LIFE-HISTORY CHARACTERISTICS OF TWO SYMPATRIC THALASSINIDEAN SHRIMPS, *NEOTRYPAEA CALIFORNIENSIS* AND *UPOGEBIA PUGETTENSIS*, WITH IMPLICATIONS FOR OYSTER CULTURE

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ABSTRACT

An investigation of the life-history characteristics of 2 thalassinid shrimps (*Neotrypaea californiensis* and *Upogebia pugettensis*) on intertidal mud flats in Willapa Bay, Washington (U.S.A.), revealed substantial differences. Both species are viewed as pests by the oyster industry due to their ability to disturb sediments. The density of *Neotrypaea* was always higher than that of *Upogebia* in the undisturbed populations sampled, and burrow opening–shrimp density relationships differed between species (1.2 burrow openings shrimp^{-1} in *Neotrypaea* and 1.5 openings shrimp^{-1} in *Upogebia*). Differences were also noted in growth rate (2–3-mm CL yr^{-1} for *Neotrypaea* versus 4–5-mm CL yr^{-1} for *Upogebia*), size at maturity, and sexual dimorphism. Male and female claw size diverged immediately in juvenile *Upogebia* (4–5-mm CL, <1 yr old), but not until sexual maturation in *Neotrypaea* (9–10-mm CL, almost 2 yr old). Average fecundity was higher for *Upogebia* (7,100 eggs) than *Neotrypaea* (3,900 eggs) and we found a distinct difference in the seasonal reproductive cycle of the 2 species of shrimps. *Neotrypaea* were ovigerous from April through August and *Upogebia* were ovigerous from October through May. Seasonal timing of postlarval recruitment was correspondingly offset; *Neotrypaea* recruited to the estuary from late summer through early fall (August–October), while *Upogebia* recruited in spring (April–June). The seasonal difference in timing of recruitment of these shrimps to the estuary has important implications for shrimp-control programs and oyster-culture practices which are currently not being considered. Control operations occur in July before settlement of postlarvae of *Neotrypaea*, enabling this species to rapidly reinfest oyster-culture areas.

Two species of burrowing thalassinid shrimps are endemic to estuaries along the Pacific coast of North America. The ghost shrimp *Neotrypaea californiensis* Dana, 1854 (formerly *Callianassa californiensis*; Manning and Felder, 1991) and the mud shrimp *Upogebia pugettensis* Dana, 1852 (hereafter referred to by generic name only) inhabit the middle to low intertidal zone from southeast Alaska to Baja California (Stevens, 1928; MacGinitie, 1930, 1934; Swinbanks and Murray, 1981; Hart, 1982). Like other thalassinid shrimps, they dig extensive gallery systems in the sediment (MacGinitie, 1930, 1934; Swinbanks and Luternauer, 1987; Griffis and Chavez, 1988), and thereby greatly influence community composition and structure (Peterson, 1977; Brenchley, 1981; Bird, 1982; Peterson, 1984; Posey, 1986a, b, 1987a, 1990; Posey *et al.*, 1991). *Neotrypaea* and *Upogebia* also adversely affect shellfish aquaculture operations in these estuaries by increasing turbidity and sediment deposition rates and reducing the compaction of

intertidal sediments. The chronic disturbance to the benthos causes oysters and other sessile bivalves to either sink into the mud or be smothered and die, particularly as settling larvae and spat (Stevens, 1929; Loosanoff and Tommers, 1948; Washington Department of Fisheries (WDF), 1970; Peterson, 1984; Murphy, 1985).

Commercial oyster farmers have controlled shrimp populations on intertidal oyster beds in Washington State (U.S.A.) since 1963 using the insecticide carbaryl (1-napthol n-methyl carbamate, brand name Sevin®) which is sprayed directly on the sediment at low tide (WDF, 1970; Buchanan *et al.*, 1985; WDF and Washington Department of Ecology (WDOE), 1985, 1992; Armstrong *et al.*, 1989). This chemical inhibits activity of the enzyme acetylcholinesterase at nerve synapses, resulting in hyperactivity, paralysis, and death (Estes, 1986). With the exception of attempts to use carbaryl to control *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991, in South America (R. B. Griffis, personal

communication), where penaeid shrimp culture is affected by the burrowing activity of this shrimp (Lemaitre and Rodrigues, 1991), the program in Washington is the only reported use of chemicals to control thalassinid shrimps as pests. The population dynamics of *Neotrypaea* and *Upogebia* in small estuaries along the Oregon coast have been described (Bird, 1982; Johnson and Gonor, 1982), and Posey (1986a, b) examined ecological relationships of *Neotrypaea* with predators and other infauna. Despite a 30-year history of shrimp control in Washington State, however, little has been done to describe life-history characteristics of *Neotrypaea* and *Upogebia* in Washington estuaries or to link these characteristics with aquaculture practices and the seasonal timing of the pesticide application program developed to control them. Without some knowledge of life history, and particularly the timing of seasonal recruitment of these two thalassinid shrimps to intertidal oyster beds, we hypothesized that control programs targeted at juveniles and adults would be less effective, and only temporary solutions to the problem.

The objectives of this study were twofold: (1) to describe and compare the life-history characteristics (growth, reproduction, and larval settlement) of *Neotrypaea* and *Upogebia* in Willapa Bay, the largest and most important estuary for oyster-culture operations in the Pacific Northwest (Conway, 1991), and (2) to identify characteristics that should be considered in design and implementation of programs to control shrimp on intertidal culture grounds. This study was part of a larger program to examine the efficacy of the pesticide carbaryl as the present control measure (Dumbauld, 1994). Characterization of the life history of the pest organism is a crucial step toward implementing any control program. It is an explicit goal of integrated pest management, which has become the preferred alternative in the recent environmental impact assessment for thalassinid shrimp control in Washington (WDF and WDOE, 1992).

MATERIALS AND METHODS

Field Collection.—Willapa Bay covers approximately 260 km², making it the largest estuary along the west coast of the United States north of San Francisco Bay
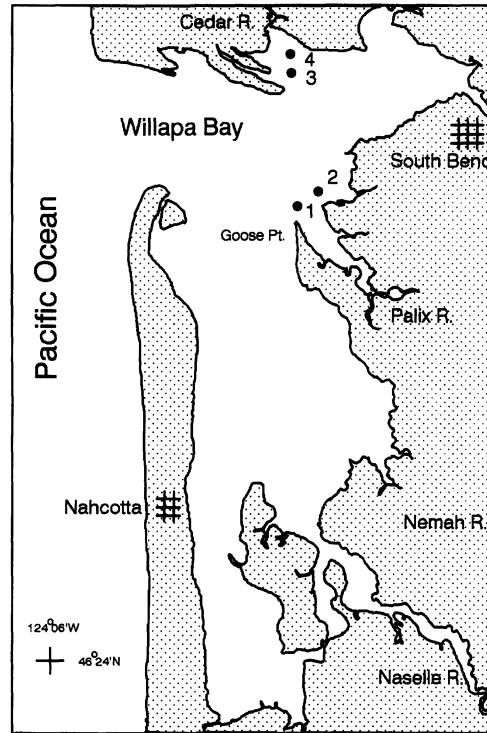

Fig. 1. Map of Willapa Bay, Washington, showing the location of the primary intertidal sampling locations, Stations 1, 2 along the Palix River Channel. Also shown are Stations 3, 4 along the Cedar River Channel.

(Hedgpeth and Obrebski, 1981). Tides are semidiurnal, ranging up to 4–5 m, and over half of the bay is exposed at low tide. Although distribution of the 2 species of thalassinid shrimps often overlaps in Willapa Bay, sampling locations were purposely selected in areas of high single-species density. Shrimps were sampled regularly from June 1988–June 1990 at 2 estuarine locations along the Palix River channel (Stations 1, 2, Fig. 1). Additional collections were made at 2 locations along the Cedar River channel in 1988 and 1989 (Stations 3, 4), and *Neotrypaea* and *Upogebia* were also sampled once each year from 1991 through 1994 at Stations 1, 4, respectively.

Neotrypaea and *Upogebia* dig burrows that range in depth from several cm as juveniles up to 90 cm as adults, but are usually less than 60 cm deep (Stevens, 1928; MacGinitie, 1930, 1934; Thompson, 1972; Swinbanks and Luternauer, 1987). Burrows have multiple openings to the surface and bulbous turnarounds enabling the shrimps to reorient themselves within their burrows. Since burrow openings are often used to estimate the density of thalassinid shrimps, we counted burrow openings at each sample location on each date before core samples were taken in order to establish a ratio between shrimp density and burrow openings. When possible, approximately 10 cores were taken per sampling trip at each station. Quantitative sampling of thalassinids in intertidal areas by previous researchers has generally been carried out with small

coring devices (10-cm diameter by 50-cm depth) or with a small pump (Hailstone and Stephenson, 1961; Bird, 1982; Posey, 1986a). In order to increase the size of a sample, relative to size and morphology of the shrimp burrow, we used a large stainless steel core (40-cm diameter by 60-cm depth for *Upogebia* and 40-cm diameter by 90-cm depth for *Neotrypaea*) and excavated contents with a shovel. The longer (90 cm) core was necessary when sampling *Neotrypaea* to stabilize the unconsolidated substrate at depth, preventing shrimp outside the sampling area from entering the core and allowing the upper 60 cm to be quantitatively sampled.

The contents of each core were sieved through 3-mm mesh and sorted for shrimps. Shrimps were measured from the tip of the rostrum to the posterior margin of the cardiac region of the carapace (carapace length, CL, to the nearest whole mm), and sex was determined for individuals larger than 4-mm CL based on presence of anterior pleopods in females. Females with eggs were recorded and a visual assessment of egg-development stage was made (i.e., color and presence of eye spots). Subsamples were frozen and saved for laboratory analyses of shrimp dry weight, egg count, and additional morphometric measurements. A smaller core (26.5-cm diameter by 15-cm depth) was periodically used during settlement periods in 1989 and 1990 to capture newly recruited individuals that passed through the 3-mm mesh. Contents were rinsed on a 1-mm mesh sieve (later a 0.5-mm mesh sieve) and sorted for shrimps.

Laboratory Analyses.—Shrimps retained for laboratory analyses were sexed and CL was measured to the nearest 0.1 mm. Morphometric measurements were taken from a subsample of male and female shrimps of both species. These included total length (TL, from the tip of the rostrum to the posterior margin of the telson), propodus length of the largest chela (PL, along the midline from insertion of the dactylus to the posterior margin), propodus height (PH, at the widest point), and carpus length and height (CAL and CAH, both measured at the widest point). Linear relationships were developed between these measurements and used to estimate size at maturity. This was particularly useful for males, since gonad development was not assessed. Shrimps with a complete complement of appendages were blotted dry for wet-weight measurements and dried at 60°C for 48 h to obtain dry weight. Eggs were removed from pleopods of females, subsampled and counted, and dried separately. Total egg count was estimated using both dry weight (g): total egg count = subsample count * dry weight subsample/dry weight total egg mass, and volumetric methods: count = volume sample/average volume of a single egg. In the latter technique, the volume of an egg ($\bar{x}$ + 1 SD in cc) was determined by using the average diameter of a subsample of 20 eggs to compute the volume of a sphere. Counts of the entire egg mass were made on females of both species to assess the accuracy of each technique. Only counts of newly extruded eggs were used in final fecundity estimates.

All data were entered into a database (Rbase by Microrim) on a microcomputer and analyzed with a commercial statistical package (Statgraphics® by Magunistics). Size-frequency analyses were performed by fitting lognormal components to the data using MIX (Release 2.3, Icthus Data Systems; MacDonald and Pitcher, 1979). Since the MIX algorithm often produced more than one set of possible lognormal distributions, graphical presentations of the means of these distributions were used to choose the most reasonable representation of growth for each species and sex. Age classes were assigned and hereafter are referred to by number starting with 0+ which identifies shrimps from the time they settle to the benthos to one year thereafter. Multiple linear regression was used to model the relationship between burrow-count density and shrimp density with time and location as factors. In most cases, standard least squares linear regression was used to determine relationships between morphometric measurements. Although iterative standard least squares regression and examination of the total residual sum of squares provided a less distinct definition of transition points than the reduced major axis technique explored by Lovett and Felder (1989), it was deemed adequate and used to determine the size at which shrimps reached maturity.

RESULTS

Shrimp Density

The average density of *Neotrypaea* at Station 1 along the Palix River increased from about 230 shrimp m^{-2} in September, 1988, to 450 shrimp m^{-2} in October, 1994 (Fig. 2). This increase was due in part to a strong settlement event and 0+ year class in 1989 which comprised 56% of the population in 1990 (1+ shrimp, 4–8-mm CL by late summer; see length frequency and growth results below) and 49% of the population (2+ shrimp, 7–12-mm CL) in 1991 (Fig. 2). The density of *Neotrypaea* at Station 3 along the Cedar River in 1988 and 1989 was comparable to that at Station 1 (214–244 shrimp m^{-2}). The average density of *Upogebia* was always lower than that for *Neotrypaea*, but there was a similar increase in density over the sampling interval from about 40 shrimp m^{-2} in 1989 to 100 shrimp m^{-2} in 1994 at Station 4 along the Cedar River (Fig. 2). The mean density at Station 2 along the Palix River was comparable to that at Station 4, fluctuating from about 85–125 shrimp m^{-2} throughout 1988 and 1989.

The density of burrow openings was highly variable, but positively and significantly correlated to shrimp density. Location and time of year had a significant effect on the relationship for *Neotrypaea* (ANCOVA, $P = 0.016$ and $P < 0.001$, respectively), while only time of year was important for *Upogebia* (ANCOVA, $P = 0.70$ and $P < 0.001$). The best relationship be-
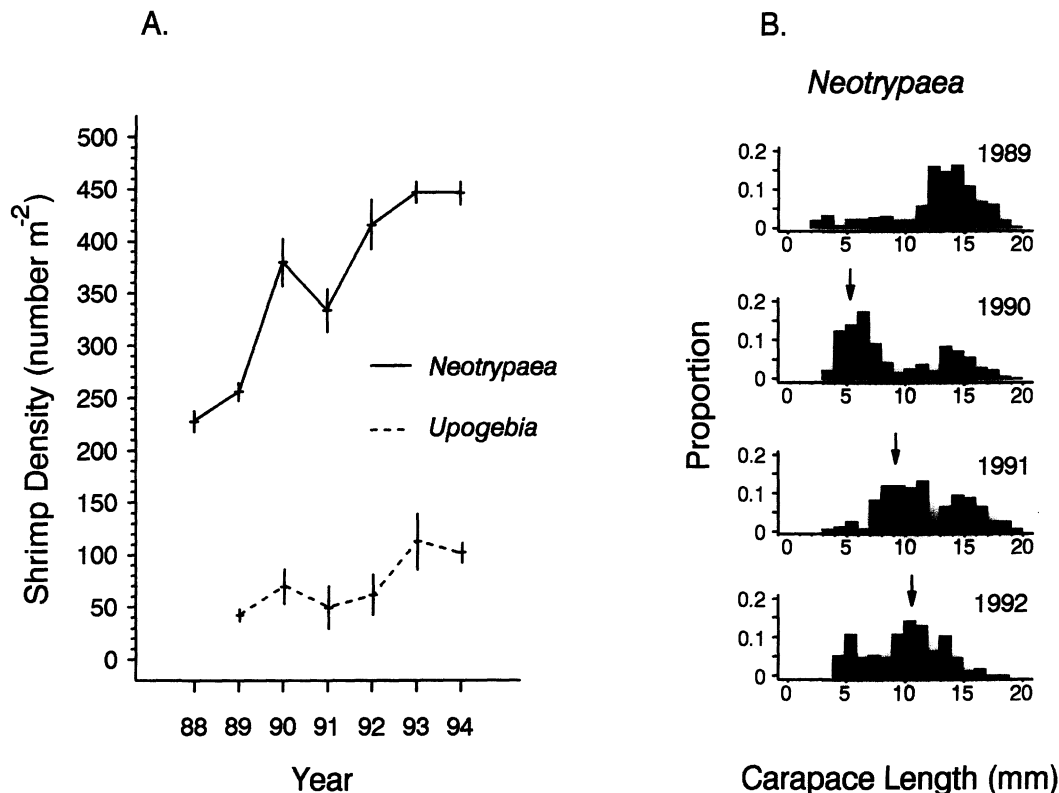
Fig. 2. (A) Average density of *Neotrypaea* at Station 1 and *Upogebia* at Station 4 from 1988–1994. Data represent means from samples (N = 5–10) taken during a single month in late summer or early fall and therefore include 0+ *Upogebia* but exclude newly recruited *Neotrypaea* (bars represent ±1 SE). Note the low density of *Upogebia* relative to *Neotrypaea* and long-term increase in density of both species. (B) Size composition of *Neotrypaea* in samples from 1989–1992. Arrows designate a large 1989 year class of shrimp first detected as 1+ (4–8-mm CL) in summer 1990 that contributed to a large population increase over the next three years.

tween average burrow count and average shrimp density was achieved by plotting only the means from warmer months (May–October, 1988–1989) at Stations 1, 2 (Fig. 3). The slope of the relationship was greater (ANCOVA, P < 0.005) for *Upogebia* (1.5 burrow holes shrimp^{-1}) than *Neotrypaea* (1.2 burrow holes shrimp^{-1}), but variability was equally high for both species, and correlation coefficients were similar (r = 0.73 and 0.75, respectively).

Size Frequency and Growth

The smallest size classes were routinely missed in the 40-cm diameter core samples processed through a 3-mm mesh screen. Samples taken with the 26.5-cm diameter core and processed through a 1-mm mesh screen in 1990, revealed that settlement of 0+ *Neotrypaea* occurred from August–October (Fig. 4) and that this species displayed

little growth until the following summer. Shrimp did not reach a size of 4–8-mm CL until August or September one year after settlement. Therefore, most individuals first appearing in the 40-cm diameter core samples were at least six months old and perhaps as much as one year old (Fig. 5). In contrast, settlement of *Upogebia* (at a location near Goose Point, see Fig. 1) occurred sometime in May and June. These shrimp grew rapidly during their first summer, allowing individuals to reach 7–9-mm CL by August of the same year (Fig. 4).

Size-frequency distributions revealed the year-round presence of several larger (≥1+) size classes of shrimps which could occasionally be visually distinguished (e.g., August 1988 for males of both species, Fig. 5), but were confirmed in all cases using size-frequency analysis. The presence of a broad range of sizes forming at least two
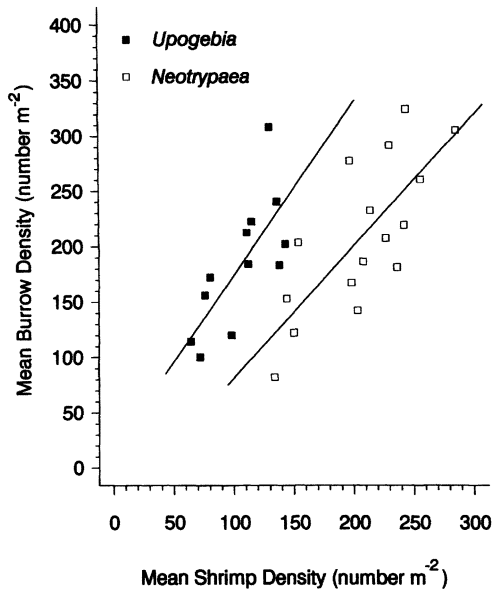
Fig. 3. Relationship between average burrow opening density and average shrimp density for both species at Stations 1, 2 during summer months (May–October). The slope of the relationship was 1.5 burrow holes shrimp^{-1} for *Upogebia* and 1.2 burrow holes shrimp^{-1} for *Neotrypaea*.

cohorts of 0+ shrimps (which differed in mean size by 1–3-mm CL) in some years made it difficult to distinguish the age of >1+ shrimps (note July 1990 size-frequency histogram showing two cohorts of *Neotrypaea* that recruited in 1989, Fig. 4). Graphical presentations of the means of the lognormal distributions produced by the MIX algorithm indicated the presence of four to five year classes of shrimps for both species and sexes (e.g., males, Fig. 6). Although growth intervals are discrete and growth rates are markedly higher during spring and summer, size-at-age data were used to estimate average annual growth rates for both species and sexes via simple linear regression on the means (Fig. 7). Average growth rates were higher for *Upogebia* (4.7- and 5.4-mm CL yr^{-1} for females and males, respectively) than for *Neotrypaea* (3.3- and 3.5-mm CL yr^{-1} for females and males, respectively). Sex and cohort were added to the model as categorical factors, and both were significant for each species (ANCOVA, $P < 0.001$). Females and cohorts settling later in the season grew more slowly than males and earlier cohorts, respectively.

Sexual Dimorphism and Maturation

Body size and claw morphometry revealed marked sexual dimorphism, particularly for *Neotrypaea* (Table 1). Carapace length (CL) was linearly related to total length (TL) and to dimensions of the chela (PH and CAH). There was little difference between sexes in the relation between TL and CL for either species, but a slight inflection was present in the relationship for females of both species occurring at approximately 13-mm CL for *Neotrypaea* and 28.5-mm CL for *Upogebia* (Table 1). The relationship between chela size (PH) and CL differed between males and females of each species, and there was a sharp inflection point for both sexes, presumably corresponding to sexual maturation (Fig. 8). Inflection points were less distinct for both sexes of *Upogebia* (26-mm CL for females and 25-mm CL for males) than for *Neotrypaea* (11-mm CL for females and 9.5-mm CL for males). Male claw size was larger than that of females for all sizes of *Upogebia* and adult *Neotrypaea* (Table 1), but similar for juvenile *Neotrypaea* (Fig. 8). The height of the carpus and propodus continued to expand in males with increasing claw length, while female claw size stopped growing (particularly for the carpus of *Neotrypaea* and the propodus of *Upogebia*). At the same PL and CL, the PH and CH were correspondingly greater for male than female *Upogebia*, while PH and PL expanded at similar rates for male and female *Neotrypaea* until maturation, when PH expanded dramatically in males. The slope of the best-fitting multiplicative relationship between carapace length and weight was also greater for males of both species, reflecting their continued growth beyond sexual maturity (Table 1).

Sex ratio was influenced by size, season, and location. The sex ratio was approximately equal for juvenile *Neotrypaea* ($\bar{x}$ = 52% males), but skewed toward females for sexually mature adults ($\bar{x}$ = 32% males). In contrast, the proportion of female *Upogebia* was greater for both juveniles ($\bar{x}$ = 43% males) and adults ($\bar{x}$ = 45% males). Seasonal differences in sex ratio were apparent, but only significant for adult male *Neotrypaea*, which were more abundant in winter months (ANOVA, $P < 0.001$). Significantly

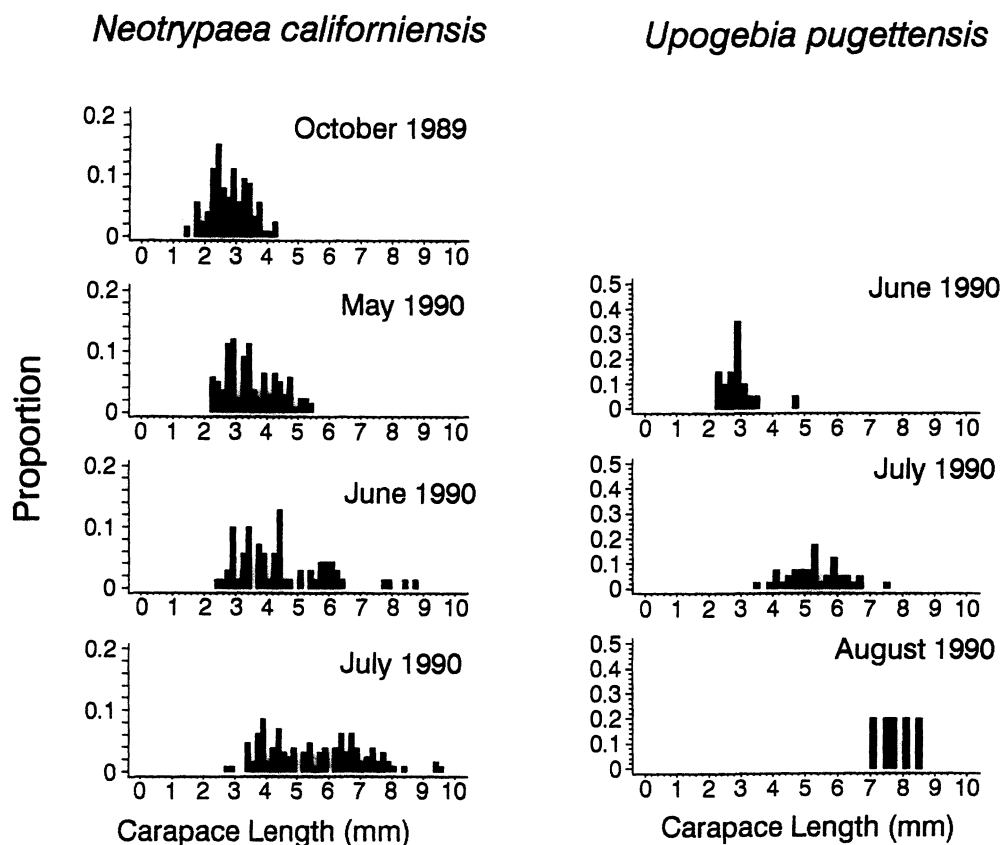## Neotrypaea californiensis

Upogebia pugettensis

Fig. 4. Size composition of newly recruited *Neotrypaea* at Station 1 along the Palix River Channel and *Upogebia* at a location just south of Station 1 near Goose Point in 1990. *Upogebia* grew rapidly from 2–3-mm CL shortly after settlement in June to 7–9-mm CL in August, while *Neotrypaea* settled later (August–October) and grew more slowly from 1–4-mm CL in October to 3–6-mm CL in July of the following year. Note the presence of 2 cohorts for both species.

more adult male *Upogebia* were present at Station 2 than at Station 4 ($P < 0.005$). No significant effects of station or season could be detected in juvenile sex ratios for either species.

Reproduction

A striking difference was observed in the reproductive cycle of the two species of shrimps. Ovigerous *Neotrypaea* were found throughout spring and summer (April–August), while female *Upogebia* carried eggs from fall through spring (October–May; Fig. 9). *Neotrypaea* extruded red eggs in spring that developed and hatched from June–August (indicated by the presence of empty egg cases on the pleopods), while *Upogebia* extruded yellow eggs in fall that developed more slowly and hatched the following spring (February–May). Average

size of ovigerous female *Neotrypaea* was 14-mm CL (range: 9–19-mm CL), while ovigerous *Upogebia* averaged 26-mm CL (range: 20–30-mm CL). Growth models indicate that the majority of ovigerous shrimps of both species were at least three years old (Fig. 7).

The volumetric method of measuring egg count consistently overestimated true egg count, while the dry weight method underestimated the count. Since dry-weight estimates were far more variable, however ($r = 0.88$ versus $r = 0.99$ for the volume method), volume estimates and the resulting relationship (a multiplicative function, egg volume $= 19.73$ count$^{0.76}$) were used to obtain fecundity estimates (Fig. 10). Fecundity increased with size for both species, but fit a much steeper curve for *Neotrypaea* due to smaller size at maturity. Fecundity

Neotrypaea californiensis

Upogebia pugettensis

June 1988

August

October

December

February 1989

May

Carapace Length (mm)
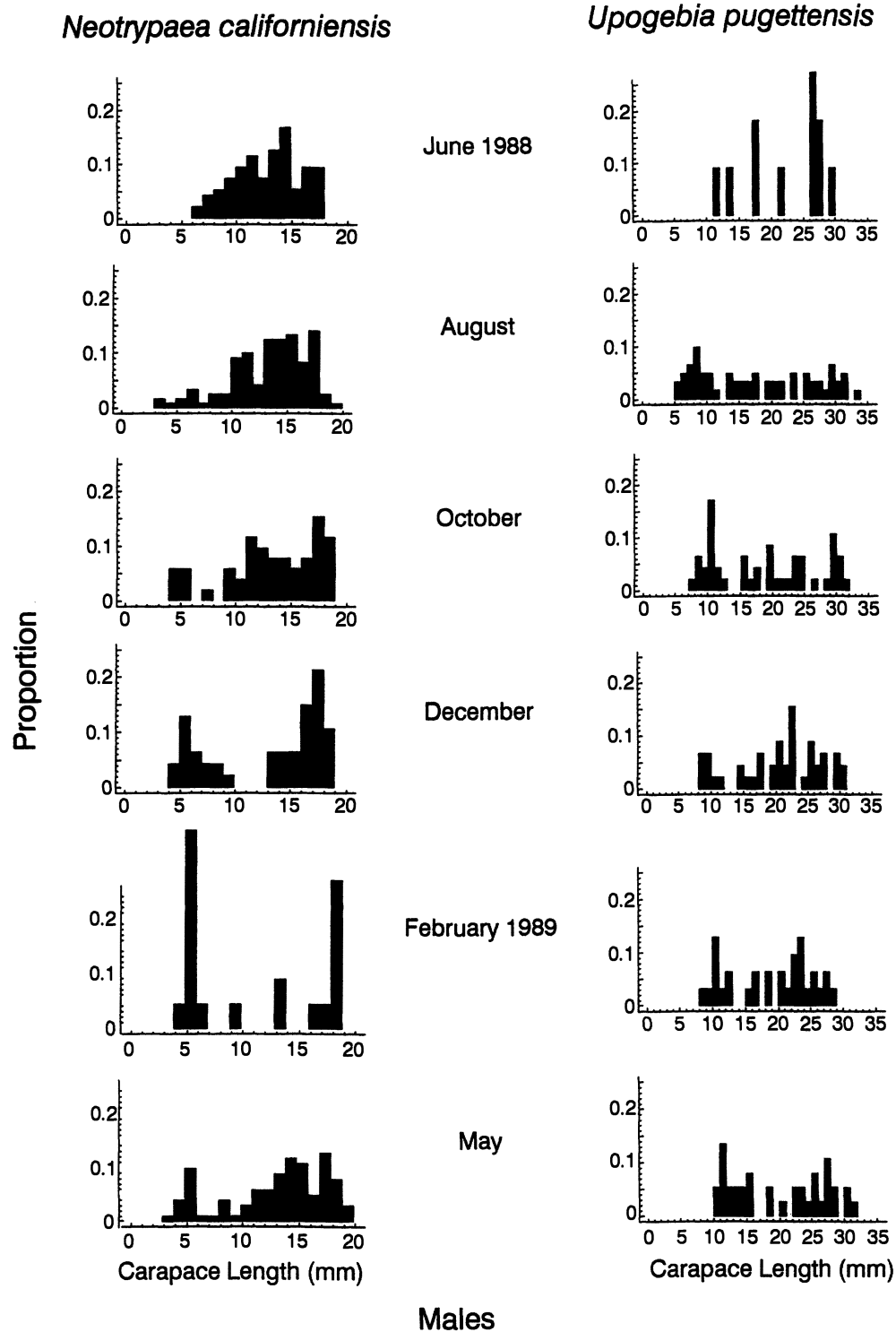
Carapace Length (mm)

Proportion

Males

Fig. 5. Size composition of male *Neotrypaea* collected at Station 1 and male *Upogebia* at Station 2 from June 1988–May 1989. Several age classes are present, but are difficult to distinguish except in certain months such as August and October.

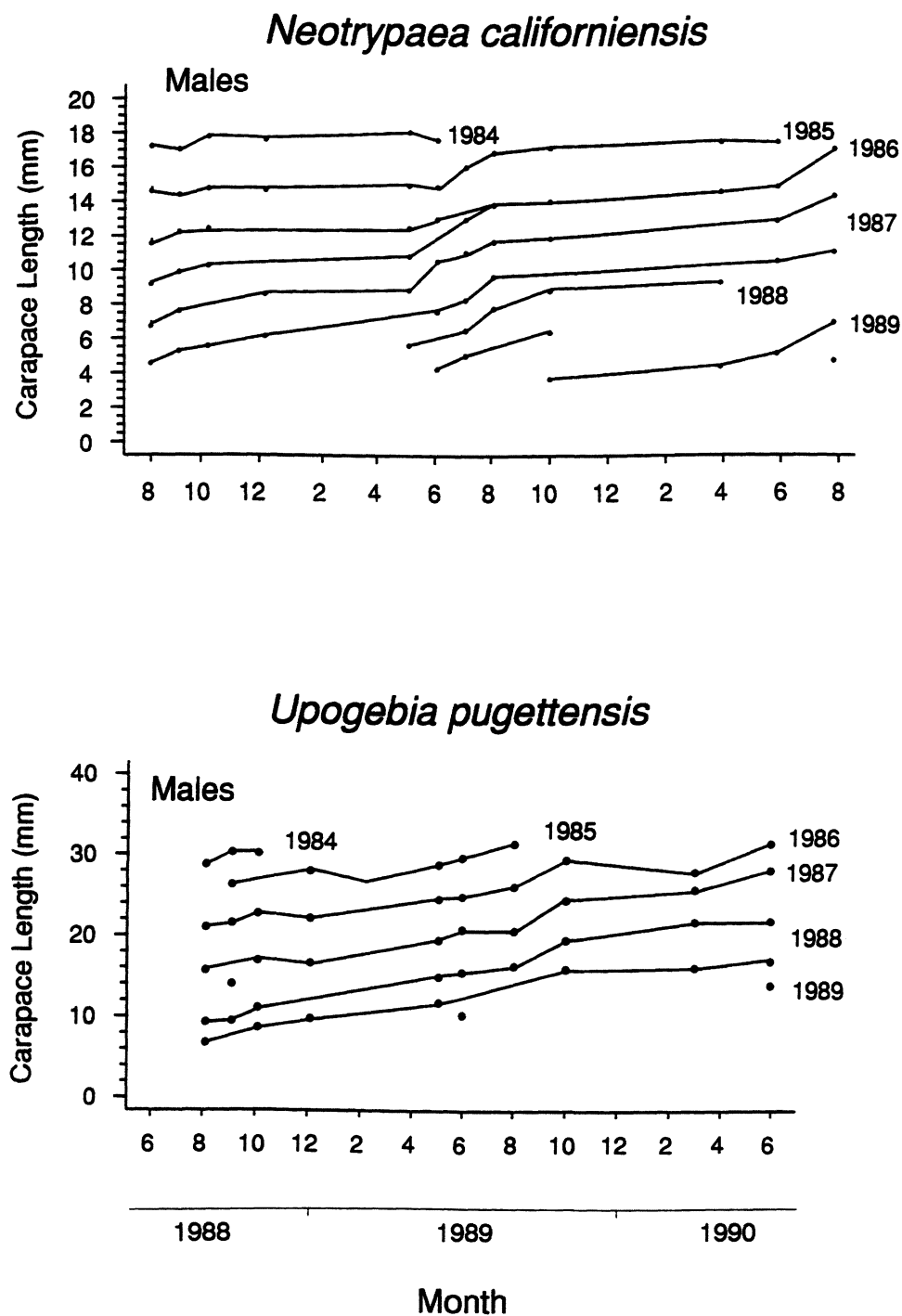JOURNAL OF CRUSTACEAN BIOLOGY, VOL. 16, NO. 4, 1996

Fig. 6. Growth scheme for individual year classes of male *Neotrypaea* and male *Upogebia* showing mean sizes (CL in mm) from size-frequency analysis. The appearance of two cohorts of 0+ shrimps in most years (particularly for *Neotrypaea*, 1–2-mm difference in size based on known size distributions from settlement experiments), makes it difficult to separate older age classes. Years shown represent best estimates of age class (estimated year of settlement).
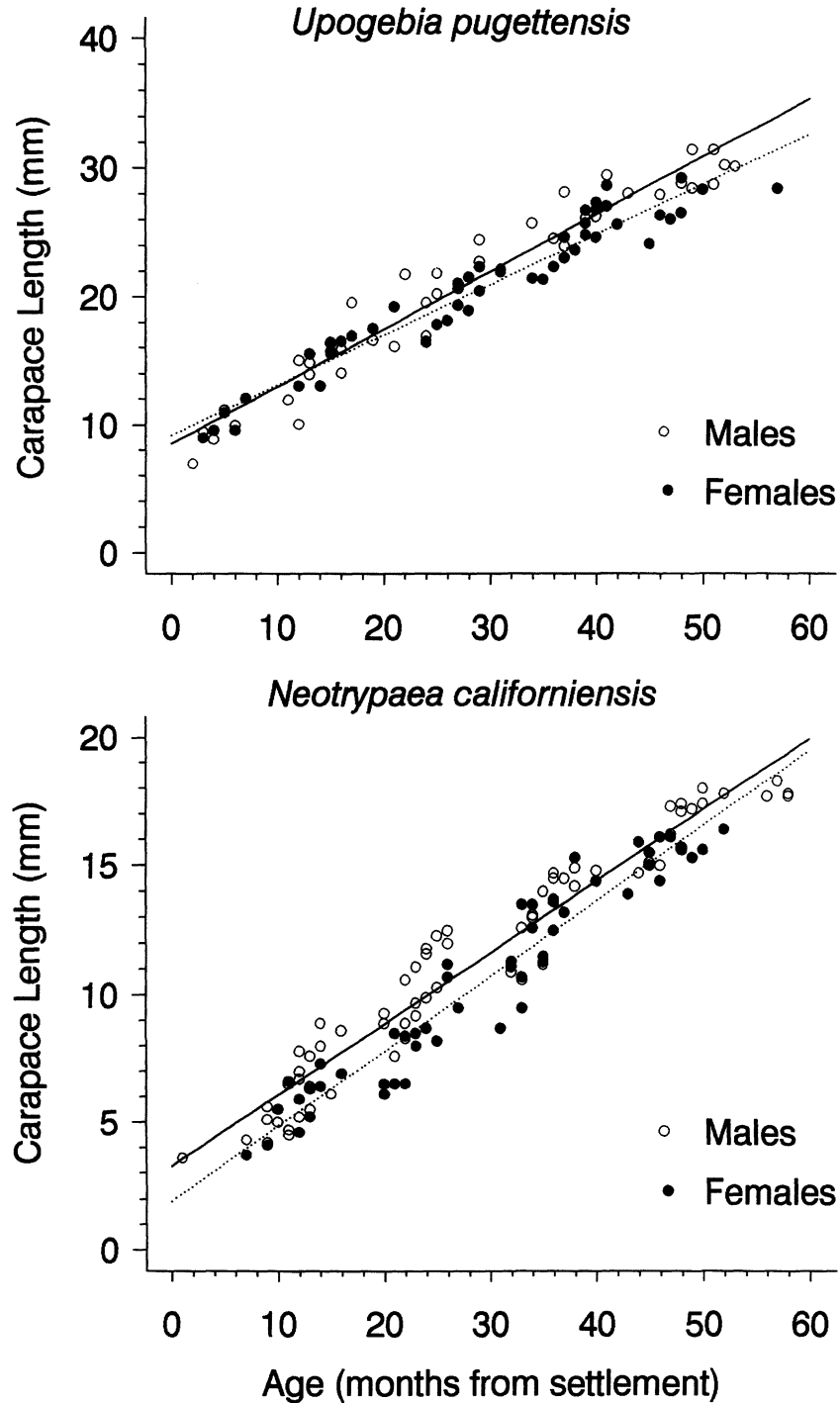
Fig. 7.   Growth rates for male and female *Upogebia* and *Neotrypaea*. Data points represent means (CL in mm) from size-frequency analysis, plotted against estimated time elapsed since settlement. Growth rate was higher for *Upogebia* (4–5-mm CL year^{-1}) than for *Neotrypaea* (2–3-mm CL year^{-1}) and significantly higher in males than in females.

Table 1. Allometric relationships. Least squares regression (untransformed data) of total length on carapace length (TL:CL), propodus height on carapace length (PH:CL), propodus height on propodus length (PH:PL), carpus height on carpus length (CAH:CAL), and multiplicative relationship ($y = ax^b$) of dry weight on carapace length (DW:CL) for both sexes of *Neotrypaea* and *Upogebia*. Data were subdivided at transition points X (CL in mm), at which the two groups yielded the lowest combined residual sum of squares. All regression models were highly significant ($P < 0.005$) with high correlation coefficients (r). Standard errors are given in parentheses.

		Lower line ≤ X				Upper line > X			
	X	Intercept	Slope	d.f.	r	Intercept	Slope	d.f.	r
Neotrypaea									
Males									
TL:CL	na	−1.62 (1.54)	4.74 (0.13)	114	0.96				
PH:CL	9.5	−0.91 (0.18)	0.56 (0.03)	64	0.93	−4.87 (0.59)	1.01 (0.04)	75	0.94
PH:PL	6.5	−1.05 (0.18)	1.11 (0.04)	79	0.94	−11.10 (2.20)	2.70 (0.29)	60	0.77
CAH:CAL	na	0.44 (0.34)	1.11 (0.03)	88	0.98				
DW:CL	na	−9.66 (0.23)	3.63 (0.10)	106	0.96				
Females									
TL:CL	13	−5.46 (3.75)	5.43 (0.36)	78	0.87	32.91 (6.11)	2.34 (0.40)	115	0.48
PH:CL	11.0	−1.33 (0.32)	0.61 (0.03)	28	0.96	2.22 (0.44)	0.33 (0.04)	104	0.71
PH:PL	na	−0.63 (0.17)	1.00 (0.02)	133	0.96				
CAH:CAL	na	1.16 (0.26)	1.00 (0.04)	133	0.92				
DW:CL	na	−8.30 (0.38)	3.08 (0.15)	185	0.83				
Upogebia									
Males									
TL:CL	na	−1.58 (1.19)	3.54 (0.05)	104	0.99				
PH:CL	25	−1.27 (0.23)	0.33 (0.01)	37	0.98	−1.08 (0.90)	0.34 (0.03)	50	0.86
PH:PL	na	−1.02 (0.24)	0.72 (0.02)	88	0.97				
CAH:CAL	na	−0.77 (0.09)	1.00 (0.02)	40	0.99				
DW:CL	na	−9.59 (0.32)	3.18 (0.11)	94	0.95				
Females									
TL:CL	28.5	5.89 (2.29)	3.16 (0.09)	158	0.95	31.92 (14.67)	2.58 (0.46)	24	0.76
PH:CL	26	−0.29 (0.41)	0.22 (0.02)	30	0.90	0.85 (0.48)	0.17 (0.02)	118	0.70
PH:PL	na	0.35 (0.21)	0.47 (0.02)	149	0.90				
CAH:CAL	na	−0.33 (0.67)	0.78 (0.10)	31	0.81				
DW:CL	na	−9.41 (0.36)	3.10 (0.01)	159	0.91				

na = transition not applicable, one regression line provided best fit.

ranged from about 200–14,000 eggs for both species, but average fecundity was higher for sexually mature *Upogebia* (≥26-mm CL, 7,100 eggs) than sexually mature *Neotrypaea* (≥13-mm CL, 3,900 eggs). There was a significant difference in the relationship between fecundity and female size for *Neotrypaea* between years sampled (ANCOVA, $P < 0.001$, Fig. 10). Average egg size was also slightly larger in *Upogebia* (0.73-mm diameter for newly extruded eggs, developing to 0.85 mm when eyed and ready to hatch) than in *Neotrypaea* (0.62-mm diameter at extrusion to 0.83 mm when eyed).

DISCUSSION

Neotrypaea californiensis and *Upogebia pugettensis* frequently coinhabit the intertidal zone within estuaries along the Pacific coast of North America. They are regarded as "pests" that must be removed in order to sustain the commercial oyster aquaculture industry and are managed as a single entity in the current control program in Washington State. We found distinct differences in their life-history characteristics that have descriptive ecological value which we outline first, but also some important implications for designing future shrimp control plans to benefit aquaculture.

Shrimp Density

The average density of *Neotrypaea* was higher (150–450 shrimp m⁻²) than that of *Upogebia* (40–140 shrimp m⁻²) in the undisturbed populations of shrimps that we sampled in Willapa Bay. These densities appear to be in the midrange for the Pacific coast, being lower than those reported by
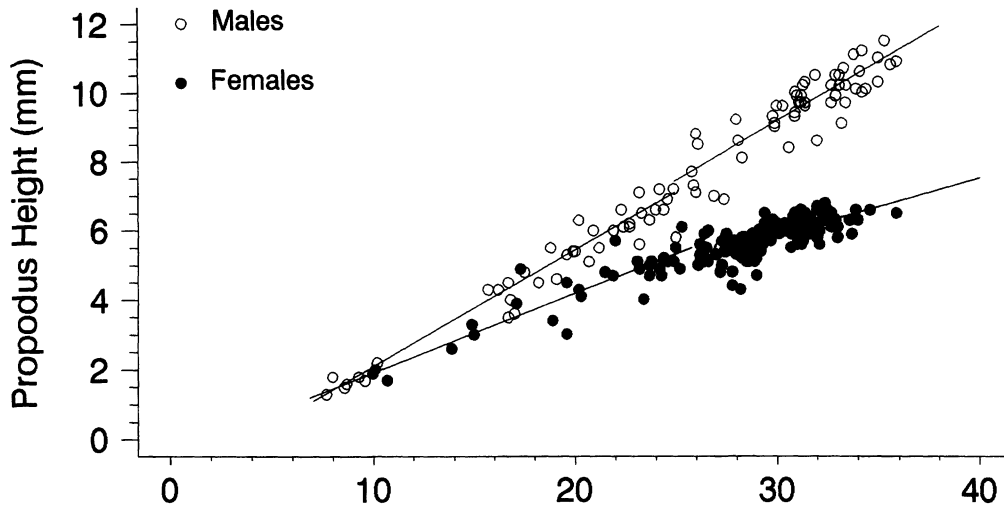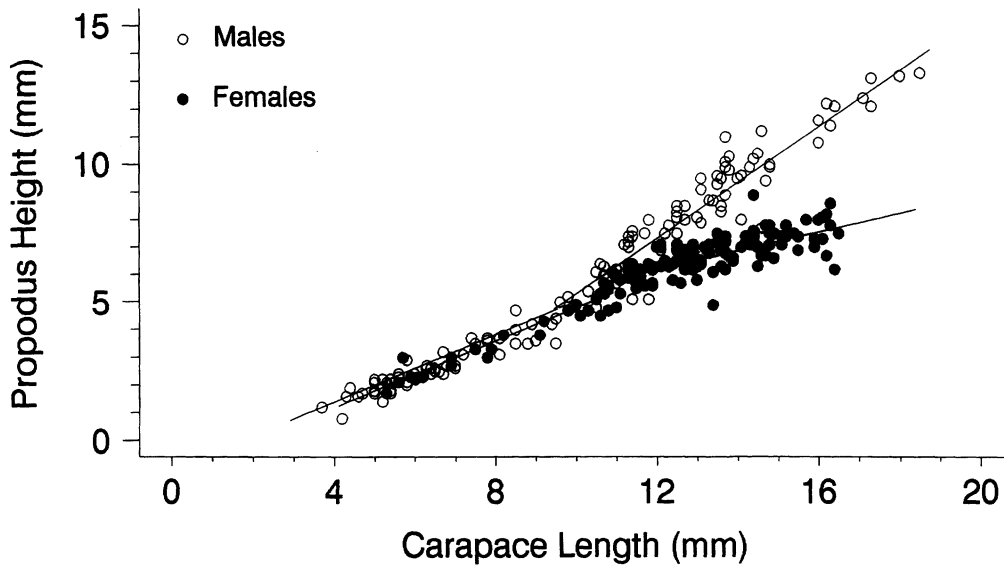
Upogebia pugettensis

Neotrypaea californiensis

Fig. 8. Comparison of the relationship between claw size (propodus height PH, of the chela) and body size (carapace length CL) for male and female shrimps of both species. Male claws exhibited increased growth at maturity, while female claws grew at a much slower rate. Transition points were noted at 25-mm and 26-mm CL for male and female *Upogebia*, respectively, and at 9.5-mm and 11-mm CL for *Neotrypaea*.

Bird (1982) and Posey (1986a) for estuaries in Oregon (300–700 shrimps m^{-2} for both species), but higher than those reported for Baha de San Quentin in Mexico (50–100 *Neotrypaea* m^{-2}; Griffis and Suchanek, 1991), for Mugu Lagoon in California (50–170 *Neotrypaea* m^{-2}; Peterson, 1977, 1984; Miller, 1984), and for the Fraser River estuary in British Columbia, Canada (140–180 *Neotrypaea* m^{-2}, 10–40 *Upogebia* m^{-2}; Swinbanks and Luternauer, 1987). Bird (1982) found that the density of *Neotrypaea*

Upogebia pugettensis
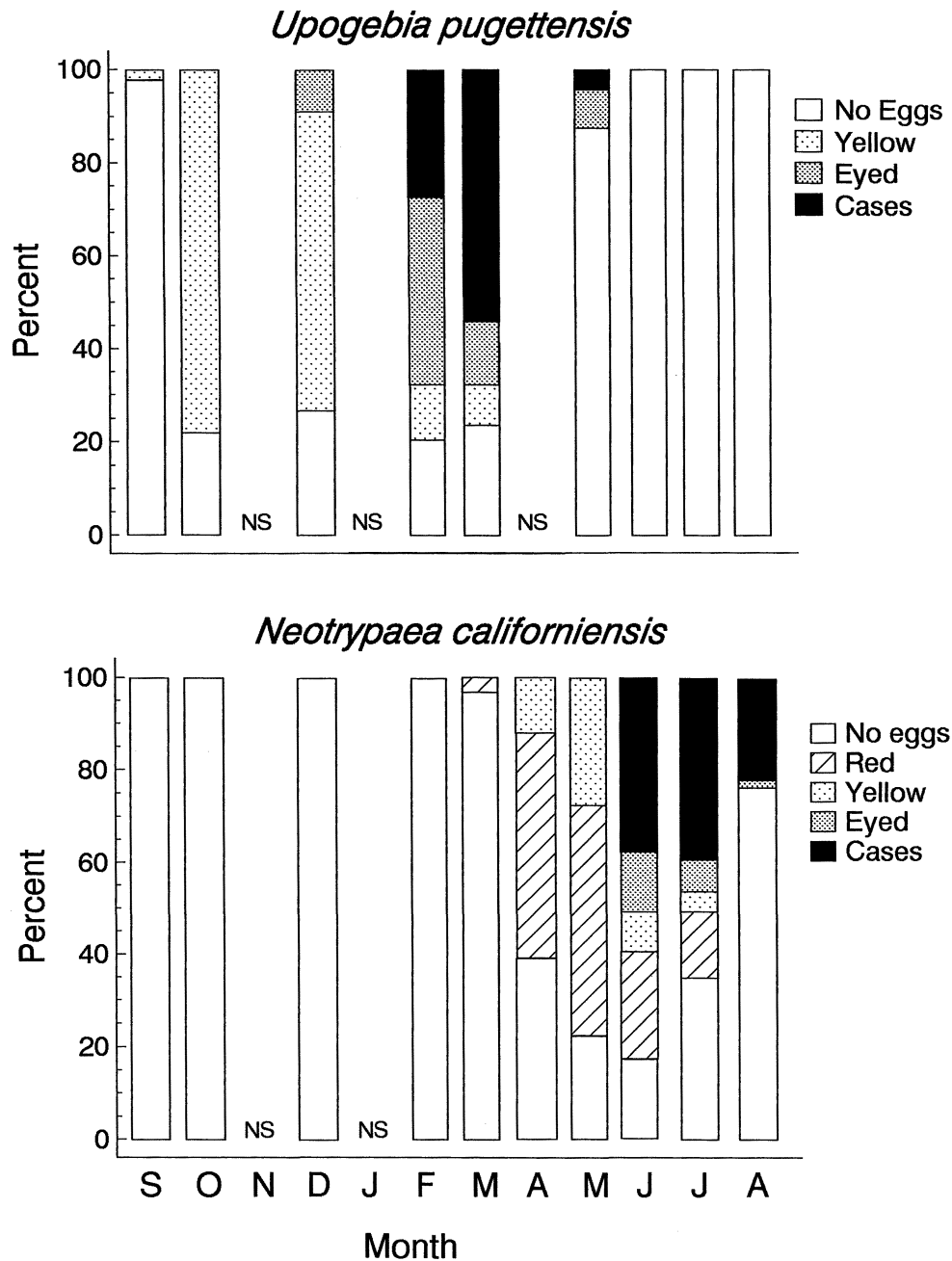

Neotrypaea californiensis

Fig. 9. Seasonal presence of ovigerous *Upogebia* and *Neotrypaea* with eggs in various stages of development: newly extruded yellow eggs (*Upogebia*) and red eggs (*Neotrypaea*), eyed eggs, and finally empty egg cases found on pleopods after hatch. Note difference in seasonal timing of reproductive cycle between species. NS = no samples taken.

decreased with increasing distance from the mouth of the estuaries that he studied, while the density of *Upogebia* was less affected. He attributed this pattern to differences in food availability and larval recruitment, suggesting that proximity to the ocean conveyed a distinct advantage with respect to growth and egg production. Limited observations suggest that similar trends in abundance occur in both Willapa Bay and Grays
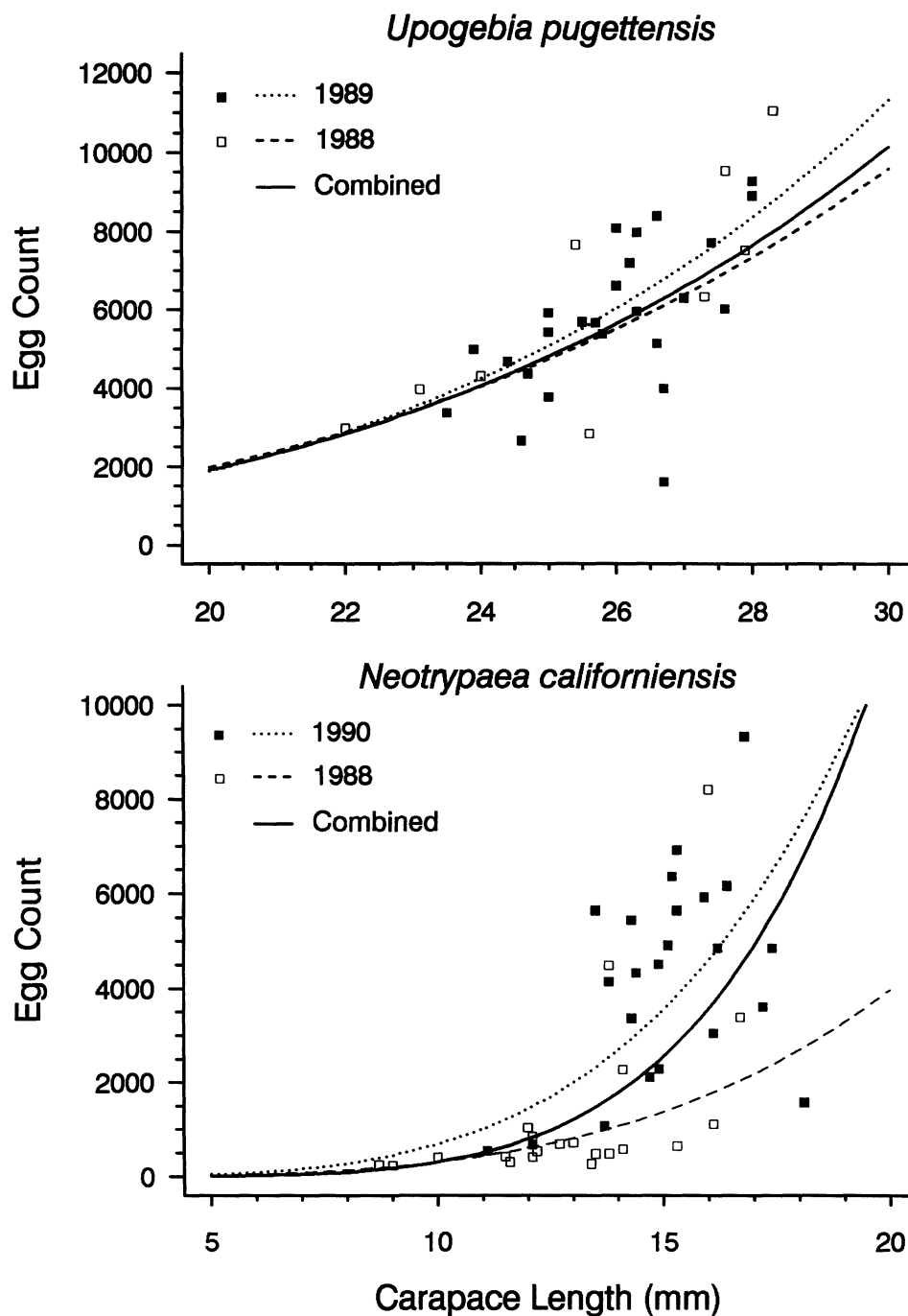
Fig. 10. Relationship between fecundity (corrected volume estimates) and size (CL in mm) for *Upogebia* and *Neotrypaea*.

Harbor, Washington (Armstrong *et al.*, 1991; B. R. Dumbauld, personal observation). Density at a given location in Willapa Bay also fluctuated with strength of annual recruitment, as demonstrated by the 1989 year class of *Neotrypaea* which contributed to a two-fold increase in density of shrimp at Station 1 during this study (Fig. 2).

Burrow counts are frequently used as surrogate measures of thalassinid shrimp

abundance, because sampling with a core is time consuming and destructive. We found an extremely variable relationship between burrow count and shrimp density for both species in this study. Seasonal variation was significant with declining burrow counts during fall and winter. Consequently, there was little correlation between burrow openings and shrimp density in this season. This was likely due to a combination of increased wave exposure, causing burrow openings to collapse (Miller, 1984; Griffis and Chavez, 1988), and decreased shrimp activity due to lower salinity and cooler temperatures (Posey, 1987b). The slopes of the best fitting relationships, 1.2 burrow openings shrimp^{-1} for *Neotrypaea* and 1.5 burrow openings shrimp^{-1} for *Upogebia* (Fig. 3) are lower than those measured by previous researchers (1.4–2.5 burrow openings shrimp^{-1}; Swinbanks and Luternauer, 1987; Bird, 1982). They are also lower than direct assessments via resin casts (2.0–2.7 burrow openings shrimp^{-1}; Stevens, 1928; Thompson, 1972; Swinbanks and Murray, 1981; Griffis and Chavez, 1988). The few casts that we made confirmed the presence of at least two openings observed by the above researchers; however, casts are even more laborious than taking cores. Given the inherent variability in burrow-count measurements due to environmental conditions, an initial characterization of shrimp density based on core samples must be made during summer to achieve an accurate density or population estimate.

Growth and Sexual Maturation

Populations of *Neotrypaea* and *Upogebia* were composed of four to five year classes of shrimps. This closely agrees with results reported by Bird (1982). Growth rates averaged 4.7-mm CL year^{-1} for female *Upogebia* and 3.3-mm CL year^{-1} for female *Neotrypaea* (Fig. 7). Bird recorded a difference in growth between species in the Siletz estuary in Oregon (5.0- and 7.7-mm CL yr^{-1} for *Neotrypaea* and *Upogebia*, respectively), but similar growth rates in other estuaries. We suspect that ambient food supply is the controlling factor, since growth rate was reduced for shrimp cohorts settling later in the season and those located farther from the mouth of the estuary. Growth rates and life span (4–5 years) doc-

umented here are comparable to those of other thalassinids in temperate waters (Hailstone and Stephenson, 1961; Devine, 1966; Dworschak, 1987; Rowden and Jones, 1994), though slightly slower and longer, respectively, than those from warmer waters (Forbes, 1977; Hanekom and Erasmus, 1988; Felder and Lovett, 1989; Tamaki and Ingole, 1993).

The size at which female shrimps were ovigerous agreed well with sexual maturation points estimated from morphometric measurements. Morphometric data on males and females indicate that both species of shrimps reached sexual maturity in approximately three years in Washington, whereas Bird (1982) indicated that *Neotrypaea* matured in two years in Oregon. Minimum size at oviposition (9-mm CL for *Neotrypaea* and 22-mm for *Upogebia*) was slightly less than the putative maturation point, as was similarly observed by Felder and Lovett (1989) for *Callianassa louisianensis* Schmitt, 1935, and it is possible that some shrimps were reproductive in Willapa Bay at two years of age as well (Fig. 7). An age of two to three years at maturity is similar to that of other temperate species of thalassinid shrimps (Dworschak, 1987).

Measurements of body size and claw morphometry indicate that both *Neotrypaea* and *Upogebia* are sexually dimorphic (Fig. 8, Table 1). Male claw size (larger chela) is larger than that of females for sexually mature individuals of both species of shrimps. In females, the segments of the major chela either continue to grow at a slower rate than the same segments in males or stop altogether after this transition, while in males the rate of growth, especially in segment height or width, increases after this transition. Although the pattern is similar for both species of shrimps, claw size diverges immediately in juvenile *Upogebia*, while claw size is similar until the maturation point in *Neotrypaea* (Fig. 8). A number of authors have documented sexual dimorphism in other thalassinids and present evidence that energy in maturing females is invested in egg production, while males devote substantial energy to the major chela, which may result in competitive advantage in interactions with other shrimp (Tucker, 1930; Hailstone and Stephenson, 1961;

Dworschak, 1988; Felder and Lovett, 1989; Rowden and Jones, 1994). Although there is little conclusive evidence to indicate whether this appendage is used in direct combat or for display in territorial and/or mating behavior, Griffis (1988) observed aggressive combative behavior for both *Neotrypaea californiensis* and *Upogebia macginitieorum* Williams, 1986, in the laboratory. Damaged chelae, skewed sex ratios, and additional laboratory observations indicate that fighting may be common in other thalassinids as well (Felder and Lovett, 1989). Sex ratio was skewed toward females for both sexually mature *Neotrypaea* and *Upogebia* in this study (32% and 45% males, respectively), possibly indicating the loss of large males from the population due to fighting or predation if males leave their burrows in search of females. The immediate divergence in claw size and correspondingly offset sex ratio in juvenile *Upogebia* may be indicative of territorial behavior at a smaller size and could be linked to feeding behavior, the more permanent burrow system, and a resource defense strategy for this species. With the exception of some work on *Upogebia affinis* Say, 1818 (see Chaud, 1984), however, mating behavior in thalassinid shrimps remains virtually undescribed.

Reproductive Cycle

The distinct difference in the seasonal reproductive cycle of *Neotrypaea* and *Upogebia* has been noted elsewhere along the Pacific coast. Ovigerous *Upogebia* were collected in Bodega Bay and Elkhorn Slough, California, from January through April coinciding with the reproductive period in our study (October–May; Mac-Ginitie, 1930; Thompson, 1972). Although MacGinitie (1934) reported year-round presence of ovigerous *Neotrypaea* in Elkhorn Slough, they were most abundant in July and August, which also coincides with our study (April–August). Bird (1982) observed similar offset periods of oviposition for *Neotrypaea* and *Upogebia* and differences in the timing of the peak egg-bearing period by location within Oregon estuaries. Populations in close proximity to the mouth of the estuary extruded eggs earlier than those located within the estuary. Similarly, we observed large females with eyed eggs

present in early spring landings of bait shrimp from the outer parts of Willapa Bay, at a time when shrimp at sampling locations in this study had just begun to extrude eggs. Despite considerable variability, older females of both species appeared to produce clutches earlier during the reproductive season. Observation of ovigerous *Neotrypaea* for a prolonged period led Bird (1982) to believe that these shrimp had multiple broods each year. No evidence was found for multiple broods in Willapa Bay, where the total proportion of ovigerous females was high for several months, but eggs progressed from early to late development stages during the months sampled (Fig. 9). Although multiple broods have been documented for other thalassinids (Hailstone and Stephenson, 1961; Devine, 1966; Felder and Lovett, 1989), there did not appear to be sufficient time for females to produce more than one brood during the reproductive season at our location, given that the egg-brooding period for these shrimp is 5–6 weeks (Bird, 1982).

Females of both species invested approximately 30–40% of their body weight in egg production. Our fecundity estimates (200–14,000 eggs shrimp^{-1}) were lower than those previously reported for both species (2,000–30,000 eggs shrimp^{-1}; Bird, 1982). This difference is most likely due to the discrepancy which we discovered between volume- and weight-based estimates. When this discrepancy between methods was accounted for, relationships between egg count and female size were comparable to those given by Bird (1982) and to those for other thalassinids (see Dworschak, 1988, for a review). Growth data suggest that ovigerous females of both species were generally at least three years old (compare Figs. 7, 10), while Bird (1982) reported that *Neotrypaea* reached maturity and were ovigerous at two years of age (see discussion of growth, above). Average fecundity of $\geq 4+$ *Neotrypaea* did not differ greatly from $\geq 4+$ *Upogebia*, but $3+$ *Neotrypaea* had much lower fecundity than $3+$ *Upogebia* due to their much smaller size.

Juvenile Recruitment

Separate recruitment periods were found for both species of shrimps, coinciding with the difference observed in the seasonal cy-

cle of egg production. Larval development occurs in the nearshore coastal ocean where *Neotrypaea* has a planktonic residence period of 6–8 weeks with five zoeal stages (McCrow, 1972; Johnson and Gonor, 1982; Pimentel, 1983) and *Upogebia* a 2–3 week period with three zoeal stages (Hart, 1937; Thompson, 1972). Postlarvae return to the estuary predominantly during nocturnal flood spring tides (B. R. Dumbauld and K. L. Feldman, unpublished data), as has been shown for other thalassinids (Makarov, 1977; Emmerson, 1983; Wooldridge, 1991). *Upogebia* settle in spring, grow quickly, and reach 7–9-mm CL by August of the same year (Fig. 4), whereas *Neotrypaea* settle from late summer to early fall and do not reach this size for almost two years (Figs. 5, 7). Differences in growth rate may be associated with this seasonal difference in recruitment period, but also feeding mode and food supply; *Upogebia* is considered a suspension feeder and *Neotrypaea* a deposit feeder (Powell, 1974; Griffis and Suchanek, 1991).

Two cohorts of 0+ *Neotrypaea* and *Upogebia* were observed in 1989 and 1990, respectively (Fig. 4). This information was used to distinguish two cohorts for both species in the growth analysis for most years. Although individual shrimps do not appear to have multiple broods per year, multiple cohorts are relatively common and have been noted for other thalassinids (Tamaki and Ingole, 1993) and other crustaceans recruiting to Pacific coast estuaries, including the Dungeness crab (*Cancer magister* Dana, 1852; Fernandez *et al.*, 1993). Differences in the size of the megalops were taken as evidence that different crab stocks might exist (Orensanz and Galucci, 1988; Dinnel *et al.*, 1992). We observed no difference in shrimp size at settlement. Instead we attribute multiple cohorts to an extended reproductive period in Willapa Bay. Moreover, recruitment periods are likely to be broad, given the asynchrony of egg hatching, the flushing of larvae from numerous estuaries along the Pacific coast into a common nearshore larval pool (Johnson and Gonor, 1982; K. L. Feldman and B. R. Dumbauld, unpublished data), and the duration of the planktonic larval period.

Implications for Aquaculture and Shrimp Control

Oyster aquaculture along the west coast of the United States has developed from a native stock fishery into a complete farming industry. Stocks of the native oyster *Ostrea lurida* Carpenter, 1864, in Willapa Bay, Washington, were depleted by the turn of the nineteenth century (Townsend, 1896; Minks, 1973; Baker, 1995) and the Pacific or Japanese oyster *Crassostrea gigas* Thunberg, 1794, became the mainstay of the industry when it was introduced in 1928 (Sayce, 1976). Today, the largest aquaculture operations utilize "ground culture," where oysters are placed directly on intertidal mud flats to grow. Juvenile oysters called "seed" are generally planted on tide flats in early spring to take advantage of phytoplankton blooms and maximum seasonal growth before overwintering (Fig. 11). After three years of growth, adult oysters are either picked by hand or harvested mechanically by dredge, with the bulk of the harvest occurring from October to March. Experimental application of the insecticide carbaryl on mud flats to control burrowing thalassinid shrimps began in 1960, after populations of shrimps expanded in the late 1950s dramatically reducing oyster production (WDF, 1970; Buchanan *et al.*, 1985; WDF and WDOE, 1985; Armstrong *et al.*, 1989). The pesticide is applied as a wettable powder by helicopter directly to the mud flat at low tide during July and August (Fig. 11).

The seasonal timing of recruitment to the benthos of *Neotrypaea* and *Upogebia* is the single most important life-history characteristic that should be considered in a management plan for their control. Both oyster-culture practices and the current shrimp-control program may inadvertently create favorable conditions for recruitment, particularly for *Neotrypaea*. When carbaryl is applied in July and August, it effectively removes both adult and 0+ *Upogebia* and kills adult *Neotrypaea*, but 0+ *Neotrypaea* which recruit in August and September are not affected (Fig. 11). *Neotrypaea* are able to recruit back to areas that have just been treated, and even to areas where *Upogebia* were formerly dominant, the carbaryl application itself thereby influencing the dis-
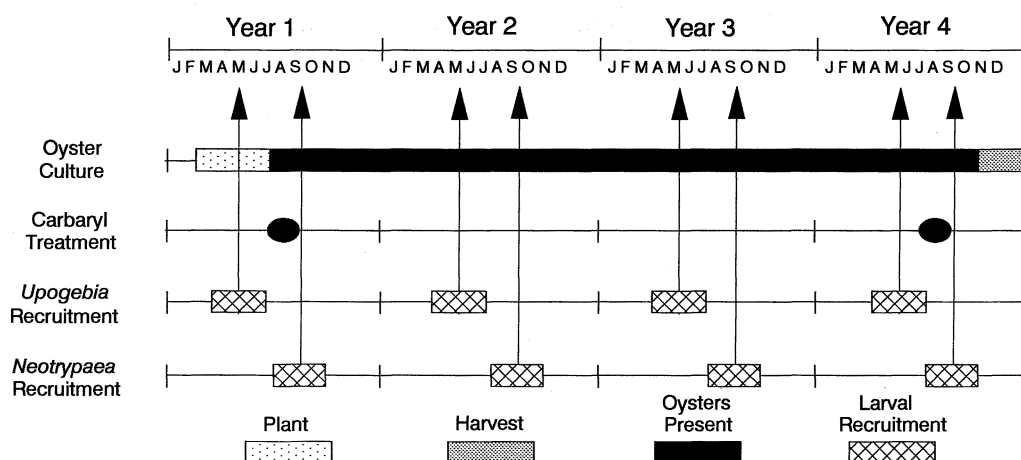
Fig. 11. Four-year cycle of oyster growing operations in Pacific Northwest estuaries. Oyster seed (young oysters or spat on a shell) are placed on a bed in spring, where they grow for three years before harvest in fall or early spring. Also shown are the typical carbaryl application period (July–August, circles) and the recruitment periods for postlarvae of *Upogebia* (April–June) and postlarvae of *Neotrypaea* (August–October) with arrows to indicate possible interactions with oyster-culture operations.

tribution of the two species of shrimps. Dumbauld (1994) found little residual pesticide toxicity toward shrimps recruiting in late August and September one month after treatment, and the density of 0+ *Neotrypaea* was higher on treated plots than on untreated plots. This sequence of control and immediate reinvasion by 0+ shrimps also occurred on commercial oyster beds investigated in 1992, where prespray density of *Neotrypaea* was 418 shrimp burrow openings m^{-2} and one-year postspray density of newly recruited individuals (mean CL = 2.8 mm) was 184 burrow openings m^{-2} (Dumbauld, 1994). In contrast to *Neotrypaea*, 0+ *Upogebia* did not reinvade treated areas until the following spring, and even then recruited in much lower density to experimental plots and commercial ground (Dumbauld, 1994).

In addition to pesticide application, the seasonal schedule of other oyster-growing practices, including harvesting by dredge, planting, and harrowing, could influence the abundance of newly settled shrimps by physically altering settlement conditions and/or postlarval behavior, disturbing the shrimps, thereby enhancing predation on them, or simply enhancing the density of predators. These processes are currently being studied and results suggest that the presence of epibenthic shell negatively influences *Neotrypaea* settlement (K. L. Feld-

man, unpublished data). Furthermore, the presence of shell, especially in a thick layer like that used by the Army Corps of Engineers to encourage crab settlement in Grays Harbor, Washington (Armstrong *et al.*, 1991; Dumbauld *et al.*, 1993; Fernandez *et al.*, 1993), and live oysters (Doty *et al.*, 1990) significantly increases the density of juvenile Dungeness crab, which consume newly recruited shrimps (K. L. Feldman, unpublished data). Seasonal planting operations that distribute shell and oysters on the tide flat and attract associated predators could, therefore, greatly influence the success of an incoming year class of shrimps.

Given the above observations, an ideal scenario for shrimp control and oyster culture would involve harvesting oysters after shrimp recruitment, immediately controlling shrimp, and then replanting seed well before recruitment occurs again, so that predators have time to colonize live oyster habitat as it develops. This would require shifting the control period to late fall through spring, between shrimp recruitment periods, to allow sufficient time for oyster growth and habitat colonization in the summer (Fig. 11). While practical and regulatory constraints are in place to prevent carbaryl application during this season, we believe that experimentation with shifts in the control period should be pursued, especially if alternatives to broad spectrum insecti-

cides like carbaryl are found, and particularly where *Neotrypaea* is concerned, given the propensity of this species to dig continuously and its ability to recolonize treated areas immediately.

In areas where they exist at high density, thalassinid shrimps are dominant members of the benthic community and greatly influence ecosystem structure by virtue of their size and ability to modify the substrate (Aller and Dodge, 1974; Rhoads, 1974; Ronon, 1975; Peterson, 1979, 1984; Suchanek, 1983; Branch and Pringle, 1987; Posey, 1986a, 1987a; Dumbauld, 1994). The framework for shrimp management and control in Washington has sought to balance the economics of oyster production on small spatial scales (5–20 ha) with a regulatory approach that involves risk assessment to resources from pesticide application. Unfortunately, neither of these approaches addresses the ecology and life history of the shrimps nor lends itself to quantification of the true impact of the shrimp, the control measures, and the subsequent oyster culture on estuarine resources at a baywide or ecosystem level. Our study suggests that these considerations are essential, if integrated pest management and sustainable oyster-culture practices are to be successfully implemented in areas where these shrimps are abundant along the Pacific coast of the United States.

ACKNOWLEDGEMENTS

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