GROWTH AND LARVAL DEVELOPMENT OF *NYCTIPHANES SIMPLEX* IN LABORATORY CONDITIONS

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ABSTRACT

Larvae of *Nyctiphanes simplex* were reared in the laboratory from second and third calyptopis stages (C_2 and C_3) to juvenile. Effects of three different diets were observed: the microalgal flagellate *Tetraselmis suecica*, nauplii of the brine shrimp *Artemia franciscana*, or a mixture of the two. Larvae receiving *Artemia* showed longer pathways of development and longer intermoult periods. The age of larvae at the start of experiment (C_2 compared with C_3) affected patterns of pleopodal development. Rate of growth (body-length increment) decayed exponentially as estimated by von Bertalanffy equation: 0.010 d^{-1} for larvae fed either microalgae or the mixture, and 0.034–0.050 d^{-1} for larvae fed only *Artemia*.

RESUMEN

Larvas de *Nyctiphanes simplex* fueron cultivadas en laboratorio a partir de los estadios caliptopis segundo y tercero (C_2 y C_3) hasta juvenil. Se observó el efecto de tres diferentes tipos de dietas en el crecimiento: el microflagelado *Tetraselmis suecica*, nauplios de *Artemia franciscana*, o una mezcla de los dos. Las larvas que recibieron *Artemia* tuvieron vías de desarrollo más largas y periodos de intermuda más prolongados. La edad de la larva al inicio del experimento (C_2 comparado con C_3) afectó los patrones de desarrollo pleopodal. La tasa de crecimiento (incremento en longitud corporal) decayó exponencialmente según estimación con la ecuación de Bertalanffy: 0.010 d^{-1} para larvas alimentadas con microalgas o la mezcla, y de 0.034–0.050 d^{-1} para larvas alimentadas con *Artemia*.

INTRODUCTION

Nyctiphanes simplex is the most abundant euphausiid in nearshore waters of the eastern subtropical Pacific, including the Gulf of California (Brinton and Townsend 1980; Lavaniegos et al. 1989). In the season of intense upwellings, larvae of this species can average more than 50 ind/m^3 over distances of hundreds of km (Brinton 1967, 1973). However, little attention has been paid to the species' population dynamics and trophic role in the pelagic ecosystem. Boden (1951) described larval development of *N. simplex* from field samples. He found great variability in number of pleopods and terminal telson spines among furcilia specimens. A detailed study of *Nyctiphanes australis* showed that variant forms could not be considered a distortion of a single, basic pathway of development, since the dominant forms can differ from one place to another (Sheard 1953). Hedgpeth (1957) pointed out that all species of the genus occupy similar subtropical warm-temperate ecological situations.

Variability in larval development has been considered an effect of environmental variability, since it is observed most frequently in species distributed through coastal or continental slope areas (Mauchline and Fisher 1969). Influences of food type on larval development and growth rate were tested in the laboratory for *Nyctiphanes couchii* from the coast of France (Le Roux 1973). In that work there was a lower growth rate and greater variability in pathways of development in larvae on a diet of the diatom *Phaeodactylum tricornutum* than in larvae on diets of mixed microalgae or *Artemia* nauplii. Similar results were obtained for *Nyctiphanes capensis* from South Africa (Pillar 1985). Though healthy individuals tended to go through particular pathways of development, no clearly dominant pathway could be traced.

Euphausiids go through three larval phases: nauplius, calyptopis, and furcilia. In the furcilia phase there may be conspicuous variation in the addition and development of the five pairs of abdominal swimming appendages, or pleopods, and in the reduction in the number of terminal telson spines. The pleopods are added in sequence from anterior to posterior abdominal segments; each pair appears first as nonsetose rudiments which become setose and functional at the next moult (Fraser 1936; Mauchline and Fischer 1969). The number of terminal telson spines decreases from seven to one through a variable number of moults. The extreme variability in larval development that characterizes *Nyctiphanes* makes it difficult to describe an onto-

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genic sequence. An approximation of developmental sequence is crucial to the determination of age and estimation of growth.

For this study I analyzed the larval development and growth in *Nyctiphanes simplex* exposed to different feeding conditions. The following terms describe furcilia development: *phase* is the complete sequence of events in furciliar development; *instar* is the form of larva between successive moults. The following furcilia stages are used:

Furcilia 1: forms with 0–4 pairs of nonsetose pleopods.

Furcilia 2: forms with any combination of nonsetose and setose pairs of pleopods.

Furcilia 3: forms with five pairs of setose pleopods and seven terminal telson spines.

Furcilia 4: forms with five pairs of setose pleopods and five or six terminal telson spines.

Furcilia 5: forms with five pairs of setose pleopods and 2–4 terminal telson spines.

Furcilia 6: forms with five pairs of setose pleopods and one terminal telson spine.

There may be one or more instars within each stage. All furcilia forms have three pairs of posterolateral telson spines. The juvenile has only two pairs of posterolateral telson spines.

METHODS

Larvae of *N. simplex* were collected on February 9, 1990, near Todos Santos Islands, Baja California (31°49'N; 116°49'W), with a net of .333-mm-mesh width. They were transferred immediately to laboratory containers. Calyptopis stages 2 and 3 (C_2 and C_3) were sorted out. Groups of 20 larvae were placed in 200-ml beakers containing 150 ml of filtered seawater (10 μm) which had been sterilized by ultraviolet light. Beakers were kept in the dark at 14 ± 0.5°C. The larvae were fed the microalga *Tetraselmis suecica*, nauplii of the brine shrimp *Artemia franciscana*, or a mixture of the two (table 1). The content of carbon in one cell of *T. suecica* is approximately $0.8 \cdot 10^{-4}$ μg (Parsons et al. 1961); in one *Artemia* nauplii it is 0.9 μg (Bruggeman et al. 1980). Therefore, when the experiment started the amount of carbon per larva was 2.7 μg in *Artemia*-fed animals and 120 μg in *Tetraselmis*-fed animals. In addition, two lots of larvae were given no food.

The seawater was changed and the food provided daily. Microalgal culture was grown in F/2 medium under constant white light at 14 ± 0.5°C. *Artemia* nauplii were hatched every day in filtered seawater at 20°C. Body lengths of *Nyctiphanes* larvae were measured daily (in a welled slide), from tip of rostrum to end of telson (including spines) with an ocular micrometer. The number of pleopods and telson spines, and the dates of moulting were recorded. Larvae in stage C_2 at the start of the experiment are designated cohort 1, and those starting at C_3 are designated cohort 2.

TABLE 1
Food Given to Larvae of *Nyctiphanes simplex* in Each Experimental Unit*

Initial stage	Diet type	Daily ration	Replicates
C_2	Without food		2
C_2	*Tetraselmis suecica*	$2 \cdot 10^5$ cel/ml	2
C_2	*Artemia franciscana*	60 nauplii	2
C_2	*T. suecica* + *A. franciscana*	$2 \cdot 10^5$ cel/ml + 60 naup.	2
C_3	*Tetraselmis suecica*	$2 \cdot 10^5$ cel/ml	1
C_3	*Artemia franciscana*	60 nauplii	1

*150 ml of filtered seawater with 20 larvae
C_2 = calyptopis 2; C_3 = calyptopis 3.

RESULTS

Survival and Duration of Development

During the first week of the experiment half of the larvae died. Only a quarter of the total remained alive into the juvenile phase. Some of the starved larvae (table 2) started pleopodal development, but none completed it. Larvae with the best survival rate were in the cohort 2 lot receiving the *Tetraselmis* diet; 10% of the initial number died before entering the furcilia phase, and 10% more died when moulting to juvenile phase. There was high mortality (40%–60%) for all other fed larvae entering the furcilia phase. Differences in survival in relation to kind of diet were important only in the moult from last furcilia stage to juvenile.

Juveniles first appeared in lots fed *Tetraselmis* or the mixed diet, after 25 days in cohort 1 and 20 days in cohort 2 (table 3). Since furcilia first appeared in the cohort 1 after 7 days and in cohort 2 after 4 days,

TABLE 2
Survival (Percentage) of *Nyctiphanes simplex* Larvae on Different Diets at Four Levels of Development

Diet type	Initial stage	First furcilia instar	First instar with 5″	First instar with 1 t.t.s.	First juvenile instar
Starved	C_2	27.5	0.0	0.0	0.0
Tetraselmis	C_2	55.0	47.5	47.5	37.5
Artemia	C_2	40.0	35.0	25.0	7.5
Mixed	C_2	47.5	35.0	35.0	35.0
Tetraselmis	C_3	90.0	90.0	90.0	80.0
Artemia	C_3	60.0	40.0	40.0	15.0

5″ = 5 pairs setose pleopods.
1 t.t.s. = 1 terminal telson spine.
C_2 = calyptopis 2; C_3 = calyptopis 3.

TABLE 3
Mean Time Elapsed (Days) ± Standard Deviation from the Beginning of Experiment for *Nyctiphanes simplex* Larvae on Different Diets at Four Levels of Development

Diet type	Initial stage	First furcilia instar	First instar with 5″	First instar with 1 t.t.s.	First juvenile instar
Starved	C_2	7±2	—	—	—
Tetraselmis	C_2	7±1	16±2	22±2	25±2
Artemia	C_2	7±1	19±5	26±2	33±0
Mixed	C_2	7±1	16±2	21±2	26±3
Tetraselmis	C_3	4±1	13±2	17±3	20±1
Artemia	C_3	3±0	14±2	22±2	33±2

5″ = 5 pairs setose pleopods.
1 t.t.s. = 1 terminal telson spine.
C_2 = calyptopis 2; C_3 = calyptopis 3.

the furcilia phase lasted 17–19 days. The *Artemia* diet produced longer periods of furcilia development (26 days for cohort 1 and 30 days for cohort 2).

Development of Pleopods

The high variability in pleopod development during the furcilia phase that characterizes other species of the genus *Nyctiphanes* was also observed in *N. simplex* (figure 1). Of the possible pleopod combinations, only forms 5′ (5 nonsetose pleopods) and 2″3′ (2 setose and 3 nonsetose pleopods) did not occur. Forms present in all lots, including starved larvae, were 0, 1′, 2′, 3′, 1″3′, and 4″1′. Considering only the lots with food, the minimum number of forms was observed in the lots receiving the mixed diet, and the maximum number in the lot of cohort 2 receiving the *Artemia* diet. However, differences in type and proportions of forms were greater between cohorts than among diets.

Of 98 larvae starting pleopodal development, 74% completed it through 25 different pathways (table 4). Only the pathway 1′ → 1″3′ → 4″1′ → 5″ was common to all treatments; it occurred in 32.9% of the larvae. However, this pathway is considered dominant only in cohort 1 (40.4% of larvae).

In cohort 2, pathways consisting of the sequence 2′ → 2″2′ → 4″1′ → 5″ or 2′ → 2″ → 2″2′ → 4″1′ → 5″ were more common (34.6% versus 6.4% in cohort 1). Another important difference between cohorts was the proportion of pathways starting with form 0 (furcilia without pleopods): 9 pathways (46.8% of cases) in cohort 1, and 2 pathways (11.5%) in cohort 2.

The number of instars per pathway was similar in the two cohorts, with feeding conditions clearly determining the pathway. Larvae fed *Tetraselmis* tended to follow shorter pathways (table 4) than larvae fed only *Artemia*.

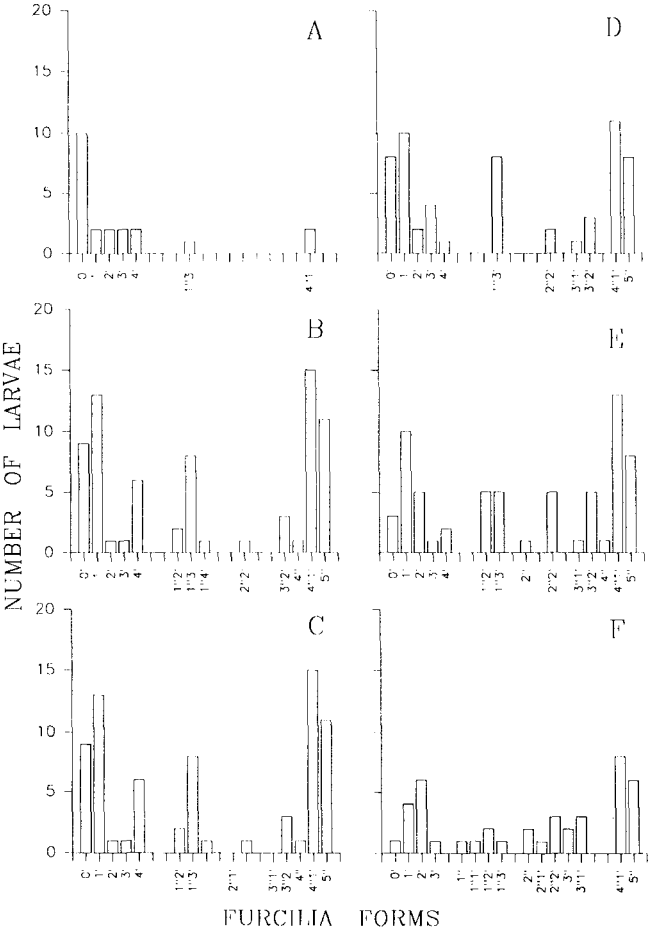

Figure 1. Frequency of furcilia forms of pleopod development in *Nyctiphanes simplex* kept under different feeding conditions: starved (*A*); *Tetraselmis* diet (*B,E*); *Artemia* diet (*C,F*); mixed diet (*D*). *A–D* are from cohort 1; and *E–F* are from cohort 2. (′) denotes a pair of nonsetose pleopods and (″) a pair of setose pleopods. All forms have seven terminal telson spines.

Reduction in Number of Terminal Telson Spines

Of 73 larvae in the first instar with five pairs of setose pleopods, 67 survived to complete the reduction of terminal telson spines (from 7 to 1). Twenty-eight larvae fed microalgae started this reduction without passing through F_3. All six possible reduced numbers of terminal telson spines (6, 5, 4, 3, 2, 1) occurred in each of the four groups that received food, with odd numbers of spines being more frequent. Most larvae required only 2 or 3 instars for complete spine reduction from 7 to 1 (table 5). Seventeen different pathways were observed in this part of development. Three pathways (7 → 5 → 3 → 1, 7 → 5 → 1, and 7 → 3 → 1) dominated, occurring in 58.2% of larvae. Sequence 7 → 3 → 1 appeared only in cohort 1.

Number of Instars in Furcilia Phase

Considering both pleopod development and the reduction of terminal telson spines, the total number

TABLE 4

Effect of Diet on Pathways of Pleopodal Development in Laboratory-Reared *Nyctiphanes simplex* Furcilia Stages 1, 2, and 3*, with Frequency Observed for Kind of Diet

Cohort 1

Instar number					Diet type and number of larvae				
1	2	3	4	5	*Tet*	*Art*	Mix	Total	%
4′	→4″1′	→5″			1	1		2	
1′	→1″4′	→5″			1			1	
1′	→1″3′	→4″1′			4		3	7	34.0
0	→ 4′	→4″1′			3	1	1	5	
0	→ 3′	→3″2′					1	1	
3′	→3″1′	→4″1′	→5″				1	1	
1′	→1″3′	→4″1′	→5″		3	5	4	12	
1′	→1″2′	→3″2′	→5″		1			1	
0	→ 4′	→4″1′	→5″		2	2		4	55.3
0	→ 3′	→3″2′	→5″		1	3	2	6	
0	→ 2′	→2″2′	→4″1′				1	1	
0	→ 1′	→1″2′	→3″2′		1			1	
1′	→1″3′	→4″	→4″1′	→5″	1			1	
0	→ 4′	→4″	→4″1′	→5″		1		1	
0	→ 2′	→2″2′	→4″1′	→5″	1		1	2	10.6
0	→ 1′	→1″2′	→3″1′	→4″1′		1		1	

Cohort 2

Instar number						Diet type and number of larvae			
1	2	3	4	5	6	*Tet*	*Art*	Total	%
3′	→3″1′	→4″1′				1		1	
2′	→2″2′	→4″1′				3		3	30.8
1′	→1″3′	→4″1′				2		2	
1′	→1″2′	→3″2′				2		2	
2′	→2″2′	→4″1′	→5″			1	2	3	
2′	→2″	→2″2′	→4″1′			1	1	2	
1′	→1″3′	→4″1′	→5″			2	1	3	50.0
1′	→1″2′	→3″2′	→5″			2		2	
0	→ 4′	→4″1′	→5″			2		2	
0	→ 1′	→1″2′	→3″2′			1		1	
2′	→2″1′	→3″	→3″1′	→4″1′			1	1	
2′	→2″	→2″2′	→4″1′	→5″			1	1	15.4
1′	→1″3′	→4″	→4″1′	→5″		1		1	
1′	→1″1′	→2″2′	→4″1′	→5″			1	1	
1′	→1″2′	→3″	→3″1′	→4″1′	→5″		1	1	3.8

*Includes all larvae with 7 terminal telson spines.
(′) = pair nonsetose pleopods; (″) = pair setose pleopods.

of developmental pathways was 52. The number of furcilia instars most frequently observed was 6 for *Tetraselmis*-fed larvae and 7 for *Artemia*-fed larvae (table 6). Statistical comparison of the number of instars (two-way analysis of variance) with factors cohort and diet, showed significant differences only for diet ($F = 8.68$, $p = 0.005$). *A posteriori* multiple range test (Student-Newman-Keuls) for means at 95% confidence interval indicated a difference ($p = 0.015$) only between the means for *Tetraselmis*-fed larvae (6.2 ± 0.3 instars) and those fed *Artemia* (6.9 ± 0.4 instars) and not between larvae fed the mixed diet and the other diets. All the larvae fed microalgae showed one instar in F_6. Only six of the *Artemia*-fed larvae reached the juvenile phase (i.e., reduction of posterolateral telson spines from three pairs to two), and they required two or three instars within F_6.

Intermoult Period and Moulting Rate

The average intermoult period for all larvae was 3 days. In each feeding treatment some extremely short or long periods occurred. Long periods were most common in *Artemia*-fed and starved larvae (figure 2). Nonparametric comparison of intermoult periods among diets, using Kruskall-Wallis test (rank sums) showed significant differences ($p < .001$) only in cohort 1. For all treatments, the intermoult period remained approximately constant through successive moults.

Regression analysis of cumulative intermoult period on number of moults (table 7; figure 3) indicated a slower moulting rate for *Artemia*-fed animals of cohort 1, but very similar rates among other diet groups (mixed diet is omitted in figure 3, since it is almost identical to *Artemia* diet). Moulting rate is

TABLE 5

Effect of Diet on Pathways of Reduction in Terminal Telson Spines in Laboratory-Reared *Nyctiphanes simplex*

Cohort 1

	Instar number				Diet type and number of larvae				
	1	2	3	4	*Tet*	*Art*	Mix	Total	%
	3	→1			5	1	3	9	
	4	→1			1			1	40.5
	5	→1			3	2	2	7	
	4	→2	→1			1		1	
	5	→2	→1		1	1		2	
7→	5	→3	→1		4	3	2	9	
	5	→4	→1				1	1	54.8
	6	→2	→1		2		1	3	
	6	→3	→1		1		4	5	
	6	→4	→1			1	1	2	
	5	→3	→2	→1	1			1	4.8
	6	→4	→3	→1	1			1	

Cohort 2

	Instar number				Diet type and number of larvae			
	1	2	3	4	*Tet*	*Art*	Total	%
	4	→1			2	1	3	
	5	→1			6	2	8	52.0
	6	→1			2		2	
7→	5	→2	→1		1	1	2	
	5	→3	→1		3	3	6	44.0
	6	→2	→1		2		2	
	6	→3	→1			1	1	
	5	→4	→2	→1	1		1	4.0

TABLE 6

Effect of Diet on Number of Instars in Furcilia Phase of *Nyctiphanes simplex*

		Number of instars				
Diet type	Cohort	5	6	7	8	9
Tetraselmis	1	3	9	6	1	
Artemia	1		4	5		
Mixed	1	1	7	6		
Tetraselmis	2	5	7	4	1	
Artemia	2		2	3	2	1
Total		9	29	24	4	1

In *Artemia* diet only the first instar in F_o (1 t.t.s.) is included because most of the larvae died before the moult to juvenile phase.

TABLE 7

Regression Parameters of Cumulative Intermoult Period on Moult Number for Larvae of *Nyctiphanes simplex*

Diet type	Cohort	*a*	Moulting rate (days/moult)	r^2
Tetraselmis	1	0 ± 1.5	2.90 ± 0.03	0.941
Artemia	1	0 ± 1.9	3.69 ± 0.04	0.942
Mixed	1	0 ± 1.4	2.82 ± 0.03	0.951
Tetraselmis	2	0 ± 1.6	2.64 ± 0.04	0.898
Artemia	2	0 ± 3.3	2.88 ± 0.09	0.819

Forcing intercept (*a*) to zero; slope = moulting rate.

defined here as number of days elapsed per moult. The regression for *Artemia*-fed larvae of cohort 2 had the poorest fitting, with the last instars sometimes showing prolonged intermoult periods, and sometimes showing short intermoult periods but more moults. Juveniles appeared first in the *Tetraselmis* diet (figure 3).

Growth Rate

Increments in body length were consistently higher in the *Tetraselmis*-fed larvae. Mean body length for furcilia forms is shown in tables 8 and 9. A comparison among forms and treatments could not be made because there were too few measurements for many of the forms and heteroscedasticity. However, for larvae with form 5″ and 7 terminal telson spines (when the development of pleopods was complete), the statistical comparison of body-length measurements among diets and cohorts produced significant differences ($F = 31.54$, $p < 0.001$; one-way analysis of variance) among treatments. *A posteriori* multiple range test (Student-Newman-Keuls) for means resulted in two groups: the diets including microalgae and the diet of *Artemia* only. A similar comparison among treatments of larvae with

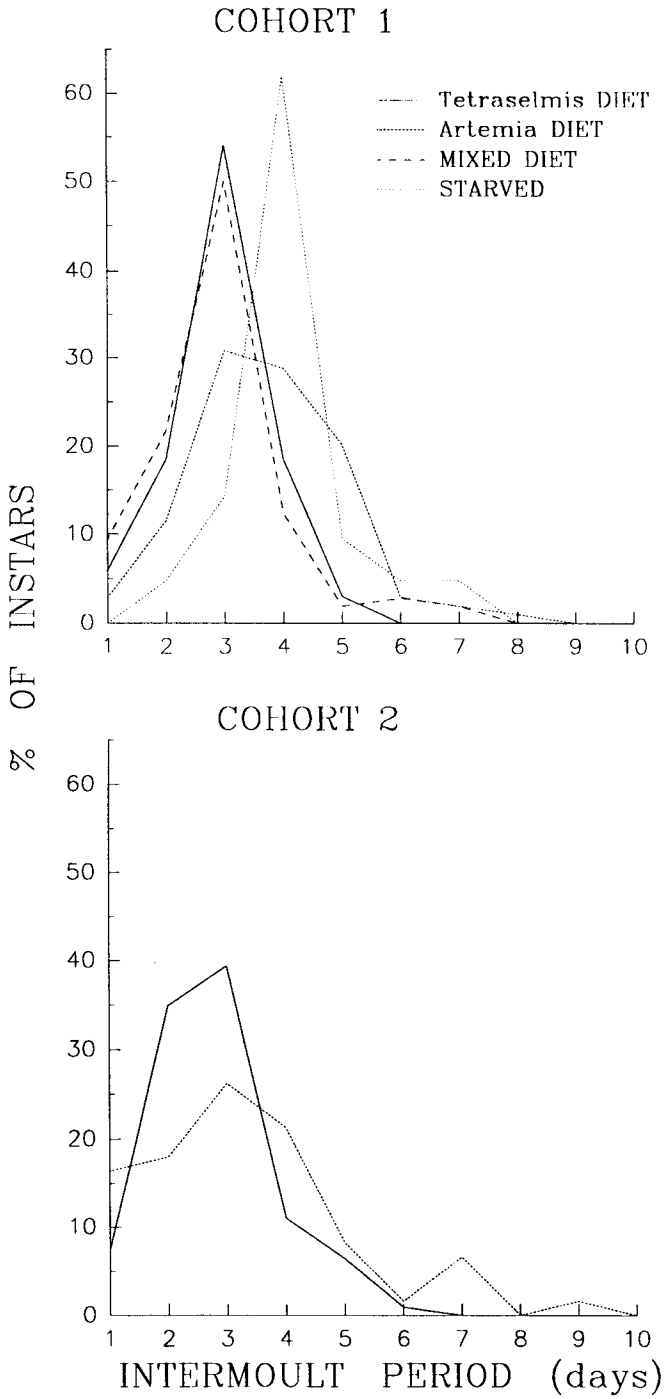

Figure 2. Relative frequency of furcilia instars having different durations in *Nyctiphanes simplex* under different feeding conditions.

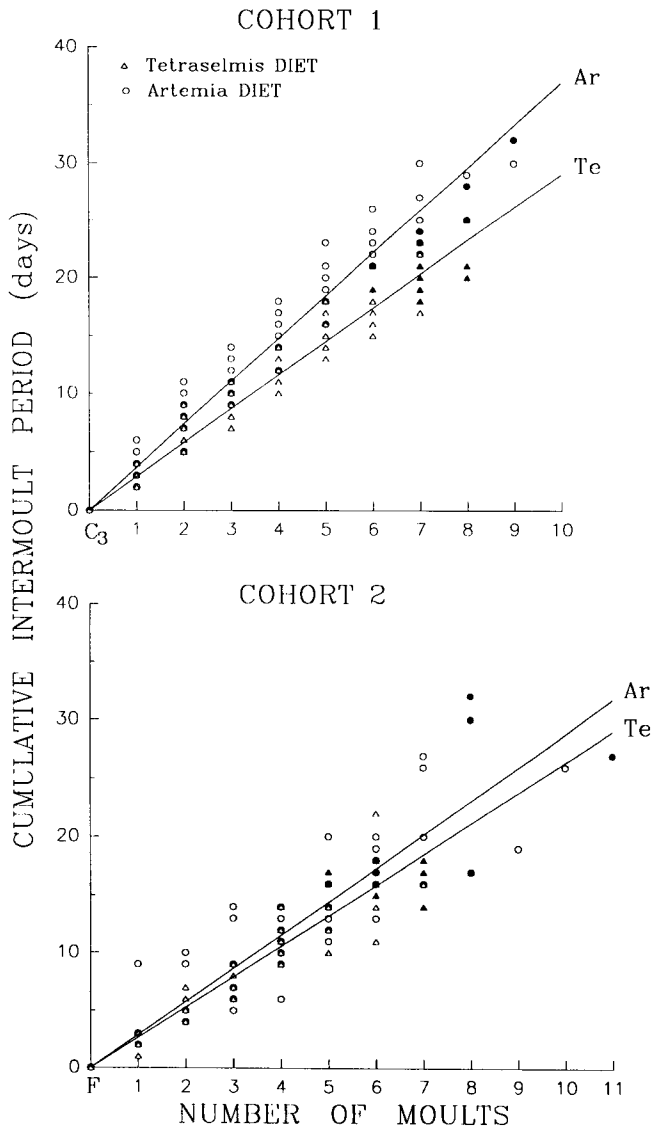

Figure 3. Cumulative intermoult period on successive number of moults for *Artemia*-fed and *Tetraselmis*-fed larvae. Mixed diet had similar values to *Tetraselmis* diet. Closed symbols indicate the appearance of juveniles. Lines are predicted values from regression analysis (Ar, *Artemia*-fed; Te, *Tetraselmis*-fed).

the form 1 terminal telson spine (when reduction in number was complete) showed significant differences also ($F = 163.27$, $p < 0.001$), and again one homogeneous group of means for microalgal diets. *Artemia*-fed larvae, however, did not form a homogeneous group, which suggests differences between cohorts.

The increment in body length on time was not linear, suggesting an exponential decay (instantaneous growth rate). The von Bertalanffy growth curve was used to estimate growth:

$$L_t = L_{\text{inf}}[1 - e^{-K(t-t_0)}]$$

where L_t = length of animal at age t; L_{inf} = asymptotic maximum length; K = instantaneous growth rate; and t_0 = age of animal when L_t is zero. In order to eliminate the last parameter to make the curves for different diets comparable, t_0 is taken equal to zero. Therefore a constant value of 8.5 days was added to values of t in cohort 1, and of 11.5 days in

TABLE 8
Effect of Diet on Mean Body Length (mm) ± Standard Deviation of *Nyctiphanes simplex* of Cohort 1

Stage	Form	Diet type: Starved	*Tetraselmis*	*Artemia*	Mixed
Calyptopis 2		1.5 ± 0.1	1.6 ± 0.1	1.6 ± 0.1	1.6 ± 0.1
Calyptopis 3		1.9 ± 0.1	2.1 ± 0.1	2.0 ± 0.1	2.1 ± 0.1
Furcilia 1	0	2.3 ± 0.2	2.6 ± 0.2	2.4 ± 0.1	2.6 ± 0.1
	1′	2.5 ± 0.1	2.7 ± 0.2	2.6 ± 0.2	2.7 ± 0.1
	2′	2.6 ± 0.2	3.0	2.8	2.8 ± 0.1
	3′	2.8 ± 0.1	3.4	2.9 ± 0.1	3.0 ± 0.2
	4′	3.0 ± 0.1	3.3 ± 0.1	3.0 ± 0.2	3.4
Furcilia 2	1″2′	—	3.1 ± 0.2	2.7	—
	1″3′	2.8	3.3 ± 0.2	3.2 ± 0.1	3.3 ± 0.1
	1″4′	—	3.5	—	—
	2″1′	—	—	2.8	—
	2″2′	—	3.3	—	3.3 ± 0.3
	3″1′	—	—	2.9	3.3
	3″2′	—	3.6 ± 0.3	3.2 ± 0.1	3.5 ± 0.2
	4″	—	3.4	3.1	—
	4″1′	3.0 ± 0.2	3.9 ± 0.2	3.4 ± 0.2	3.8 ± 0.2
Furcilia 3	7 t.t.s.	—	4.3 ± 0.3	3.6 ± 0.3	4.2 ± 0.3
Furcilia 4	6 t.t.s.	—	4.4 ± 0.2	3.4 ± 0.1	4.3 ± 0.1
	5 t.t.s.	—	4.4 ± 0.1	3.8 ± 0.3	4.4 ± 0.3
Furcilia 5	4 t.t.s.	—	4.5 ± 0.1	3.9 ± 0.2	4.9 ± 0.1
	3 t.t.s.	—	4.8 ± 0.2	4.0 ± 0.3	4.6 ± 0.2
	2 t.t.s.	—	4.8 ± 0.2	4.1 ± 0.2	4.9
Furcilia 6	1 t.t.s.	—	5.0 ± 0.3	4.3 ± 0.3	5.1 ± 0.3
Juvenile 1*		—	5.4 ± 0.3	4.9 ± 0.1	5.5 ± 0.3

(′) = pair nonsetose pleopods; (″) = pair setose pleopods; (t.t.s.) = terminal telson spines.
*For *Tetraselmis* and mixed diets, measurements after day 24 (when 50% larvae had moulted to juvenile) are excluded.

TABLE 9
Effect of Diet on Mean Body Length (mm) ± Standard Deviation of *Nyctiphanes simplex* of Cohort 2

Stage	Form	Diet type: *Tetraselmis*	*Artemia*
Calyptopis 3		2.1 ± 0.1	2.2 ± 0.1
Furcilia 1	0	2.5 ± 0.2	2.2
	1′	2.6 ± 0.2	2.4 ± 0.2
	2′	2.7 ± 0.2	2.5 ± 0.2
	3′	2.5	2.5
	4′	3.2 ± 0.1	—
Furcilia 2	1″	—	2.7
	1″1′	—	2.7
	1″2′	3.1 ± 0.2	2.9 ± 0.1
	1″3′	3.2 ± 0.3	3.1
	2″	3.0	2.8 ± 0.1
	2″1′	—	2.8
	2″2′	3.3 ± 0.2	3.0 ± 0.2
	3″	—	2.8
	3″1′	3.3	3.1 ± 0.2
	3″2′	3.6 ± 0.2	—
	4″	3.1	—
	4″1′	3.8 ± 0.2	3.4 ± 0.2
Furcilia 3	7 t.t.s.	4.3 ± 0.3	3.8 ± 0.3
Furcilia 4	6 t.t.s.	4.2 ± 0.2	3.6
	5 t.t.s.	4.4 ± 0.2	3.8 ± 0.1
Furcilia 5	4 t.t.s.	4.2 ± 0.4	3.9
	3 t.t.s.	4.7 ± 0.1	3.8 ± 0.1
	2 t.t.s.	4.6 ± 0.3	4.1
Furcilia 6	1 t.t.s.	5.1 ± 0.3	4.0 ± 0.3
Juvenile 1*		5.2 ± 0.4	4.5 ± 0.2

(′) = pair nonsetose pleopods; (″) = pair setose pleopods; (t.t.s.) = terminal telson spines.
*For *Tetraselmis* diet, measurements after day 20 (when 50% of larvae had moulted to juvenile) are excluded.

cohort 2. These values are assumed to be the mean ages for stages C_2 and C_3 respectively, from hatching to the midpoints of C_2 and C_3, assuming that (1) the larvae had spent one day becoming metanauplii after leaving the maternal ovisacs in the form of pseudometanauplii, and (2) each successive instar of the calyptopis phase lasted 3 days. When parameters L_{inf} and K were estimated for each treatment (table 10; figure 4) there was a remarkable similarity in K for the *Tetraselmis*-fed larvae and those fed the mixed diet, indicating a reduced growth rate of 0.01 per day. The asymptotic body length predicted for these treatments is consistent with the maximum sizes occasionally found in field samples of adults (17–19 mm). In contrast, the *Artemia*-fed and starved larvae showed a drastic decay in growth rate and a small asymptotic body length, indicating that such larvae would probably die in subsequent larval or juvenile stages.

A duration of 4–5 weeks for the larval phase is predicted by von Bertalanffy's equation under optimal feeding conditions (from pseudometanauplius to the first juvenile). The *Artemia*-fed larvae could require 7–8 weeks. The number of moults produced with a constant moulting rate is 12 in the first case. For *Artemia*-fed larvae of cohort 2 the estimated number of 18 moults could be too high, indicating that a constant moulting rate should not be assumed.

TABLE 10

Parameters of von Bertalanffy's Growth Equation, and Age Estimated at End of Larval Phase (L_t = Body Length of First Juvenile Stage)

Diet	Cohort	L_{inf} (mm)	K (d^{-1})	r^2	Larval phase	
					Days	Moults*
Tetraselmis	1	18.6	0.010	0.929	34	12
Artemia	1	5.8	0.034	0.864	56	15
Mixed	1	20.2	0.009	0.953	35	12
Starved	1	3.4	0.067	0.729	—	—
Tetraselmis	2	19.6	0.010	0.890	31	12
Artemia	2	4.9	0.050	0.847	52	18

*Number of moults is calculated with moulting rates from table 7.

DISCUSSION

The influence of feeding conditions on larval growth and development of other *Nyctiphanes* euphausiids reared in the laboratory (Le Roux 1973, 1974; Pillar 1985) indicates that the environment does indeed affect ontogenesis, as suggested by the many studies of euphausiid furcilia of various genera based on field samples (Lebour 1926; Macdonald 1927; Rustad 1930; Fraser 1936; Boden 1951; Sheard 1953; Mauchline 1965; Mauchline and Fisher 1969). However, variation in pathways of pleopodal development is not exclusive to larvae subjected to poor feeding conditions, as observed here for *Nyctiphanes simplex* and previously for *N. couchii* (Le Roux 1973) and *N. capensis* (Pillar 1985). The number of larvae handled in experiments of this kind may be inadequate for extracting general conclusions as to dominant pathways, but the results still indicate that, under controlled conditions, there are several preferential routes. Furthermore, dominant pathways in *N. simplex* following different experimental starting points (cohorts C_2 and C_3) were more different than in groups distinguished by diet. Whether developmental pathways are affected by the precapture history of larvae or differing adaptations to laboratory conditions is difficult to answer.

Feeding history was reflected more in the duration than in the route of pathways. Healthy larvae of *N. simplex* seem to require 6 or 7 instars in the furcilia phase for developing pleopods and reducing the number of terminal telson spines before moulting to juvenile. Boden (1951) described six furcilia stages, two based on pleopodal development (with variable number of forms) and four based on reduction in number of terminal telson spines, as well as segmentation of the second antennal endopod (table 11). In this study, spine reduction was usually completed in 2–3 instars; only three larvae required 4 instars (table 5). Experimental results for *N. capensis* indicated a dominant sequence of 3 instars to reduce the number

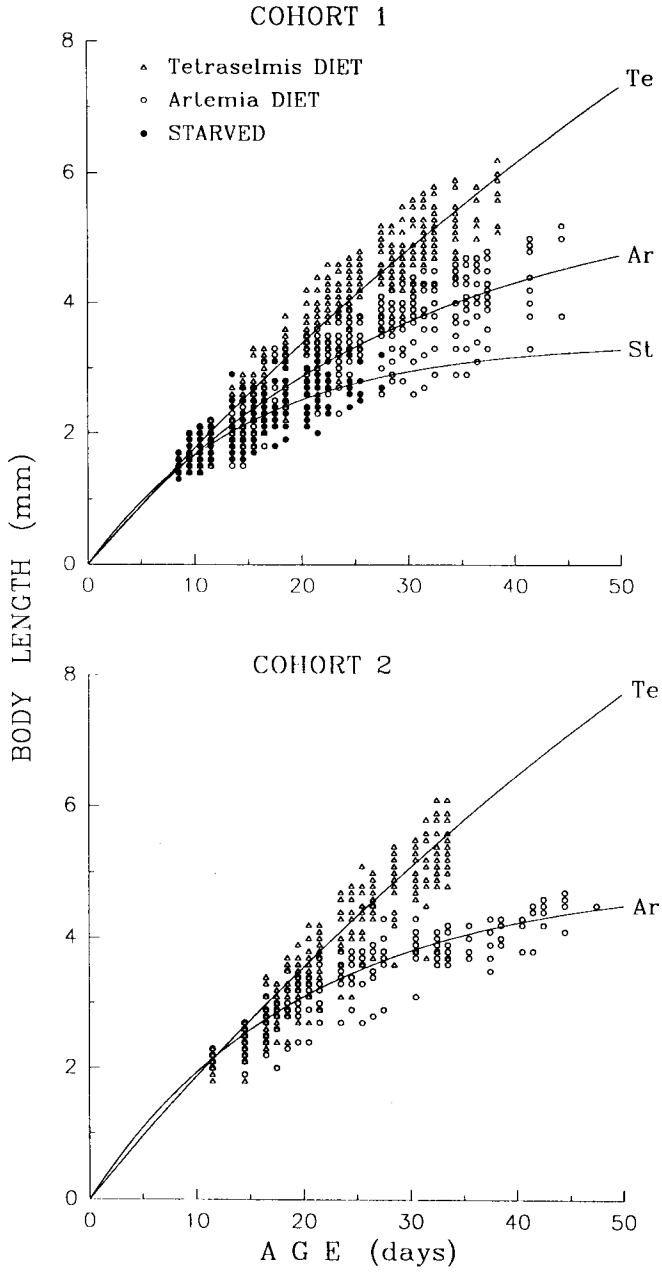

Figure 4. Body length of *Nyctiphanes simplex* larvae reared under different feeding conditions (*symbols*) and von Bertalanffy growth curves (*lines*) estimated for *Tetraselmis*-fed (Te), *Artemia*-fed (Ar), and starved (St) larvae. Mixed diet had similar values to *Tetraselmis* diet.

of terminal telson spines; no sequences of only 2 instars were noted (Pillar 1985). In *N. couchii* (Le Roux 1973) a 2-instar sequence was more frequent. Boden (1951) used segmentation of the antennal endopod to separate furcilia stages of *N. simplex* (table 11). In the experiment reported here, segmentation occurred when larvae moulted from penultimate to last furcilia instar (68% of the larvae)—i.e., when terminal telson spines were reduced to one, independently of the precedent form. Because this anatom-

TABLE 11
Diagnostic Characters Used to Classify Furcilia Stages of Development

Furcilia stages	Boden (1951)	This study
F_1	Forms with nonsetose pleopods; 7 terminal telson spines. 2nd antennal endopod unsegmented.	Forms with nonsetose pleopods; 7 terminal telson spines.
F_2	Combination of nonsetose and setose pleopods or all setose; 7 terminal telson spines. 2nd antennal endopod unsegmented.	Combination of nonsetose and setose pleopods; 7 terminal telson spines.
F_3	Five setose pleopods; 5–6 terminal telson spines. 2nd antennal endopod unsegmented.	Five setose pleopods; 7 terminal telson spines.
F_4	Five setose pleopods; 3–4 terminal telson spines; 2nd antennal endopod unsegmented.	Five setose pleopods; 5–6 terminal telson spines.
F_5	Five setose pleopods; 3–4 terminal telson spines; 2nd antennal endopod segmented.	Five setose pleopods; 2–4 terminal telson spines.
F_6	Five setose pleopods; 1–2 terminal telson spines; 2nd antennal endopod segmented.	Five setose pleopods; 1 terminal telson spine.

ical feature does not synchronize with telson spine reduction, I have omitted it in the diagnosis of furcilia forms.

A major advance in our understanding of moulting processes is needed to explain why, under poor feeding conditions, some larvae lengthen the intermoult period and others increase the number of moults. The intermoult period observed for healthy larvae of *N. simplex* is similar to that for *N. couchii* under temperatures of 15°–16°C (Le Roux 1973). In *N. capensis* a long intermoult period (5 days) was recorded most frequently at 12°C (Pillar 1985). Longer intermoult periods in *N. couchii* and *Meganyctiphanes norvegica* were found to be induced by limited food and low temperatures (Le Roux 1973, 1974).

The condition of larvae is expressed here by body length. Size differences among specimens of a particular form seem to depend on each individual's place in its pathway of development, since significant differences between diets were more important than between cohorts. Experimental studies permit us to know exact ages and to estimate growth rates. A constant growth rate was assumed by Le Roux (1973) for *N. couchii*, with estimates of 0.10–0.13 mm/d for larvae fed abundant *Artemia*. Similar values were estimated for *N. capensis* larvae fed *Artemia* mixed with copepod nauplii or microalgae (Pillar 1985); when both species were reared with a diet of the diatom *Phaeodactylum tricornutum* mean growth was only 0.05 mm/d. Differing growth rates among species of *Nyctiphanes* fed only *Artemia* may have resulted from the amount of this food offered to the larvae. In the experiment discussed in this paper, the ration offered (60 larvae per lot per day) was always completely consumed; thus the diet's effect may have resulted from its quantity as well as quality.

Body-length growth cannot be assumed constant, and the logarithm of length regressed on moult number (Mauchline 1977) has been used to estimate growth rate in several species. Fitting of data to this model seems inadequate in some cases, including *Nyctiphanes simplex*. The von Bertalanffy equation provides a better fit. For larvae of cohort 1 fed *Tetraselmis* (K = 0.010 d^{-1}; L_{inf} = 18.6 mm), ages predicted for average sizes of C_3, F_3, F_6, and juvenile are 12, 26, 31, and 34 days, respectively; this means pleopodal development takes 14 days (mean growth = 0.159 mm/d); reduction of terminal telson spines takes 5 days (mean growth = 0.138 mm/d); and advance to the juvenile phase takes 3 days (mean growth = 0.137 mm/d). Similar calculations for *Artemia*-fed larvae (K = 0.034 d^{-1}; L_{inf} = 5.8 mm) result in periods of 17 days for pleopodal development, 11 days for reduction of terminal telson spines, and 16 days for advance to juvenile phase (mean growth being 0.098, 0.062, and 0.040 mm/d, respectively). Mean growth rates for *Tetraselmis*-fed larvae of *N. simplex* are higher than those recorded for furcilia stages of another California Current euphausiid species, *Nematoscelis difficilis* (0.10–0.12 mm/d reared on *Artemia* mixed with diatoms; Gopalakrishnan 1973). However, *N. difficilis* needs only 3 furcilia-phase moults to reach the juvenile form, though with somewhat longer intermoult periods.

Considering the mean length of an immature adult (males with petasma scarcely apparent and females with ovaries not showing oocytes) of *Nyctiphanes simplex* to be 7.5 mm, its age estimated from the von Bertalanffy equation with parameters K = 0.010 d^{-1} and L_{inf} = 18.6 mm is 52 days, indicating a short juvenile phase of only 18 days. A maximum size of 17 mm (though the most frequently observed value has been 14 mm) would require 245 days. Therefore, at most, the adult phase would last 6–7 months. One-year-old individuals should be considered exceptionally long-lived. Whether or not the decay in growth rate (K) adequately expresses the use of energy for reproduction instead of increasing body length needs to be explored. Cohort analysis

of field samples of larvae, juveniles, and adults of *N. australis* from southeastern Tasmania indicated a life span of approximately 140 days for a 14-mm adult, and 240 days for a 17-mm adult (Ritz and Hosie 1982). A similar study by Gros and Cochard (1978) using only adults suggested an average of one year of life for *N. couchii*, and perhaps two years for the largest specimens. The latter period seems improbable because growth rates estimated from laboratory experiments with *N. couchii* and its congeners *N. capensis* and *N. simplex* and from field samples of *N. australis* point to a shorter life span.

CONCLUSIONS

Growth and larval development of *Nyctiphanes simplex* were followed for the first time in the laboratory. A diet of the microalga *Tetraselmis suecica* produced better growth and shorter developmental pathways than a diet of *Artemia* nauplii. According to the van Bertalanffy growth equation, the time required to reach the juvenile phase was 31–34 days with the first diet and 52–56 days with the second diet. The average life span predicted by this model is 6 or 7 months. This short life span may be an adaptation to coastal upwelling ecosystems where production of food is irregular.

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