temperature in 3 offshore-onshore sections (lines 110, 120 and 130 in the CalCOFI grid; Fig. 3) illustrate seasonal effects of upwelling. In winter the mixed upper layer extended to depths of 70 to 100 m. During summer the mixed layer was less than 30 m in depth offshore, with upward tilting of isotherms near the coast. In Vizcaíno Bay

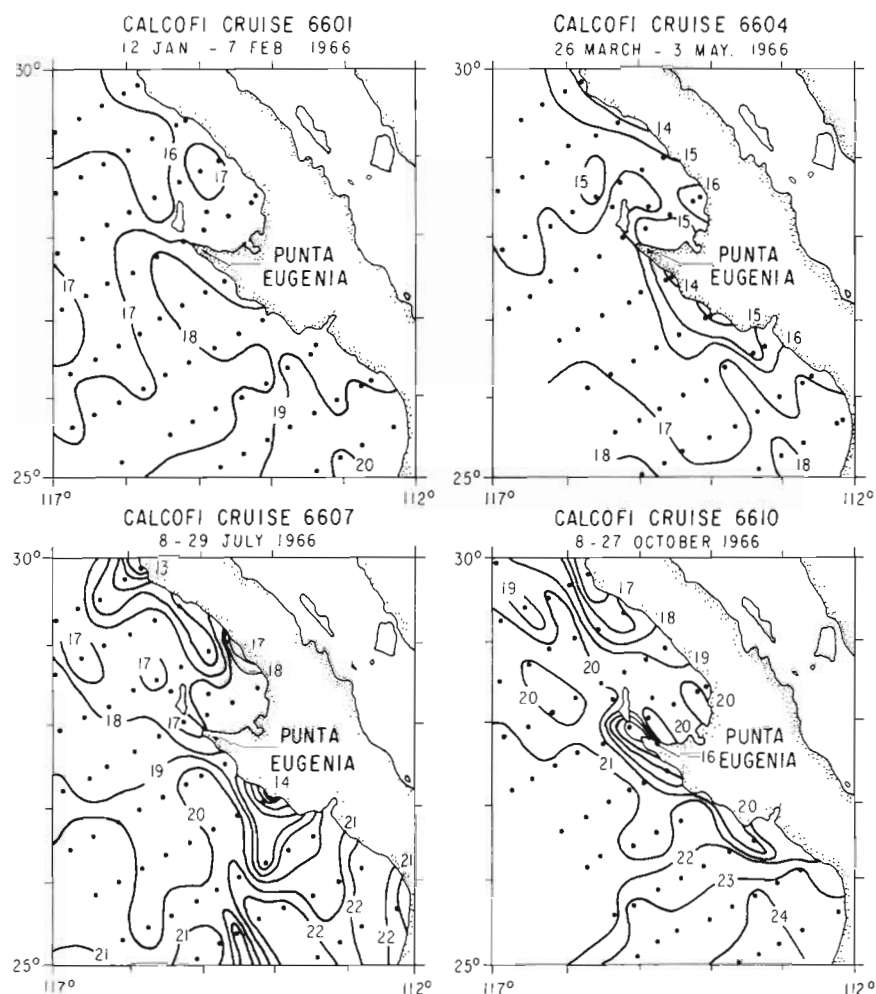


Fig. 2. Temperature distributions ($^{\circ}\text{C}$) at 10 m. Dates are of the complete cruises (after SIO Data Report 1968a, b, 1969)

(Stn 119.33) the mixed layer extended deepest in winter, possibly from the stirring action of the eddy.

Highest salinity (at 10 m) was observed in winter when values between 33.8 and 34.4‰ along the coast indicated influence of the California Countercurrent. In the other seasons salinity >33.8 ‰ was restricted to south of Point Eugenia (SIO Data Report 1968a, b, 1969). The California Countercurrent is known as the Davidson Current to the north of Point Conception (34.5°N) (Reid et al. 1958, Hickey 1979, Huyer 1983), where it is near the shore, but south of Point Baja (30°N) it is more offshore, and a near-shore flow to the southeast is observed throughout the year (Schwartzlose 1963). Beneath this countercurrent was water of the California Current, separated from the deeper Equatorial Water by a halocline near 100 to 150 m. In summer the Countercurrent disappears and a 2-layer structure is present (SIO Data Report 1968b). Thus, the upwelled water usually had characteristics of California Current Water.

Zooplankton volume

Zooplankton displacement volumes from night-time and daytime stations were similar among the cruises, apart from April (Table 1) when 95% confidence intervals (Tukey HSD method) were biased by 2 high values (47.6 and 67.9 ml m^{-2}) off Point Baja (Fig. 4). Excluding those values, values were $<30.0\text{ ml m}^{-2}$ year round. Lowest volumes occurred in January and April with 60 to 70% of the stations yielding $\leq 10.0\text{ ml m}^{-2}$. In July highest volumes (20 to 30 ml m^{-2}) were found northwest of Cedros Island and consistently offshore. Ekman transport was then strong. Highest volumes were recorded at Vizcaíno Bay in October.

Differences in zooplankton volumes among cruises (excluding outlying values) were significant ($F = 5.00$, $p = 0.002$; 1-way analysis of variance). A *posteriori* comparison of means (Tukey HSD) at 95% confidence intervals separated means for January (8.7 ml m^{-2}) and April (7.8 ml m^{-2}) from the mean for July (12.7 ml m^{-2}).

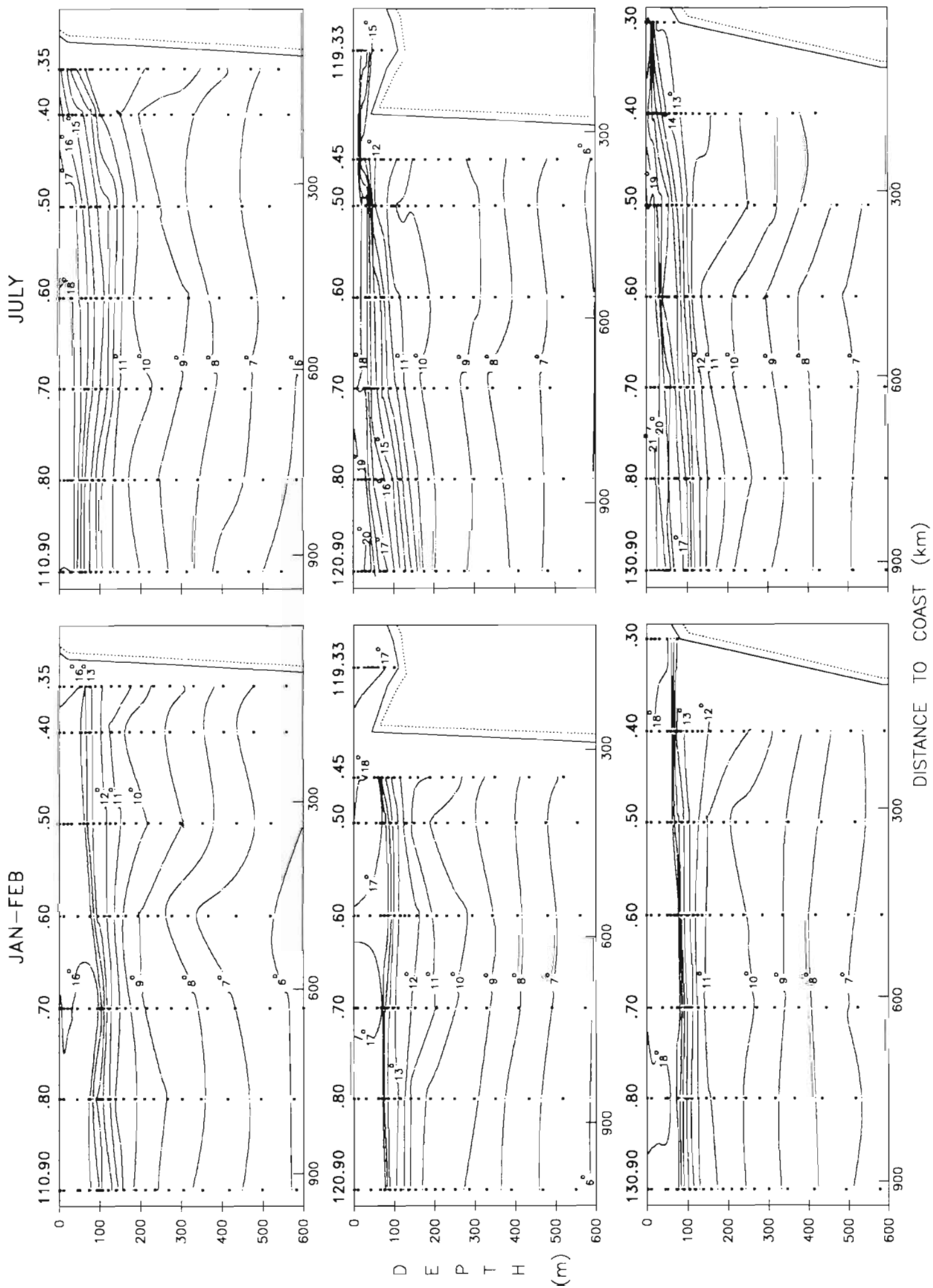


Fig. 3. Temperature profiles ($^{\circ}\text{C}$) along station lines 110, 120 and 130 of CalCOFI cruises 6601 (January-February) and 6607 (July) (data from SIO Data Report 1968a, b)

Table 1. *Nyctiphanes simplex*. Day and night means of zooplankton volumes and abundances of life phases. N = D: probability of night mean being equal to day mean (ANOVA). Confidence limits (CL) estimated with the Tukey HSD method. Data of abundance were log-transformed

	Date	Night ^a		Day ^b		N = D p
		\bar{x}	95% CL	\bar{x}	95% CL	
Zooplankton volume (ml m ⁻²)	25 Jan–2 Feb	8.0	(6.0–10.0)	9.3	(7.3–11.3)	0.521
	19–26 Apr	14.8	(10.6–19.0)	7.4	(4.1–10.7)	0.053 ^d
	17–27 Jul	14.6	(12.2–16.9)	10.9	(8.7–13.2)	0.123
	18–25 Oct	10.9	(9.1–12.7)	11.0	(9.2–12.9)	0.932
Abundance of larvae (ind. m ⁻²) ^c	25 Jan–2 Feb	74.2	(36.2–151.2)	37.6	(18.1–77.0)	0.355
	19–26 Apr	36.9	(15.7–84.8)	13.3	(6.5–26.2)	0.189
	17–27 Jul	118.2	(58.4–238.2)	47.0	(23.7–92.3)	0.185
	18–25 Oct	182.6	(92.9–358.1)	51.1	(24.8–104.2)	0.071
Abundance of juveniles (ind. m ⁻²)	25 Jan–2 Feb	3.3	(1.9–5.3)	2.1	(1.1–3.6)	0.415
	19–26 Apr	1.5	(0.8–2.3)	0.2	(0.0–0.5)	0.009 ^d
	17–27 Jul	4.9	(2.9–7.8)	1.1	(0.4–2.1)	0.011
	18–25 Oct	8.8	(5.4–14.0)	1.3	(0.5–2.5)	0.001 ^d
Abundance of adults (ind. m ⁻²)	25 Jan–2 Feb	2.5	(1.4–3.9)	0.7	(0.2–1.5)	0.055 ^d
	19–26 Apr	1.8	(1.0–3.0)	0.3	(0.0–0.7)	0.012 ^d
	17–27 Jul	2.9	(1.7–4.5)	0.4	(0.0–1.0)	0.005 ^d
	18–25 Oct	10.7	(6.2–18.0)	0.8	(0.1–1.9)	<0.001 ^d

^aNos. of night stations were 21 (January–February), 16 (April), 20 (July) and 22 (October)
^bNos. of day stations were 21 (January–February), 26 (April), 22 (July) and 20 (October)
^cIncludes calyptopis and furcilia stages
^dBartlett's test for homogeneity of variances was rejected. The Kruskal-Wallis test based on ranks gave similar results, with probabilities < 0.005 in all cases, except for April volumes (p = 0.140) and January–February abundances of adults (p = 0.205)

Abundance of life phases

Nyctiphanes simplex was present in 91% of the samples. Larvae were most frequently in the range of 100 to 1000 ind. m⁻² (ca 50% of stations) in winter, summer and fall. In spring larval abundance was lowest with < 100 ind. m⁻² at 70% of the stations. Hauls with more than 1000 ind. m⁻² occurred in 2 to 10% of stations per season. Day-night differences in larval abundance were not significant (1-way analysis of variance with log-transformed data) (Table 1). That was expected, as the known depth range of larvae (Brinton 1967b) is within the depth of tow. All samples were used to describe distributions of larvae.

Juveniles and adults showed significantly (1-way analysis of variance) higher numbers in night samples (Table 1). Variances were not homogeneous but the Kruskal-Wallis test based on ranks produced a similar result.

Considering only night stations, the range of highest abundance was 1 to 10 ind. m⁻² for both juveniles (31 to 48% of samples) and adults (25 to 32% of samples). However, in July and October abundances were > 10 ind. m⁻² in 2 times as many stations as in January and April. In October large aggregations of adults (> 1000 ind. m⁻²) were found over the continen-

tal shelf, but in the other cruises they were more frequently over the continental slope. High numbers of larvae were consistently found near the coast. Juveniles had similar abundances in shelf and slope waters at all times except July when upwelling was strongest; then juveniles tended to occur most frequently in slope stations.

Distribution by developmental stage

Distributions of *Nyctiphanes simplex* larvae by developmental stages, as defined by Lavaniegos (1992), showed differences between regions and within regions (between cruises) (Fig. 5). Calyptopis stages were probably undersampled, due to escapement through meshes of the net (mean in coastal stations was 14 to 26% of the total population per cruise). However, oldest calyptopes (C₃) larvae were found at most of the stations where the subsequent furcilia stages occurred within similar ranges of abundance. Abundance of furcilia 1 and 2 (F₁ and F₂) was higher than the other stages (F₃ to F₆) in all seasons. These are expected to be better retained by the net (they are > 0.5 mm wide) than calyptopes, and the duration of these stages can be longer when there is more than 1 instar per stage.

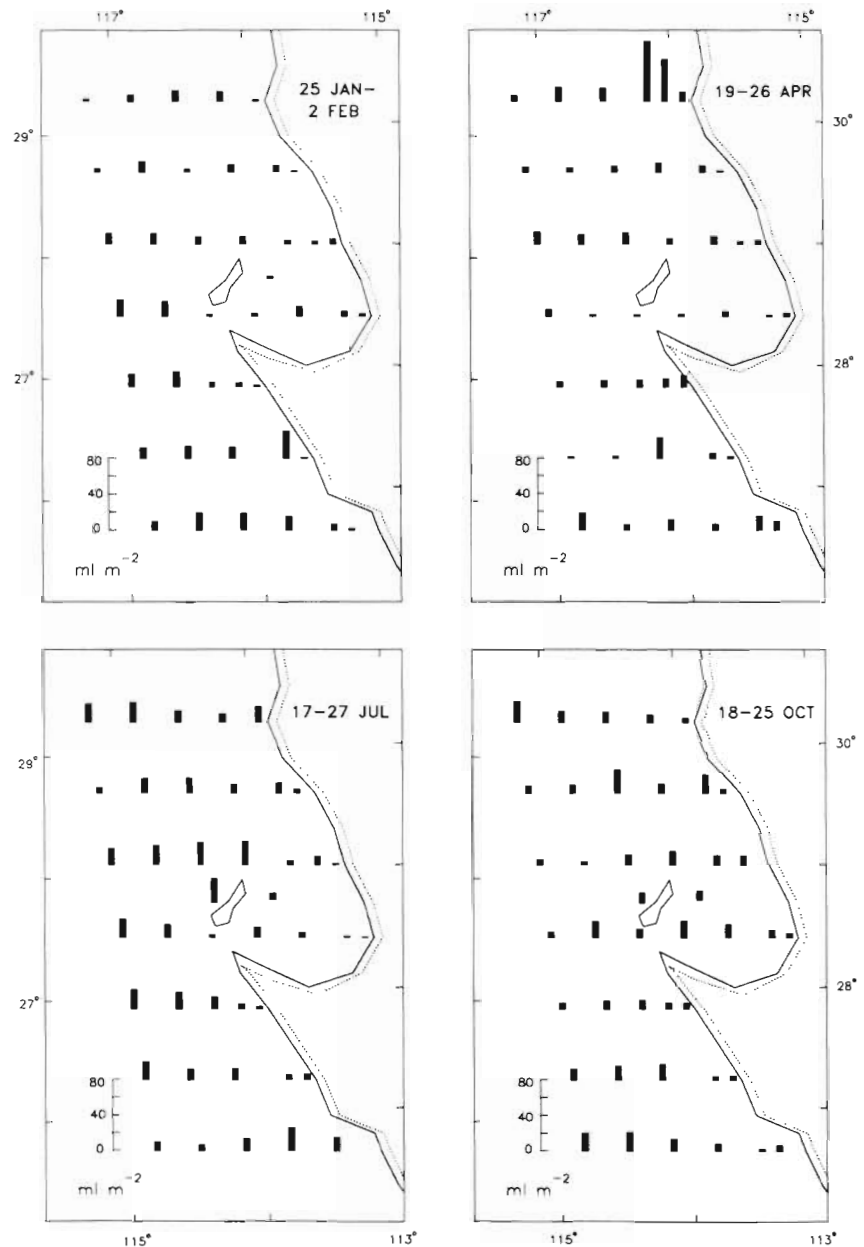


Fig. 4. Zooplankton displacement volume (ml m^{-2}) in 1966 (unpubl. data)

Based on C_3 and F_1 distribution (Fig. 5), there was intensive recruitment along the coast in January–February, where temperatures (10 m) were 16 to 19°C. In April most C_3 and F_1 were found south of Point Eugenia with low numbers in the northern area, except at Point Baja. In July F_1 larvae were more abundant than C_3 . This was the only cruise with high recruitment in the northern offshore area, where temperatures were near 17°C, between the upwelling zone near Point Baja and a tongue of warm water from the south. During October this area became warmed to 19 to 20°C and reproduction was centered in Vizcaíno Bay and to the south of Point Eugenia, where a strong thermal

front was observed (Fig. 2). Distribution of F_2 larvae was similar to that of F_1 .

Later furcilia stages (F_3 to F_5) showed the same distribution trends observed for younger larvae, but with sharp decreases in abundance. This is interpreted as being due to (1) high mortality in preceding stages and (2) stages F_3 to F_5 each usually requiring only a single instar, or with certain stages (sometimes F_3 and often F_5) skipped altogether (as observed in the laboratory; Lavaniegos 1992). Later furcilia might be expected to be better swimmers than earlier larvae and, therefore, daytime avoiders. However, Brinton & Townsend (1981) found consistently better daytime

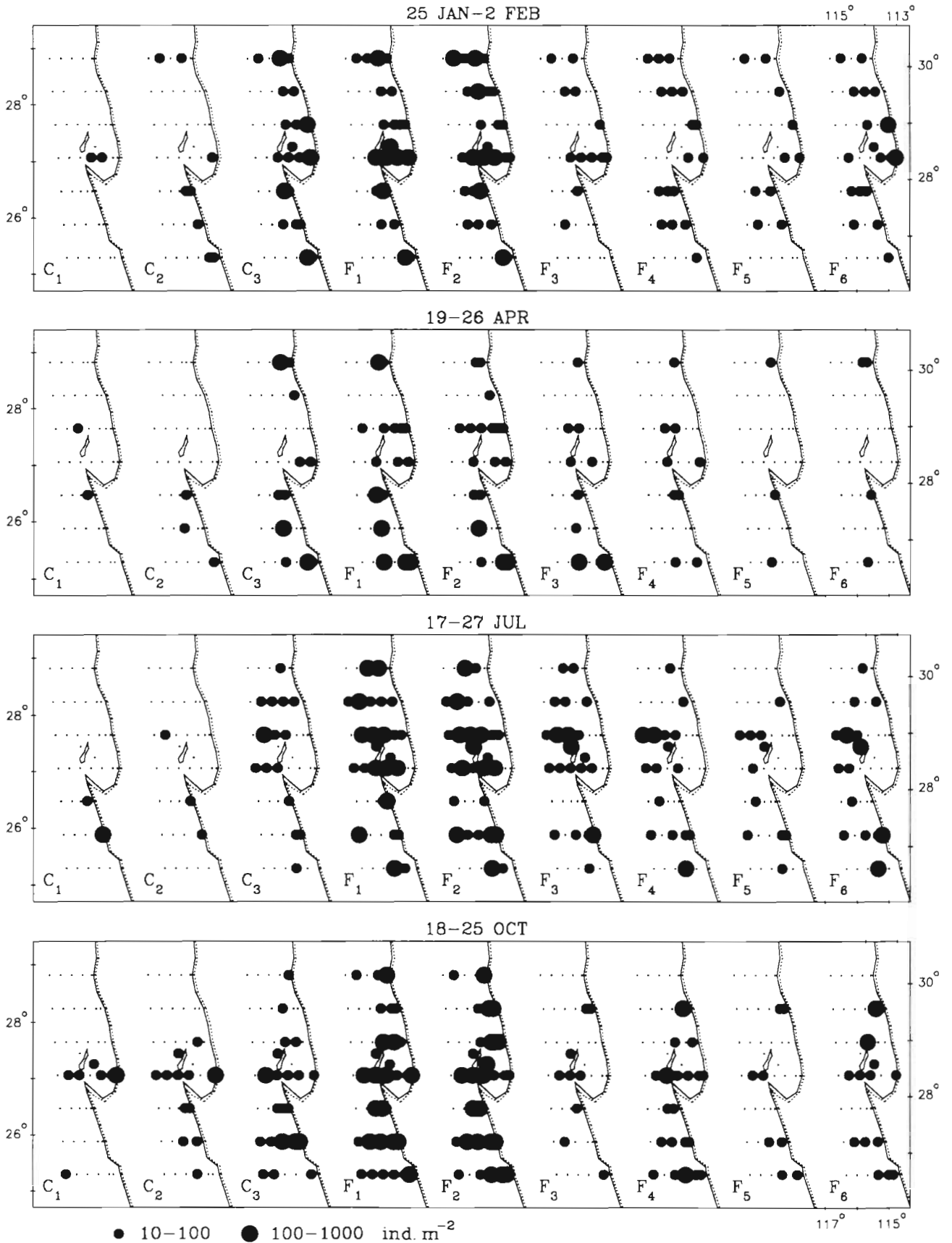


Fig. 5. Distribution of larval stages in 1966

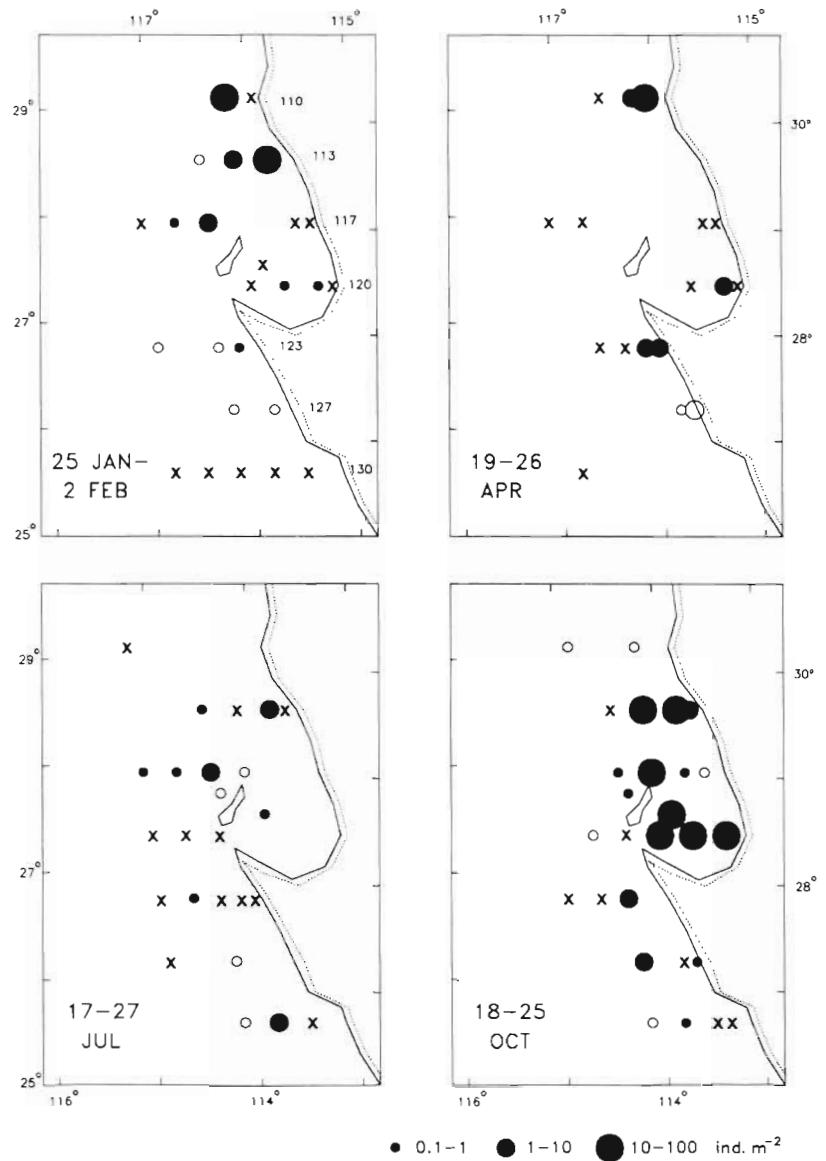


Fig. 6. Distribution of reproductive females (including females with mature oocytes, with external eggs and spent). Closed symbols: nightly aggregations; open symbols: diurnal aggregations. (Night stations without reproductive females are indicated by **x**; numbers to the right of the coastline in the upper left chart are station lines)

captures of 3 to 7 mm *Euphausia pacifica* larvae than at night.

Mature female aggregations

Mature females (here comprising fecund females, those having mature oocytes, those carrying external eggs or those that are spent) showed a trend toward abundance in certain regions (Fig. 6). In winter, there were swarms (>10 females m⁻²) off Point Baja and Point Canoa. In April, only 1 dense swarm was sampled, off Point Baja, but 2 low-density occurrences (1 to 10 females m⁻²) were observed south of Point Eugenia, where parallel isotherms near to the coast indicated upwelling (Figs. 2 & 3). Only a few dispersed mature females were found in July. The maximum number of

stations with mature females was in October when swarms were distributed over the coastal shelf from Point Canoa (or perhaps from Point Baja where there were daytime catches of adults) southward to Point Eugenia.

When body length of mature females is considered, there are differences in swarm structure (Table 2). In spite of high variability among stations the largest females were consistently observed in April and July. During April, spawning off Point Baja and Point Eugenia was by females ca 12 to 13.5 mm long, contrasting with Vizcaíno Bay, where the few spawners were ca 9.5 mm. In July mean sizes of mature females increased southward. In October as in January only small females (9.2 to 11.1 mm) were spawning. The winter group contained females significantly larger than the fall group, both females with mature oocytes

Table 2. *Nyctiphanes simplex*. Body length of females (mean \pm SD) in swarms of different density. 'F:M': ratio of total no. of females to total no. of males (only night stations were considered)

Abundance (females m ⁻²)	Month	Station	Females with mature oocytes		Spawners ^a		F:M	
			mm	N	mm	N		
10–100	Jan–Feb	110.35	10.8 \pm 1.0	3.6	11.8 \pm 0.7	10.7	1.0	
		113.30	11.2 \pm 0.9	11.1	11.2 \pm 1.1	29.6	3.7	
	Apr	110.33	12.1 \pm 0.8	9.5	13.4 \pm 0.4	2.4	1.3	
	Oct	113.30	9.1 \pm 0.5	6.8	9.4 \pm 0.8	16.7	4.3	
		113.35	8.4 \pm 0.7	4.8	9.0 \pm 0.5	11.5	1.2	
	117.35	10.6	3.9	10.0 \pm 0.7	43.1	1.6		
	119.33	10.5 \pm 0.8	3.9	9.9 \pm 0.6	12.1	2.2		
	120.25	11.4 \pm 1.2	0.9	10.6 \pm 0.8	14.3	16.7		
	120.30	11.2	2.3	11.1 \pm 0.8	25.2	1.2		
	120.35	10.0 \pm 1.5	13.9	10.6	2.3	2.1		
	1–10	Jan–Feb	113.35	10.0	0.6	11.1 \pm 0.8	6.2	3.4
117.40			7.9 \pm 1.3	2.1	11.0 \pm 1.0	6.4	1.1	
Apr		110.35	–	–	12.4 \pm 0.7	3.1	1.5	
		120.25	6.9	0.3	9.5 \pm 1.1	1.2	2.2	
		123.36	13.1 \pm 0.6	3.4	12.8 \pm 1.3	2.7	2.3	
123.37		14.9 \pm 2.5	1.1	–	–	1.5		
Jul		113.30	7.4 \pm 0.6	1.2	–	–	0.8	
		117.40	10.5 \pm 1.1	2.0	10.8 \pm 0.4	4.6	1.6	
		130.35	12.8 \pm 1.1	6.8	13.5 \pm 0.8	0.9	2.6	
Oct		113.29	9.1 \pm 0.3	3.9	9.8 \pm 0.2	0.5	2.0	
		123.42	8.8 \pm 0.5	2.1	9.6	0.3	1.6	
		127.40	9.0 \pm 0.4	1.9	9.5	0.6	0.3	
0.1–1		Jan–Feb	117.45	10.0	0.6	12.3	0.3	1.8
			120.25	11.3	0.3	–	–	1.1
			120.30	11.2 \pm 0.4	0.5	–	–	4.3
	123.37		8.2 \pm 0.1	0.6	–	–	4.0	
	Jul	113.40	–	–	11.9 \pm 0.4	0.6	0.7	
		117.45	–	–	14.4	0.3	3.9	
		117.50	–	–	10.6	0.3	F ^b	
		119.33	–	–	10.6	0.3	0.5	
		123.45	9.7 \pm 0.2	0.6	15.8	0.3	2.7	
	Oct	117.30	–	–	9.6	0.3	2.4	
		117.40	10.2	0.3	–	–	1.0	
		127.33	9.6	0.3	9.4	0.3	2.0	
		130.35	–	–	9.2 \pm 0.4	1.0	1.8	

^aSpawners are females with external eggs or spent

^bOnly females

($F = 12.42$, $p < 0.001$) and spawners ($F = 54.84$, $p < 0.001$) from the large swarms. Body length of females in October increased from Point Canoas southward to the middle of Vizcaíno Bay. Spawning frequencies are not known.

Patterns of larval development

Development of pleopods

Pleopods develop in the first 3 furcilia stages. During F_1 , 1 or more pairs of buds (nonsetose pleopods) appear, or there can be a first furcilia form with no

pleopods. In the latter case a second instar, with pleopod buds, is required to complete the stage. In F_2 , buds acquire setae (setose pleopods) and new pairs of nonsetose pleopods are added. Stage F_3 has only 1 form: 5 pairs of setose pleopods. An example of the patterns of development is: 1' \rightarrow 1"3' \rightarrow 4"1' \rightarrow 5". Here, the first furcilia form had 1 nonsetose pleopod; the second, 1 setose pleopod and 3 nonsetose; the third, 4 setose pleopods and 1 nonsetose; and the fourth, 5 setose pleopods. In field samples real sequences are unknown but the dominant frequencies of certain forms indicate probable pathways of development.

Stations with early furciliars (F_1 to F_3) ≥ 50 ind. m⁻² were selected to compare relative frequencies of

forms. The maximum number of different forms of furcilia F_1 to F_3 was found in January and the minimum number in April (Table 3). Forms 1", 2", 3", 1"1', and 2"1' did not occur in 1 or more cruises and, when present in other cruises, constituted only a small percentage of total F_1 to F_3 larvae. Forms 1"2', 1"4', 3"1', and 4" were observed in all cruises, but in April none of these reached 3% of the total in any station. The other 11 F_1 to F_3 forms appeared at all times in spite of highly variable proportions among cruises. These 11 relatively abundant forms were used to explore affinities among stations per season using the Pearson correlation coefficient. Arcsine transformation was applied to normalize the data [$x' = \arcsin(x^{0.5})$, where x = relative proportion]. Correlation coefficients among stations were calculated for each cruise. Cluster analysis of the correlation coefficients was done starting with pairs of stations with the highest values. The criterion of the maximal average of correlation coefficients was applied to join pairs in larger clusters. Clusters with average correlation coefficient with probability < 0.05 were considered significant.

A dendrogram of affinity obtained in the cluster analysis for January–February (Fig. 7) showed 3 clusters at significance $p = 0.050$ ($r \geq 0.602$). One cluster comprised coastal stations around Point Eugenia (Group C in Fig. 7). A histogram of mean relative frequency of forms in Group C had peaks in forms 2' and 2"3'. Therefore the dominant pathway of pleopodal development was probably a sequence of 3 moults

(2' \rightarrow 2"3' \rightarrow 5"). The other 2 groups (A and B) included stations at the north and south of Point Eugenia, and peaks were in forms 1', 1"3' and 4"1'. Here 4 moults were required to complete 5 pairs of setose pleopods. The difference between Groups A & B rested in secondary peaks, but the connecting steps within secondary pathways were not always obvious. Since furcilia without pleopods (form 0) made up more than 10% of these groups, secondary pathways 0 \rightarrow 3' \rightarrow 3"2' \rightarrow 5" for Group A and 0 \rightarrow 2' \rightarrow 2"2' \rightarrow 4"1' \rightarrow 5" for Group B could be considered. Stn 117.25, in Vizcaíno Bay, showed no significant relationship with other stations, suggesting even longer pathways. Stn 120.24, also in Vizcaíno Bay, similarly had no significant coefficients, while peaks in frequency of forms 2', 3', 2"3' and 3"2' indicated 2 likely pathways, each of 3 instars (2' \rightarrow 2"3' \rightarrow 5" and 3' \rightarrow 3"2' \rightarrow 5"). Therefore, during January–February, Vizcaíno Bay–Point Eugenia appears to be a separate area, with the shortest developmental pathway following the 17°C isotherm (Fig. 2) and the stable upper layer (Fig. 3).

In April, only 16 stations with more than 50 ind. m^{-2} of F_1 to F_3 larvae were found. However the most clusters resulted at these stations (Fig. 8). Affinity in the proportion of larvae per form was stronger among stations located along lines parallel to rather than perpendicular to the coast. Again Vizcaíno Bay was grouped apart (Group A), but development of pleopods appeared to require 4 instars instead of the 3 in January. The dominant pathways in Group A may be 1' \rightarrow 1"3' \rightarrow 4"1' \rightarrow 5"

Table 3. Frequency of stations with presence of furcilia forms and range of percentage with respect to the group of early furcilia (F_1 to F_3). Only stations with > 50 ind. m^{-2} of F_1 to F_3 were selected

Stage	Form	Jan–Feb		Apr		Jul		Oct	
		N	Range (%)	N	Range (%)	N	Range (%)	N	Range (%)
F_1	0	19	(1.1–33.6)	3	(3.0–3.7)	10	(1.2–5.9)	25	(1.2–20.0)
	1'	21	(1.9–53.3)	10	(1.6–38.6)	22	(1.2–51.7)	26	(2.7–47.5)
	2'	20	(1.0–34.9)	12	(2.0–31.7)	21	(7.8–33.9)	23	(1.0–17.2)
	3'	18	(1.2–13.2)	12	(1.2–64.8)	16	(1.3–28.8)	23	(0.6–14.8)
	4'	17	(0.6–14.7)	10	(1.0–15.8)	8	(1.3–8.0)	23	(0.7–17.4)
F_2	1"	2	(0.6–1.7)	–	–	–	–	–	–
	1"1'	5	(0.2–6.2)	–	–	–	–	3	(1.1–3.3)
	1"2'	13	(0.4–14.3)	3	(0.4–2.2)	2	(0.6–0.7)	15	(0.5–8.2)
	1"3'	20	(0.9–29.2)	11	(1.1–16.9)	20	(0.9–32.4)	24	(1.0–40.3)
	1"4'	11	(0.4–12.4)	5	(1.0–2.1)	7	(0.6–9.2)	5	(1.0–4.5)
	2"	1	(0.2)	–	–	–	–	–	–
	2"1'	5	(1.1–3.5)	–	–	1	(0.7)	1	(0.5)
	2"2'	18	(0.8–7.9)	10	(0.8–13.5)	23	(0.7–24.7)	22	(0.7–13.0)
	2"3'	12	(0.2–26.3)	13	(1.2–18.9)	24	(1.5–22.9)	17	(0.5–9.0)
	3"	2	(0.6–2.5)	–	–	–	–	2	(0.8–1.1)
	3"1'	7	(0.4–4.8)	2	(0.4–2.2)	2	(0.6–1.4)	10	(0.6–30.7)
	3"2'	16	(0.5–11.8)	10	(1.4–39.1)	22	(0.7–22.1)	25	(0.6–20.0)
	4"	4	(0.2–3.8)	1	(0.4)	1	(0.6)	7	(1.0–7.4)
	4"1'	20	(0.9–34.8)	14	(0.7–28.8)	25	(0.7–36.0)	26	(5.0–36.0)
F_3	5"	18	(1.1–39.8)	14	(0.6–38.0)	25	(1.6–79.3)	19	(1.3–19.0)

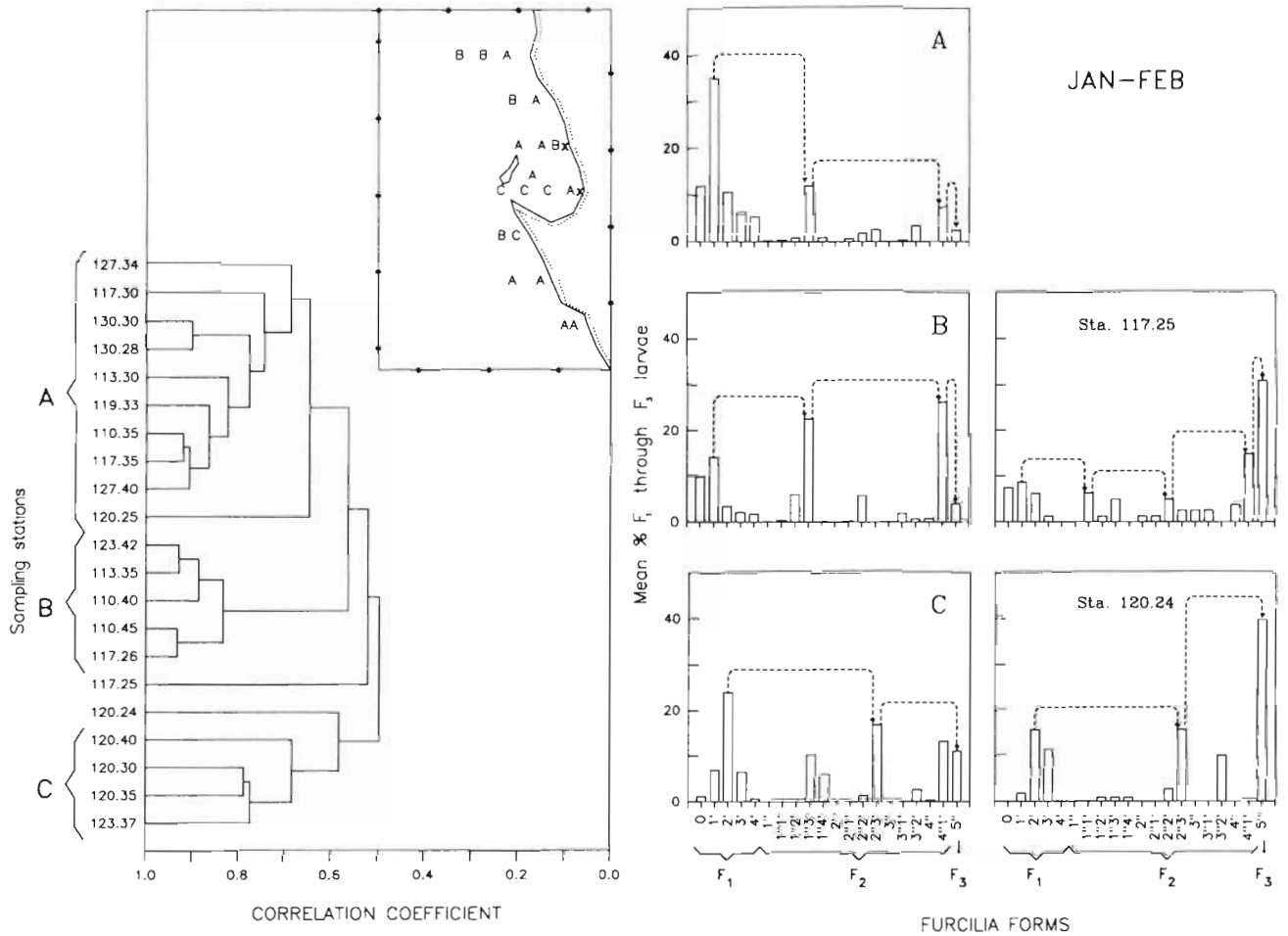


Fig. 7. Affinity among stations in composition of furcilia forms during January–February. Significant ($p = 0.05$) clusters are indicated by braces and letters. Geographic location of stations is shown in the inset map by the letter corresponding to its affinity group (x: stations not forming significant clusters). Mean percentage of forms corresponding to each cluster is shown in the histograms, including stations without significant correlations with others. Forms included belong to stages F_1 to F_3 . Dashed arrows indicate dominant pathways in development of pleopods

and $2' \rightarrow 2''2' \rightarrow 4''1' \rightarrow 5''$. Stn 120.40 showed only the first of these sequences. Shorter pathways tended to be offshore: Clusters B, with pathways $2' \rightarrow 2''3' \rightarrow 5''$ and $3' \rightarrow 3''2' \rightarrow 5''$; and Clusters C & D, with the second of these sequences.

In July 2 large clusters of stations were present (Fig. 9). Group A had stations located preferentially in zones with temperatures $>17^\circ\text{C}$, while Group B corresponds with (1) the cool northern offshore area and (2) the upwelling area off San Hipolito in the south. The developmental pathway suggested in the cool-water group was $2' \rightarrow 2''3' \rightarrow 5''$ and in the warm group, $1' \rightarrow 1''3' \rightarrow 4''1' \rightarrow 5''$. Stn 127.40 had peaks in forms $3'$, $4'$, $3''2'$ and $4''1'$. Pathways $3' \rightarrow 3''2' \rightarrow 5''$ and $4' \rightarrow 4''1' \rightarrow 5''$ are therefore possible.

The strongest affinity group was found in October (Group B), with significant ($p = 0.050$) correlation coefficients among 20 stations (Fig. 10). The dominant

pathway was $1' \rightarrow 1''3' \rightarrow 4''1' \rightarrow 5''$. Form 0 (without pleopods) in stage F_1 was prominent in Group A and at Stn 120.35, an indication of many possible pathways from that starting point, all longer than 4 instars.

Reduction in number of terminal telson spines

When pleopod development is completed, the furcilia starts a sequence of reduction in the number of terminal telson spines (TTS) from 7 to 1. Seven TTS are present in F_1 to F_3 . Forms with 6 or 5 spines correspond to stage F_4 . Forms with 4, 3 or 2 spines correspond to F_5 , and 1 spine to F_6 . In the next moult the telson loses 1 of the 3 pairs of posterolateral spines, becoming a juvenile.

Mean relative frequencies of TTS forms in stages F_4 through F_6 per affinity group were estimated, excluding stations with low abundances ($<5 \text{ ind. m}^{-2}$ of F_4

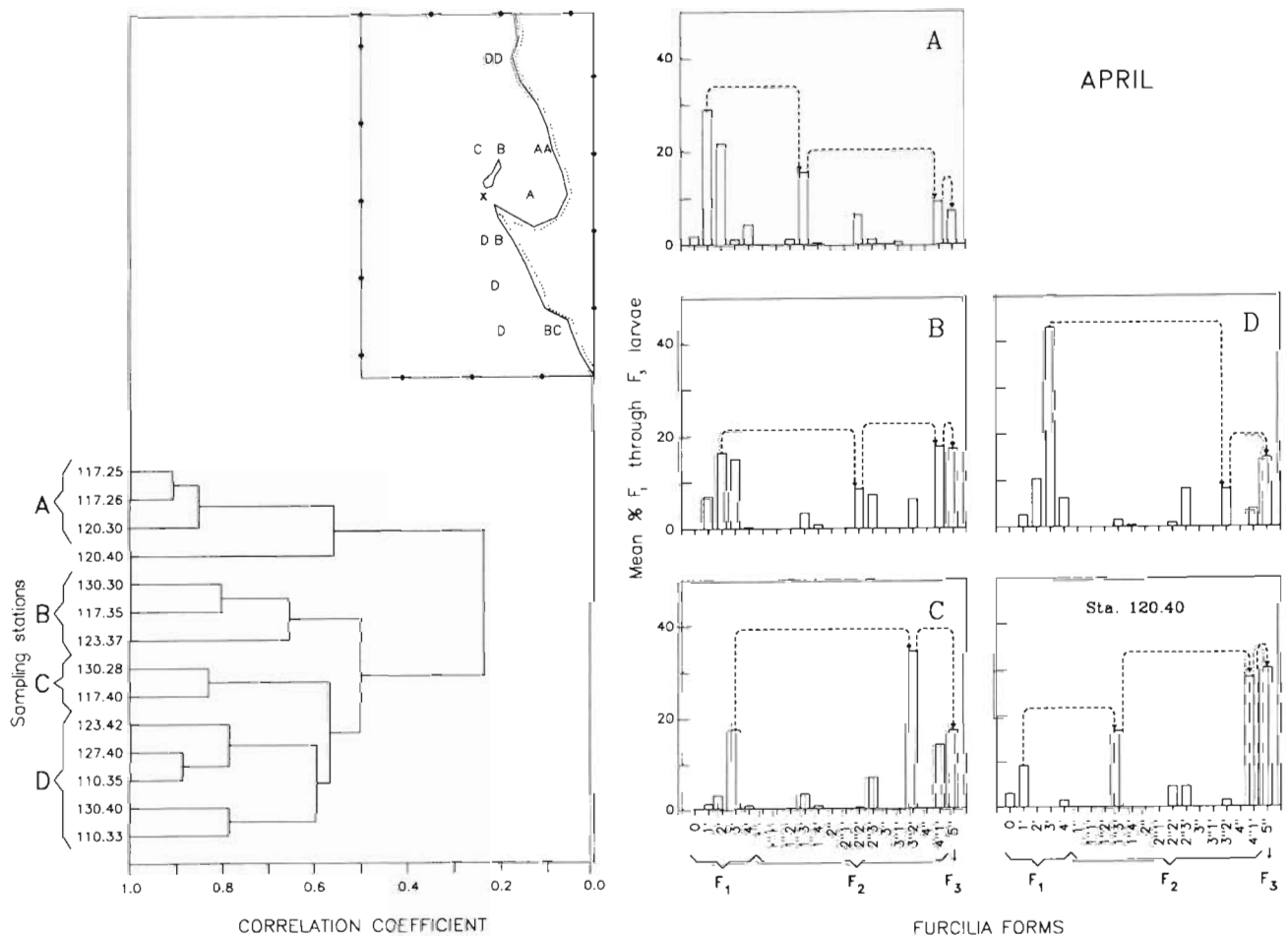


Fig. 8. Affinity among stations in composition of furcilia forms during April (for explanation see Fig. 7 legend)

to F_6). Histograms show 2 peaks in most groups, one at form 5TTS and another at form 1TTS (Fig. 11). Therefore, the dominant trend in TTS reduction would require 2 moults ($7 \rightarrow 5 \rightarrow 1$). However, other forms were important in some groups. In Group C from January, forms with 4 and 3TTS comprised 26.5%. Since form 5TTS was the maximum (40.7%), it could be assumed that an extra moult (F_5) was required to reach 1TTS. Group B from April also had a secondary peak at form 3TTS. Group A in the same season had the same proportion (21.7%) of larvae in forms 5TTS and 3TTS. We do not know with certainty if this indicates that some furciliars are in the pattern $5TTS \rightarrow 1TTS$ and others through $3TTS \rightarrow 1TTS$, because $5TTS \rightarrow 3TTS \rightarrow 1TTS$ is also possible. It is interesting to note that shorter developmental pathways, both in development of pleopods and in reduction of TTS, took place in April (in the coldest season) and in July (in the strongest upwelling season).

Seasonal differences in body length

Body length comparisons in time and space must take into account noise produced by the ontogenetic variability described above. If stages of development are considered, a mixture of forms of very different sizes is used to estimate mean body length of a stage. A finer approach would use mean body length per instar. Considering this, should the differences in number of instars required to complete larval development produce differences in body-length increment? And, should developmental pathways involving similar numbers of instars be expected to produce similar body-length increments in different seasons? To address these questions, certain dominant furcilia forms observed in affinity groups described in the preceding sections were selected to estimate mean body length per instar.

The minimum number of furcilia instars observed was 5. In January the affinity Group C had the

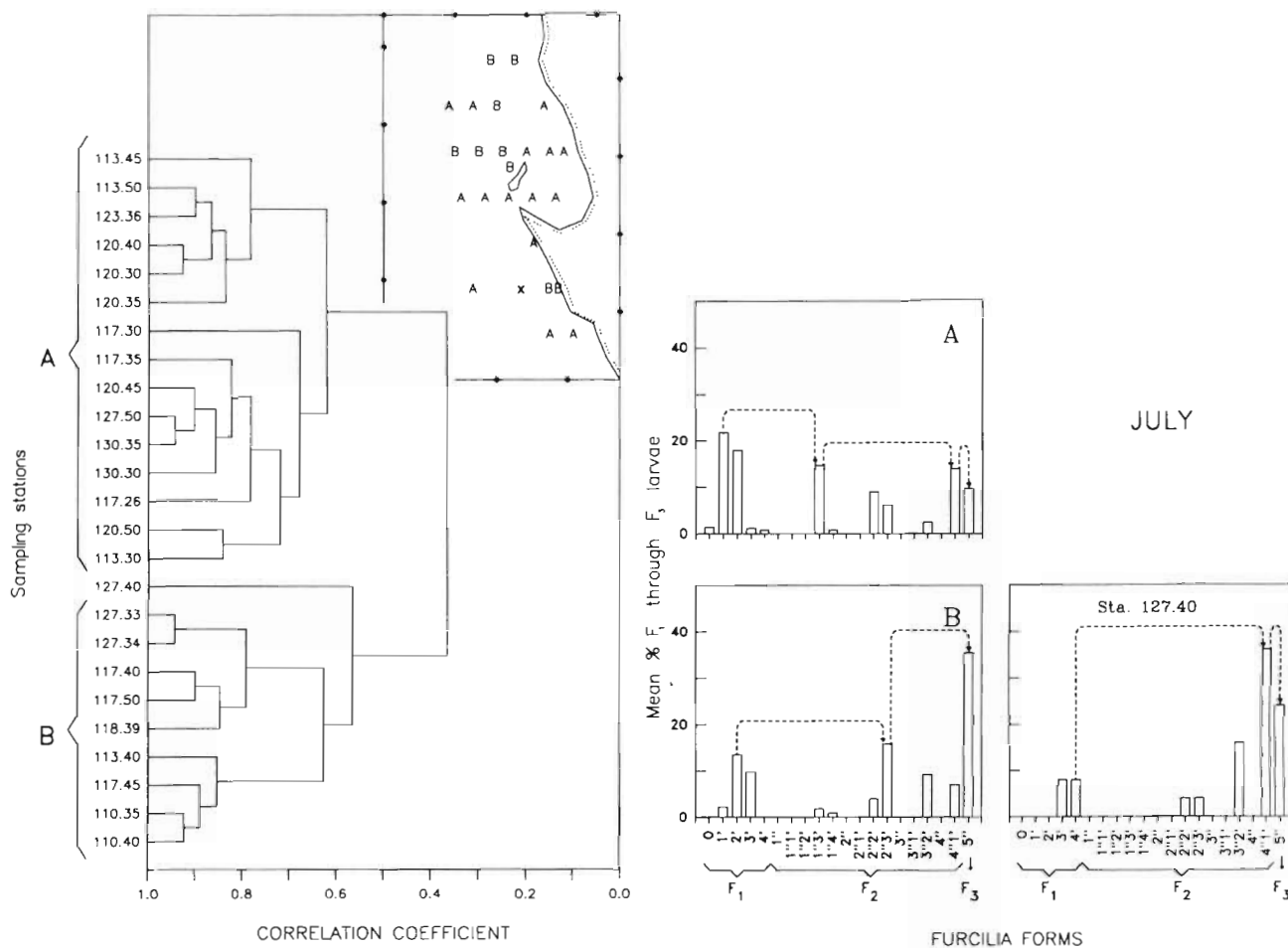


Fig. 9. Affinity among stations in composition of furcilia forms during July (for explanation see Fig. 7 legend)

sequence 2' → 2"3' → 5" → 5 TTS → 1 TTS. The same pathway was observed in Group B of July. Therefore forms 2', 2"3', 5", 5 TTS and 1 TTS were selected to calculate mean body length, in addition to the calyptopis stages (Fig. 12A). High standard deviations in body length associated with later stages (F₄ to F₆) are evidently because not all the larvae passed through the same developmental pathway. Nevertheless, the main contributors to these later stages must be larvae from the dominant F₁ to F₃ sequence. Better growth occurred in July than in January. In Group D from April a pathway equivalent to 5 furcilia instars was observed: 3' → 3"2' → 5" → 5 TTS → 1 TTS. Body-length increments in this group were similar to July. The upwelling in these months seems to have been associated with not only shorter developmental pathways but also bigger larvae.

For an inspection of body-length increments in pathways of 6 instars, the sequence 1' → 1"3' → 4"1' → 5" → 5 TTS → 1 TTS was selected using groups where it was dominant. Similar growth was found among all

months (Fig. 12B). In the case of still longer pathways it is difficult to find similar sequences among months. Comparing pathway 1' → 1"1' → 2"2' → 4"1' → 5" → 5 TTS → 4 TTS → 1 TTS observed at Stn 117.25 from January and pathway 0 → 3' → 3"1' → 4"1' → 5" → 5 TTS → 1 TTS found in Group A from October, smaller sizes were recorded in some instars during October.

Considering the body length reached in F₆ in pathways of different duration, only in April was the F₆ after 5 instars (Group D) greater than F₆ from a 6 instar pathway (Group A).

DISCUSSION

Surveys off Baja California have indicated high abundances of *Nyctiphanes simplex* year round (Brinton 1967a, 1973). Based on abundance of larvae, the most important reproductive sites have been Vizcaíno Bay, the adjacent shelf southwest of Point Eugenia and the shelf between Point Abrejos and Magdalena

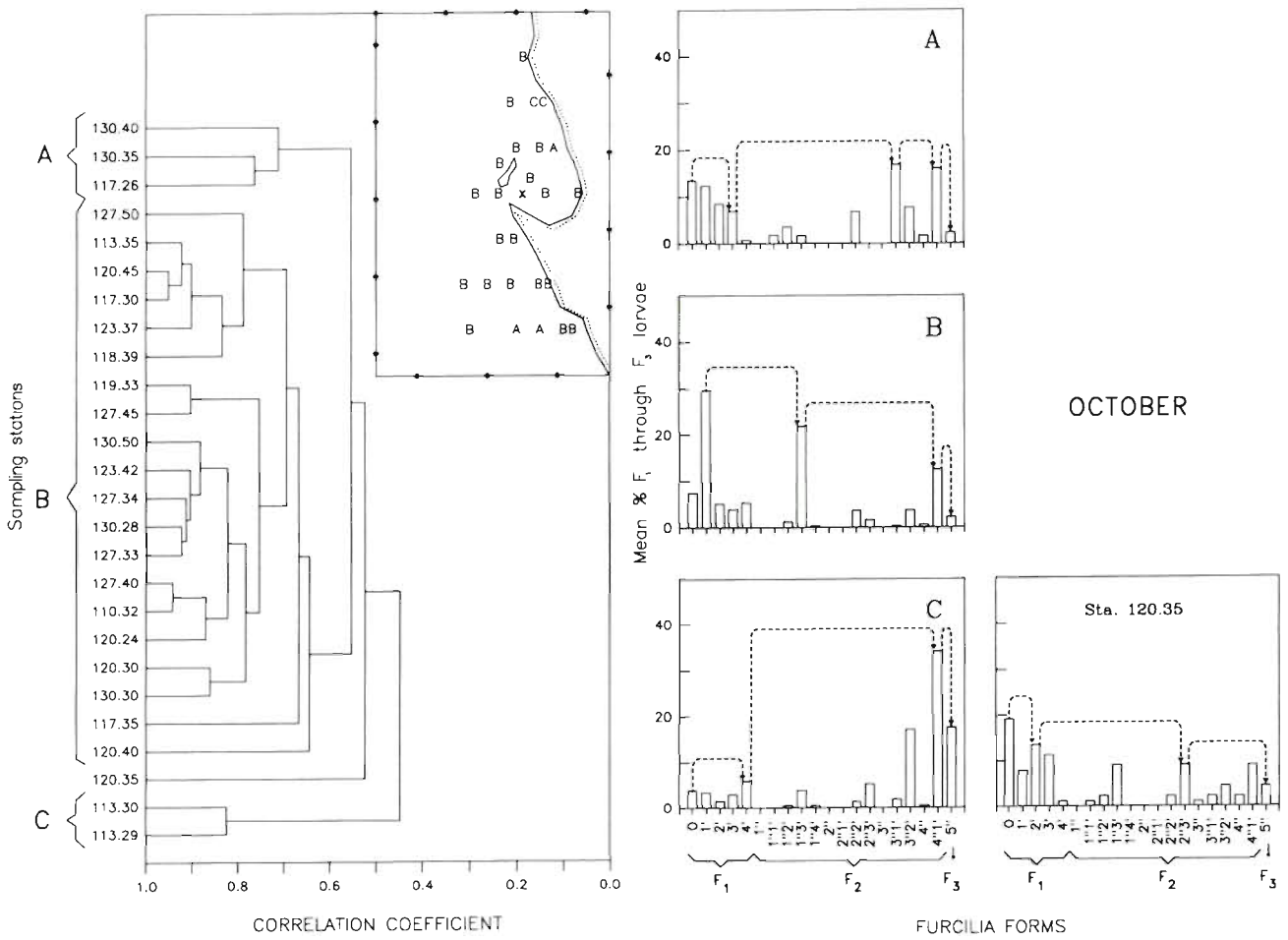


Fig. 10. Affinity among stations in composition of furcilia forms during October (for explanation see Fig. 7 legend)

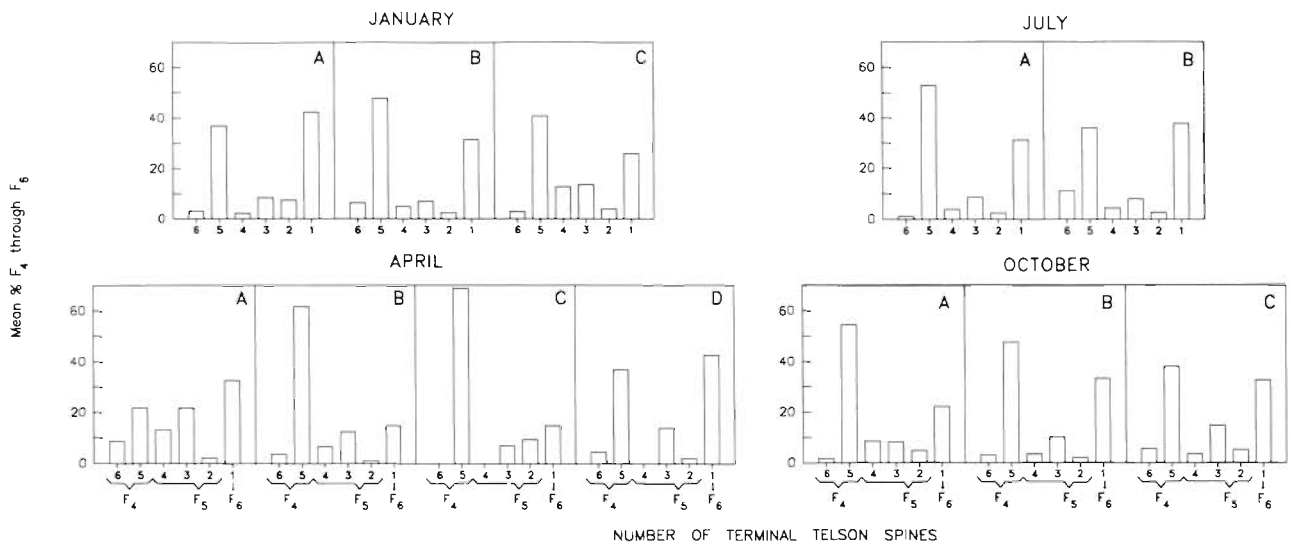


Fig. 11. Mean frequency of forms F₄ through F₆ within the affinity groups defined in the cluster analysis (Figs. 7 to 10)

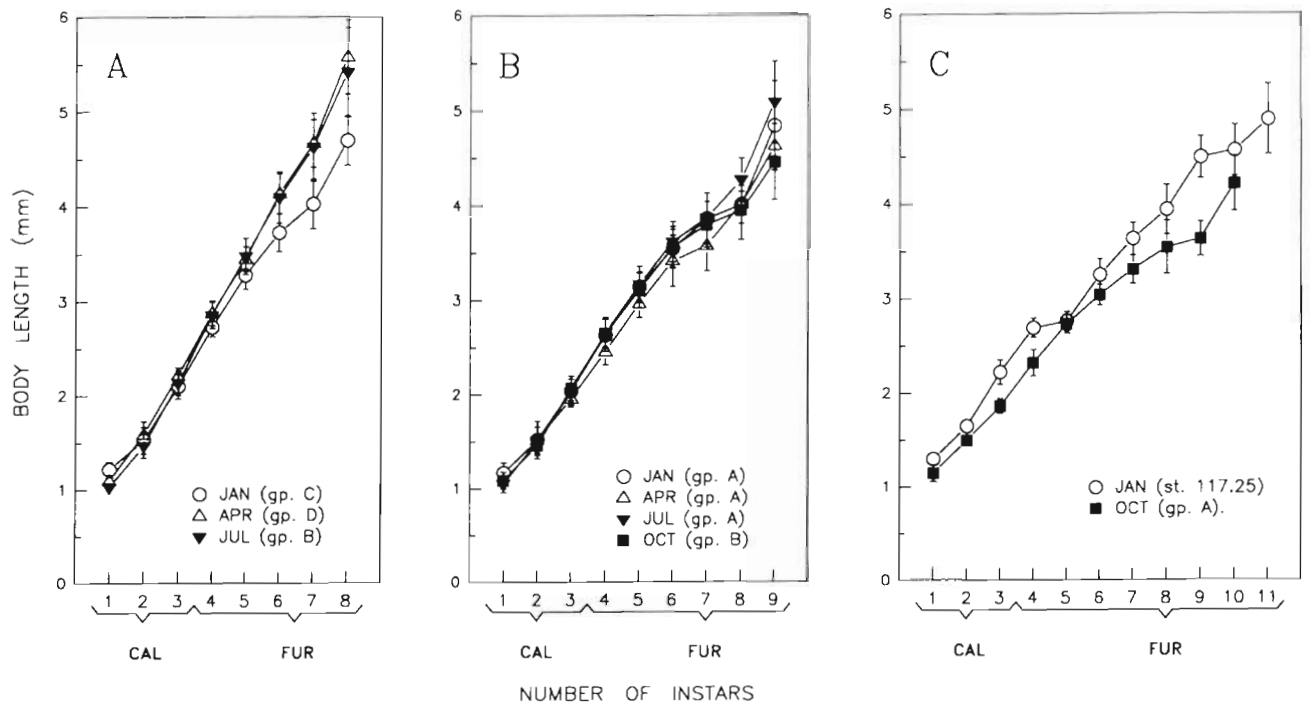


Fig. 12. *Nyctiphanes simplex*. Mean body lengths and standard deviations for larvae by instar, in sequences of: (A) 8 larval instars (pathway of furcilia development of January and July is 2' → 2"3' → 5" → 5 TTS → 1 TTS, and in April is 3' → 3"2' → 5" → 5 TTS → 1 TTS); (B) 9 larval instars (pathway of furcilia development in all months is 1' → 1"3' → 4"1' → 5" → 5 TTS → 1 TTS); (C) 10 or 11 instars (pathway of furcilia development in January is 1' → 1"1' → 2"2' → 4"1' → 5" → 5 TTS → 4 TTS → 1 TTS and in October is 0 → 3' → 3"1' → 4"1' → 5" → 5 TTS → 1 TTS). Letters in parenthesis represent affinity group (defined in Figs. 7 to 10). Cal: calyptopes; Fur: furcilia

Bay (25 to 27° N). However, when population structure was considered, a complex regional dynamic became evident. Since reproduction of *N. simplex* is continuous and there is evidence of a life span of less than a year (Lavaniegos 1992), as in *Nyctiphanes australis* from the western Pacific (Ritz & Hosie 1982), we cannot expect to be able to follow the development of individual populations (cohorts) through the year based on only the 4 surveys. Instead, the focus here is on regional trends in biological processes in different periods of the year.

While recruitment occurred through the 4 seasons, there were changes in intensity per region. In winter, recruitment occurred along the coast, as indicated by calyptopes at the stations over the coastal shelf. Mature females were then concentrated near Point Baja–Point Canoas indicating a preferential spawning site. Does this mean that the small calyptopes rapidly disperse southward to a Vizcaíno Bay nursery area? Schwartzlose (1963) estimated the southeastward flow off northern Baja California, with drift bottles, to be 0.2 to 0.3 knots (10 to 15 cm s⁻¹), during January 1959. In a straight line, 16 to 23 d would then be required to reach Cedros Island from Point Baja. If moults occur every 3 to 4 d, as observed in laboratory (Lavaniegos

1992), a metanauplius hatched near Point Baja could reach Vizcaíno Bay in stage F₁ or F₂ (Fig. 5) and then remain trapped in the central eddy of the Bay until the end of larval development. In March 1972, during the upwelling season, drogue measurements off Point San Hipolito (27° N) produced an estimate of 30 cm s⁻¹ for southward surface flow (Walsh et al. 1974). A still higher velocity (50 cm s⁻¹) was estimated in June 1976, using slopes of isopycnals off Point Colonet (31° N) (Barton & Argote 1980). With the higher values of surface flow, the arrival of larvae in Vizcaíno Bay could occur in the calyptopis phase since only 5 to 8 d would be required for transport from Point Baja.

High velocities of surface flow in the upwelling period are coincident with shortest developmental pathways in the furcilia phase, allowing a short time to reach the juvenile phase when the euphausiids enter the slope zone. There, the vertical migratory behavior of postlarvae (Brinton 1967b) may help them to avoid offshore and southerly flow at the surface. The velocity of flow tends to decrease with depth, in the layer above the undercurrent, which has been detected at 250 to 300 m flowing northward near Point Colonet during August 1966 (Wooster & Jones 1970) and again in June 1976 (Barton & Argote 1980). In the upwelling region of the Benguela

Current, where *Nyctiphanes capensis* occupies a similar niche, downward migration of maturing individuals was suggested as a mechanism to reduce advective losses from the population (Barange & Pillar 1992).

Some larvae certainly were hatched inside the Bay where a few females were found together with small calyptopes (C_1). However, south of Point Eugenia, the presence of early stages cannot be explained in terms of dispersion from the north. Daytime catches of mature females off the narrow shelf between Point Eugenia and Point Abrejos indicate spawning activity, though the small numbers suggest it is less intensive than in the northern region. Swarming behavior of *Nyctiphanes simplex* in the Gulf of California was explained as serving the process of reproduction, since a high percentage of adults in breeding condition was found during spring, in daytime surface swarms (Gendron 1992).

At the end of the main upwelling season, around September, the eddy inside Vizcaíno Bay develops and persists through fall and winter (Dawson 1952, Wyllie 1960, Mancilla-Peraza et al. 1993). The role of the Countercurrent or Davidson Current in northward transport of plankton is less understood. This Countercurrent is nearest to the coast from Point Baja northward and contributes to isolation of the Vizcaíno Bay region. Ship drift reports of a northward countercurrent are lacking in the region from Point Baja to Point Eugenia, coincident with negative wind-stress curl (Bakun & Nelson 1977). Based on these data, separate cyclonic gyres in the regions of positive wind stress curl off the Los Angeles Bight and south of Point Eugenia have been suggested (Bakun & Nelson 1977).

In 1966 the maximum observed recruitment of *Nyctiphanes simplex* was in January and October along the coast, and relatively restricted offshore in the northern region. Heating of offshore waters was at a maximum in October, although upwelling persisted off Point Baja and Point Eugenia. Both of the latter locations supported fecund females. Body length of spawning females was minimal in October in relation to other seasons but was somewhat greater in Vizcaíno Bay than at the upwelling points. More larvae per female would then be expected inside the Vizcaíno Bay eddy. During April and July large mature females >13 mm were found outside Vizcaíno Bay. The biggest spawning female was 15.8 mm, found in July off Point Eugenia. Greater sizes have been recorded in other species of the genus. Females up to 21 mm of *N. australis* were found in Storm Bay, Tasmania (Ritz & Hosie 1982) and of *N. capensis* in the Benguela Current off Namibia (Barange & Stuart 1991).

Analysis of ontogenetic patterns and mean body length of dominant furcilia forms also indicated differ-

ences in development and growth rate among months. Shorter pathways and larger sizes appeared during spring and summer, when upwelling is most intense. We do not know the duration of intermolt periods in the field, but they may be longer in cold periods as experimental studies have shown. At 14°C larvae of *Nyctiphanes simplex* moulted at 3 to 4 d intervals (Lavaniegos 1992). The same intermolt period was found for *N. couchii* of the northeastern Atlantic, at 15 to 16°C (Le Roux 1973), and was 5 d for *N. capensis* of South African waters, at 12°C (Pillar 1985). However, the laboratory studies also showed that feeding conditions affect intermolt period. Therefore, 1 or 2 extra moults to complete the furcilia phase do not necessarily mean longer periods of growth if the intermolt periods are short; however extra moults seem likely to be associated with slow growth since larvae then expend energy in the production of additional exuviae. Smaller furcilia have less rapid natatory capacity than larger furcilia and therefore there may be a higher probability that they will be preyed upon. Sustained slow growth rate will then produce smaller females, resulting in less fecundity.

Variability in pleopod development induced by environment has been reported in many euphausiid species: in the genus *Nyctiphanes* (Lebour 1926, Boden 1951, 1955, Sheard 1953). In larvae of *Euphausia pacifica*, Knight (1984) used percent similarity index to determine similarity between the percent frequency of pleopod forms within stages F_1 and F_2 from the Southern California bight. She found shorter pathways ($2' \rightarrow 2''3'$) in spring and early summer than in winter and late summer ($1' \rightarrow 1''3' \rightarrow 4''1'$). Minimum values of temperature and maximum of chlorophyll occurred during June–July. Similar conclusions have resulted for *N. simplex* in the present study: pathways $2' \rightarrow 2''3'$ or $3'' \rightarrow 3''2'$ dominated in spring and summer and $1' \rightarrow 1''3' \rightarrow 4''1'$ in fall and winter. We have no data on chlorophyll from the 1966 cruises, but for 1969, Owen (1974) found values of chlorophyll $a > 30 \text{ mg m}^{-2}$ integrated to 150 m depth along Baja California in summer, with a maximum of 230 mg m^{-2} at Point Baja. In other 1969 seasons chlorophyll a was 10 to 30 mg m^{-2} in most of the area (Owen 1974). Zooplankton volumes were also at a maximum in summer (Fig. 4) when upwelling was most intensive.

The great variability in larval development always present in *Nyctiphanes simplex* appears to result from environmental instability associated with the upwelling system. This species, like others of the same genus, shows a fast response to availability of food, shortening developmental pathways. A natatory capacity reached rapidly could be an advantage to avoid drift far away from coast when Ekman transport

is strong. Juveniles remaining near the coast might continue growing in good food conditions. A lower number of surviving females in such periods is counterbalanced by larger sizes (and higher fecundity) reached by females.

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