

EVALUATION OF ALTERNATIVE LIFE HISTORY HYPOTHESES FOR THE SAND SHRIMP *CRANGON FRANCISCORUM* (DECAPODA: CARIDEA)

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A B S T R A C T

Caridean shrimps are unique among decapod crustaceans in showing a great diversity of sexual systems, including gonochorism, protandry, protandry with primary females and simultaneous hermaphroditism. *Crangon franciscorum* (Stimpson, 1859) (Crangonidae), an ecologically and economically significant species from the Pacific coast of North America, has been assumed to be gonochoristic. Earlier population studies concluded that average lifespan is longer in females than in males, and that the latter die in or emigrate from estuaries after mating. This was believed to explain a recurrently observed “shrinking” of average male size starting during the fall of the first year of life. We investigated an alternative hypothesis according to which this species is a protandric hermaphrodite, and disappearance of large males from the population reflects sex change rather than death or emigration. We present several pieces of evidence in support of the alternative hypothesis: (i) ovarian development in males undergoing sex change, (ii) presence of atrophied vas deferens in secondary females, and (iii) observation of sex change in individuals kept in captivity. Our results are supported by histological study of the gonads, careful description of secondary sexual characters, and monthly sampling of an estuarine population (Grays Harbor, Washington). Tracking an identifiable year-class (1980) and combining field and laboratory data allowed us to assemble a life history schedule, including growth and a calendar of significant reproductive events. We discuss the implications of our results for the interpretation of survey data and studies on population dynamics.

INTRODUCTION

Caridean shrimps exhibit a diversity of sexual systems and associated pathways in their life history (Bauer, 2000; Bergström, 2000; Correa and Thiel, 2003). Gonochory is one of the most common sexual systems found in caridean shrimp, but there are also many hermaphroditic species. Five different types of protandry are known to occur in 32 species, while among members of *Lysmata* (Hippolytidae) individuals undergoing sex change retain male gonad and ducts, becoming out-crossing functional simultaneous hermaphrodites (Bauer and Holt, 1998; Bauer, 2000, 2002b, 2004; Bauer and Newman, 2004). Among crangonids, simple protandrous hermaphroditism, in which all adult individuals reproduce first as males and later in life as females, has been reported for *Notocrangon antarcticus* (Pfeffer, 1887) (Correa and Thiel, 2003). *Argis dentata* (Rathbun, 1902) and *Crangon crangon* (Linnaeus, 1758) have a system known as “protandry with primary females” (Bauer, 2000) or “partial protandric hermaphroditism with primary females” (Correa and Thiel, 2003). Individuals are either primary females (they reproduce as females throughout their life) or protandric hermaphrodites (they reproduce first as males and later as secondary females); at the age of first reproduction some members of a cohort are females and the rest males. Other species of *Crangon* have been implicitly or explicitly assumed to be gonochoristic (Birkely and Gulliksen, 2003). A species profile of *C. franciscorum* (Stimpson, 1859) states that “males are believed to die soon after copulation” (Siegfried, 1989), implying gonochory.

Population studies on *C. franciscorum* conducted in coastal embayments from Central California to Washington (Israel, 1936; Krygier and Horton, 1975; Hoeman, 1982) revealed a recurrent pattern: males are always smaller than females; their average size starts to decline during the fall of the first calendar year of life, while females of the same age keep growing. By late spring of the cohort’s second year of life, males vanish from the population while females (mostly ovigerous) continue to be present through early summer. Thus, males appear to have a shorter lifespan than females (approximately 1 versus 1.5 years, respectively). Explanation of this pattern is consistent with at least two different hypotheses. According to the current default hypothesis the species is gonochoristic, implying that all females are “primary” females. Males and females grow at different rates. Males reach sexual maturity at a smaller size than females, reproduce, and then the largest among them die or emigrate, this resulting in the observed reduction of mean size (Israel, 1936; Krygier and Horton, 1975; Hoeman, 1982; Siegfried, 1989). We advance an alternative hypothesis: populations include both “primary” and “secondary” females. Males and females do not necessarily grow at different rates. The largest males reproduce and then change sex during the fall and winter, this resulting in the observed decrease of mean size. If true, *C. franciscorum* would not be gonochoristic; rather, its sexual system would be similar to that documented for *C. crangon* (Boddeke et al., 1991).

The implications of these two hypotheses for studies of the dynamics of populations of *C. franciscorum* are

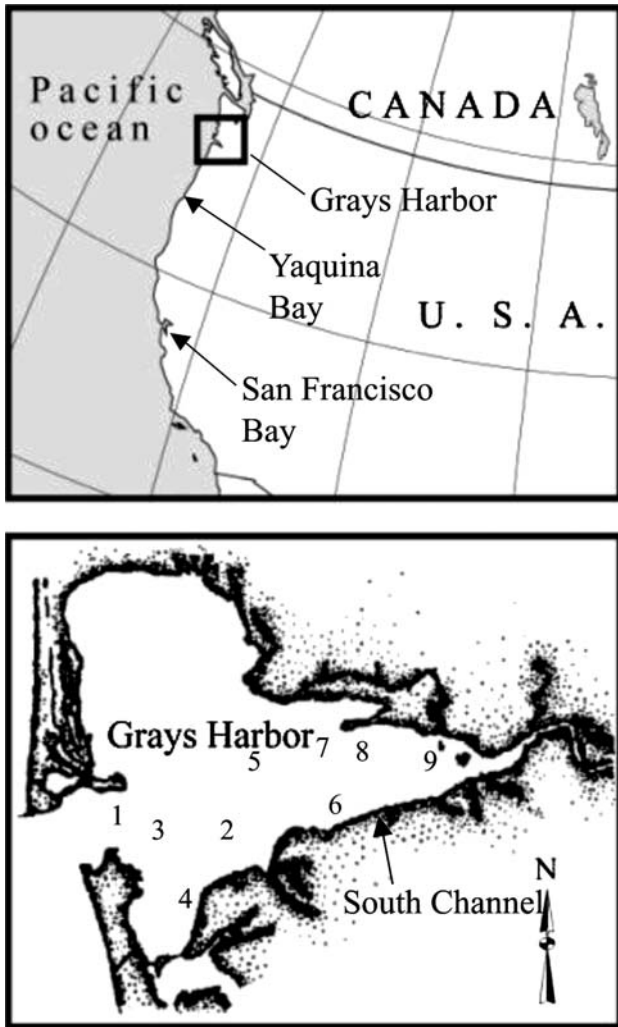


Fig. 1. Grays Harbor estuary with indication of sampling stations.

non-trivial, particularly considering that this species is a significant component of estuarine ecosystems along the west coast of North America (Stevens et al., 1982; Armstrong et al., 1995), and has even supported local food- or bait-oriented fisheries (Siegfried, 1989).

In this study, we describe the secondary sexual characters and reproductive system of *C. franciscorum* and evaluate evidence of sex change based on laboratory and field observations. We define a sequence of life history stages easily recognizable from external characters and present new information on the population of Grays Harbor. Data on the life history of *C. franciscorum* are reassessed in the light of new findings about its reproductive biology, and the consistency of those data with alternative life history models is discussed.

MATERIAL AND METHODS

Study Area and Field Collections

Grays Harbor (Fig. 1), the study area, is an estuarine environment located on the outer coast of Washington. Substrate ranges from mud with leafy debris to hard sand. Temperature and salinity vary greatly depending on season and location; salinity is influenced by rain fall and the discharge of six major rivers (Feldman et al., 2000). Specimens of *Crangon*

franciscorum were collected during the spring, summer and winter of 1992-93 at South Channel (Station 6, 46°56'N, 123°59'W; Fig. 1), where mean water temperature varied between 15°-18°C during summer and 8°C in winter. Sampling gear was a beam trawl described in detail by Gunderson and Ellis (1986).

Morphological Studies

Laboratory Procedures.—Measurements recorded were: carapace length (CL) from the posterior-most part of the orbit to the posterior mid-dorsal margin of the carapace, the length of the endopod (EL) of the first pair of pleopods and the appendix masculina (AM) on the second pair of pleopods. Size is always expressed in terms of CL in mm. A subsample from each collection was fixed in Bouin's solution for 48 hours and transferred to 70% ethanol for further microscopical study.

Identification of Stages.—Sex was assessed externally by the presence or absence of the AM on the endopod of the second pair of pleopods, and by the size and shape of the endopod of the first pair of pleopods (Butler, 1980; Boddeke et al., 1991). A total of 1279 specimens were staged based on macroscopic external characters, including 797 males, 118 immature and 364 mature females. Dissections were done on 43 males, 27 immature and 85 mature females to investigate the macroscopic anatomy of the reproductive system.

Finer staging was based on the shape and size of the first and second pair of pleopods and their setae, and on the histological study of the reproductive system. Setae considered in this study are of pinnate and non-pinnate types. The latter were classified into "primordial" (early development), "spur-like projections" (short, present in non-spawning intermolt periods), and "ovigerous" (long, present during spawning and egg-carrying periods) (Yonge, 1955). Reproductive condition of females (spawning or non-spawning) was assessed externally by the presence of either ovigerous setae or spur-like projections on the basis and endopod of the first pair of pleopods (Yonge, 1955; Butler, 1980).

Microscopical Observations.—Tissues of 43 individuals selected for histological study were embedded in paraffin, sectioned (4 µm to 6 µm), and stained with haematoxylin-eosin. Developmental stages of the ovary were categorized following Cuzin-Roudy and Amsler (1991) and Minagawa et al. (1993):

Young primary oöcytes: with the basophilic chromatin condensed as chromosomes and thin cytoplasm.

Oöcyte 1: presence of basophilic nucleolus near the center of the nucleus and cytoplasm still thin.

Oöcyte 2: oil droplets in the cytoplasm.

Oöcyte 3: the cytoplasm is widened by the accumulation of yolk. The nucleus-cytoplasm ratio (diameter) was used as an indirect measurement of the physiological stage of the ovary; a high ratio indicates early oogenesis, and low ratio, vitellogenesis (Cuzin-Roudy and Amsler, 1991).

Tissues for SEM observations were treated with Peldri II® as sublimation dehydrant. Specimens were coated with gold-palladium, and micrographs were taken with a JEOL 840A electron microscope.

Relative linear growth of the endopod (EL) and carapace (CL) was assessed using linear regression. Parameters estimated for the two sexes were compared by means of covariance analysis.

Observations in Captivity.—A total of 147 specimens (42 males, 46 non-ovigerous mature females, 16 immature females and 43 ovigerous females) were kept in the NOAA station at Mukilteo (Washington), during the summers of 1992 and 1993, to record molting events and any external evidence of sex change. All individuals were held in single containers with running seawater and fed daily with fresh fish meat. Water temperature varied from 13° to 14°C. Illumination was natural. Individuals were measured (CL) before and after molting. Color of the ovary (green or white) was recorded in the case of mature females.

Only data from shrimp that molted during the first week after collection were used for growth analysis. Growth increments were represented in the form of Hiatt diagrams (pre-molt versus post-molt size; Somerton, 1980). Growth was compared between sexes by means of covariance analysis, with initial size as covariate and sexes as factors. Intermolt period in the laboratory was recorded during the summer of 1992. Data used correspond to individuals that molted twice in the laboratory. The EL of the first pair of pleopods was measured after they were sacrificed.

Table 1. *Crangon franciscorum*. Definition of stages.

Stage	Characteristics
Juveniles (J)	Sex indeterminable on the basis of external morphology
Mature Males (MM)	Appendix masculina present on the second pair of pleopods, endopod of the first pair of pleopods short and pointing inwards. Third and fourth sternite bilobed, fourth sternal spine of the thoracic sternum acute, with lateral rows of non-pinnate setae. With paired androgenic glands; testis with spermatogonia, sperm and vas deferens full of sperm
Transitional Males (TM)	First and second pair of pleopods similar to MM. Vas deferens full of sperm. Androgenic gland present. Incipient ovarian development (oögonia in early stages of development and follicular cells arranged inside the gonad) co-exists with spermatogonia
Immature Secondary Females 1 (ISF ₁)	No appendix masculina, endopod of the first pair of pleopods short and straight. Fourth sternal spine of the thoracic sternum subtriangular, with pinnate setae. Third sternite weakly bilobed, fourth rounded. Ovary thin and translucent, with immature oöcytes. No testis or androgenic glands present; with a pair of atrophied vas deferens
Immature Secondary Females 2 (ISF ₂)	Similar to ISF ₁ , but with the endopod of the first pair of pleopods longer (yet not reaching adult size). Fourth sternal spine of the thoracic sternum subtriangular with pinnate setae. Third sternite weakly bilobed, fourth rounded
Mature Secondary Females (MSF)	Endopods of the first pair of pleopods completely developed to carry eggs. Ovary mature. With atrophied vas deferens. Fourth sternal spine of the thoracic sternum subtriangular, with pinnate setae. Third sternite weakly bilobed, fourth rounded
Immature Primary Females (IPF)	No appendix masculina, endopod of the first pair of pleopods short and straight. Ovary immature. No atrophied vas deferens
Mature Primary Females (MPF)	Endopod of the first pair of pleopods completely developed to carry eggs. Ovary mature. No atrophied vas deferens

Population Studies

Two data sets were used for the analysis of Grays Harbor population: those from Hoeman's (1982) study and new data obtained as part of this study.

Sampling Protocol Followed in Hoeman's Study (1980-81).—Regular trawl samples were collected biweekly from June through October 1980, and monthly from November 1980 through May 1981. Shrimp were collected using a semi balloon otter trawl (Hoeman, 1982) at nine stations distributed along the estuary (Fig. 1). Data were pooled for the construction of size frequency distributions (SFDs). Stations 1-5 were considered "outer harbor stations", and stations 6-9 "inner harbor stations", the latter with lower salinities and extreme seasonal temperature changes (Hoeman, 1982). Measurements recorded were CL from the posteriormost part of the orbit to the posterior mid-dorsal margin of the carapace, and, in males, the length of the AM. Stages identified based on external morphology were: [1] Juveniles (J); CL less than 5.0 mm, [2] Male: individuals larger than 5.0 mm CL with presence of the AM on the endopod of the second pair of pleopods, [3] Female: individuals larger than 5.0 mm CL lacking AM. Females were classified as ovigerous or non-ovigerous.

Samples from the South Channel Study Site (1992-93).—Data were always collected near Hoeman's station 6 (Fig. 1) in March, July, August and September 1992, and January, February and June 1993. Measurements were recorded and categories identified as above. Following Boddeke et al. (1991) and common usage in the literature (Charnov and Bergström, 1987; Gherardi and Calloni, 1993), individuals that first mature as females are defined as primary females (PF), and individuals which mature as females after having passed through a male stage are defined as secondary females (SF). The diagnostic character used to separate primary from secondary females was the presence in the latter of atrophied vas deferens (Boddeke et al., 1991; Frechette et al., 1970). Subsamples were saved for detailed morphological and histological studies (described above). Throughout the text sex-specific average size in a given month is expressed as $\bar{CL}_{\text{sex}}^{\text{month}}$.

RESULTS

Morphological Typology of Stages

Juveniles.—Sex could not be established for shrimp smaller than 5 mm (CL). Three conditions were characteristic of Js: absence of the AM, endopodite of the first pair of pleopods extremely short with no definite shape to be specified, and no setation pattern along its inner margin and tip (Table 1).

Males.—In addition to the presence of the AM (Fig. 2A), the shape and setation of the fourth thoracic sternal spine (located between the coxae of the fifth pair of pereopods) and sternal pereion is also diagnostic of sex (Tables 1, 2). In males the fourth spine is acute, with an arrowhead outline; its tip is close to the base of the third spine, and has lateral rows of long non-pinnate setae originating close to its base (Fig. 2B). The shape of the third and fourth sternites is remarkably bilobed, with the sternal spines located medially between both lobes, at the level of the fourth and fifth pairs of pereopods. The endopod of the first pair of pleopods is short and sigmoid, with a row of short setae along its inner margin, and a tuft of long setae at its tip (Fig. 2C). The EL/CL ratio of the first pair of pleopods is in the range 0.05-0.15 (Fig. 3, Table 3). Linear morphometric relations (least squares estimates) of the first male EL and AM versus CL are summarized in Table 3.

Internally, the testis extends from above the cardiac stomach to the first abdominal segment, partially covering the hepatopancreas. Spermatogonia are arranged along one side of the tube, separated from spermatids and spermatozoa on the other side. The testis of males as small as 6 mm CL contain different stages of development of sexual cells, including spermatocytes and spermatozoa, the latter also present in the vas deferens. The vas deferens is partitioned into two chambers by a non-cellular septum; sperm is contained in one of them, while in the other a stratified epithelium is folded to form a typhlosole. The androgenic glands are attached by connective tissue and muscle fibers to the intermediate portion of each vas deferens.

Transition from Male to Secondary Female.—The histological study of mature males revealed the existence of two stages, indistinguishable from each other on the basis of external characters alone. Longitudinal sections of the gonad of eight transitional males (TM) showed that the anterior part was a developing ovary, while the rest was still a mature testis with spermatids and sperm. In the male-female

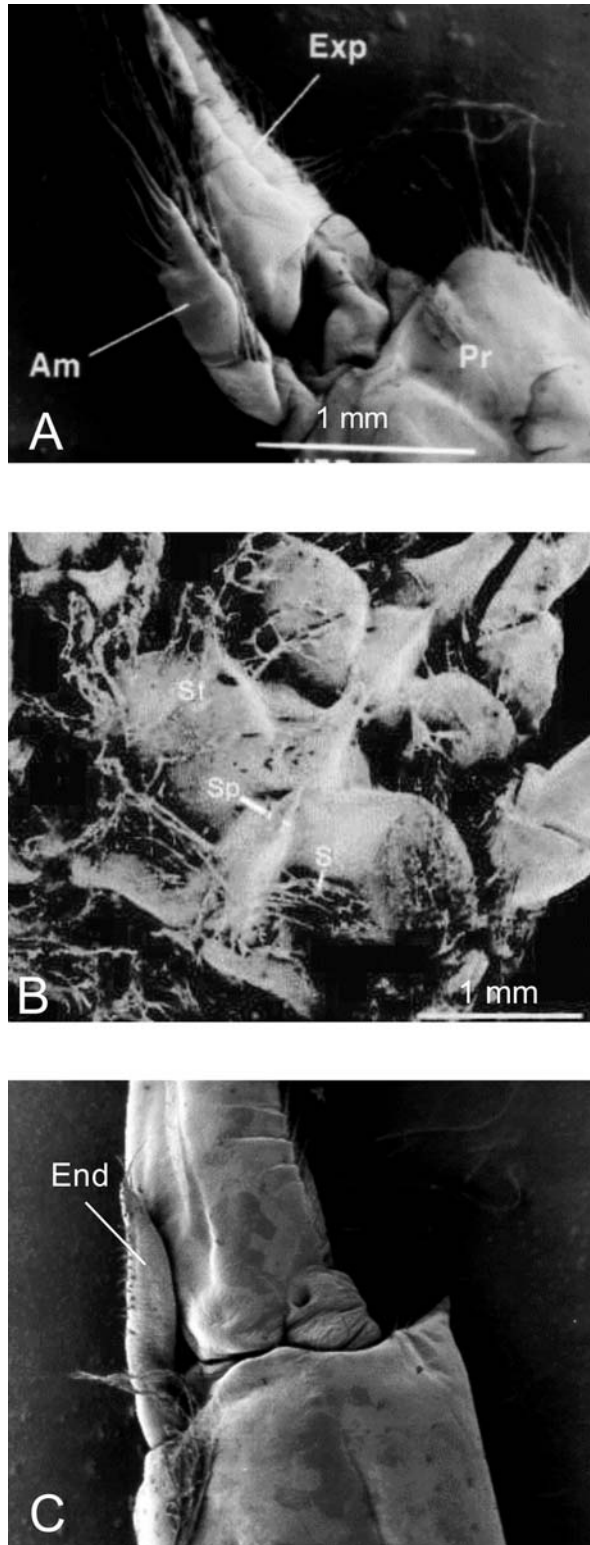


Fig. 2. *Crangon franciscorum*. Male secondary sexual characters, SEMs. A) Second pleopod with the appendix masculina (Am), Exp (exopod) and protopod (Pr). B) sternal pereon with bilobed sternites (St), showing the shape of the fourth spine (Sp) with long non-pinnate setae (S). C) First pleopod showing the endopod (End).

portion the spermatogonia were typically located on one side of the tube, and the oögonia on the other. In the male-only portion, sperm were located close to the proximal vas deferens associated with many lytic cells. In an advanced stage, males (8-9 mm CL) showed the presence of oögonia along the whole testis (Fig. 4A). The vas deferens was full of sperm and the androgenic glands were still present.

Two males (6.2 mm and 7.5 mm CL) that molted in captivity (final size 7.5 and 8.8 mm CL respectively) showed external evidence of sex change, including the shape and length of the endopod of the first pair of pleopods, and loss of the AM. Histological study of those individuals showed that the gonad was an immature ovary (Fig. 4B) with young oöcytes and oöcytes 1 coexisting with atrophied vas deferens (Fig. 4C).

Immature Secondary Females (ISFs).—Two stages in the development of secondary females could be defined based on characters associated with the first pair of pleopods: length of the endopod, and setation of the basis and endopod (Tables 1, 2):

ISF₁: Bases of the first pair of pleopods without any type of setae (Table 1). The EL/CL ratio is 0.10-0.15 (Fig. 3, Tables 2, 3). No primordial or ovigerous setae are present.

ISF₂: Bases of the first pair of pleopods with primordial setae present in the same location where ovigerous setae will develop in mature females (Fig. 5A); no fully developed ovigerous setae are present. The EL/CL ratio ranges from 0.18-0.27 (Fig. 3, Tables 2, 3).

The fourth sternal spine of ISFs is subtriangular in outline, its base forming a transversal ridge across the sternum, in sharp contrast to the male type. In males, the tip of the fourth spine reaches the basis of the third spine while in females it does not. Also different from males is the presence of only pinnate setae in the area surrounding the fourth spine, and the shape of the third (weakly-lobed) and fourth (rounded) sternites.

Dissection of the reproductive system showed a thin, translucent ovary with oögonia and oöcytes 1. Androgenic glands were not present. The reduced vas deferens, always present, are identifiable by their anatomical position and histological structure. A columnar epithelium is still present, but the striated musculature associated with the vas deferens of males is atrophied.

There were significant differences between the slopes of males and ISFs (ANCOVA, $F = 32.8$, $df. = 1,115$, $P < 0.001$), and between ISFs and MSFs (ANCOVA, $F = 4.48$, $df. = 1,56$, $P < 0.05$).

Immature Primary Females.—IPFs (CL = 5.9-6.9 mm) could be recognized by the absence of atrophied vas deferens. Externally they exhibit primordial or spur-like setae on the basis of the first pair of pleopods. The ovary is thin and translucent, extends only to the first pleomere, and has oögonia and oöcytes 1.

Mature Females.—MPFs and MSFs could not be separated on the basis of external characters; the only diagnostic character was the presence/absence of atrophied vas deferens. Mature females differ from ISFs or IPFs in the presence of fully developed setae on the basis and endopod

Table 2. *Crangon franciscorum*. Summary of character states of the different stages of individuals sampled in 1992-93. J: Juveniles, M: males, TM: transitional males, ISF₁: immature secondary females 1, ISF₂: immature secondary females 2, IPF: immature primary females, MSF: mature secondary females, MPF: mature primary females.

Characteristic	Stage							
	J	M	TM	ISF ₁	ISF ₂	MSF	IPF	MPF
CL (mm)	< 5.0	6-11	6-9	6.5-9.2	7-11	9-13	5.9-6.9	7.0-?
Endopod of the first pleopod	extremely short	short, curved, pointed	short, curved, pointed	short, straight, pointed	intermediate, straight, pointed	long, straight, spatulate	short, straight, pointed	long, straight, spatulate
EL/CL ratio		0.05-0.15	0.05-0.15	0.10-0.15	0.18-0.27	>0.28	0.10-0.22	>0.28
Shape and setation of basis	smooth	smooth	smooth	smooth	smooth; setae: primordial, basal group	bulged; setae: spur-like or ovigerous, basal and distal groups	smooth; setae: primordial, basal group	bulged; setae: spur-like or ovigerous, basal and distal groups
AM (2nd. pleopod)	—	present	present	—	—	—	—	—
4th thoracic sternite: spine and setae		arrowhead; 2 rows of non-pinnate setae	arrowhead; 2 rows, non pinnate	sub-triangular	sub-triangular	sub-triangular	sub-triangular	sub-triangular
3rd sternite		lobulate	lobulate					
Vas deferens	present	present	present	present (atrophied)	present (atrophied)	present (atrophied)	—	—
Androgenic gland		present	present	—	—	—	—	—
Gonad and color		testis, white	ovotestis, white	ovary, translucent	ovary, translucent to white	ovary, ivory to green	ovary, translucent to white	ovary, ivory to green
Gonial cells		spermatogonia spermatocytes spermatids spermatozoa	spermatogonia oögonia	oögonia oöcytes 1	oögonia oöcytes 1 oöcytes 2	oöcytes 2 oöcytes 3	oögonia oöcytes 1	oöcytes 2 oöcytes 3

of the first pleopod (Figs. 5C, D, Tables 1, 2). The endopod is long and straight, with a spatulate tip. The ratio EL/CL is higher than 0.28 (Tables 2, 3). The inner base of the basis of the first pleopod is bulged, while it is smooth in immature females. Setae of spawning and berried females include ovigerous and pinnate types. Eggs are attached to ovigerous setae of bases 1-4 and of endopods of the first pair of pleopods. In non-spawning females the only setae present

are spur-like projections (Fig. 5C). These setae are located along the inner margin of the endopod, while at the tip there is a tuft of non-pinnate setae not involved in egg-carrying. The setae of the bases (ovigerous setae or spur-like projections) are arranged in two groups, basal (4-6 setae) and distal (2-3 setae). In addition to ovigerous setae found in pre-spawning and ovigerous females, the surfaces of the bases of pleopods 1-4 and the endopod of the first pleopod

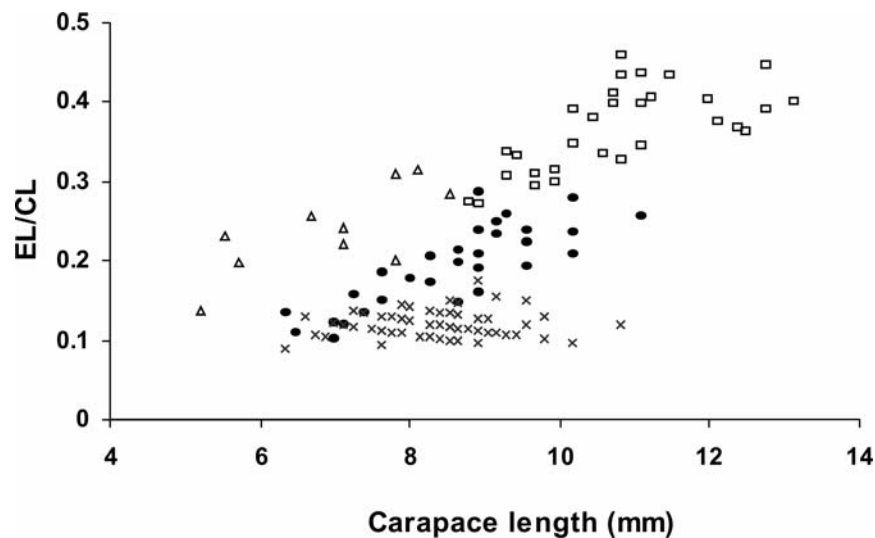


Fig. 3. *Crangon franciscorum*. Relationship between the length of the endopod of the first pleopod and carapace length; (X) males, (●) immature secondary females, (□) mature secondary females, (△) primary females. Individuals were sexed by dissection of the gonads.

Table 3. *Crangon franciscorum*. Results of regressions of the length of the appendix masculina (AM, males only) and the endopod of the first pair of pleopods (EL) vs. carapace length (CL). a: intercept, b: slope, R: correlation coefficient, N: number of individuals. ISF = immature secondary females, MSF = Mature secondary females, PF = Primary females.

Group		a	b	R	P	N	EL/CL
AM	Males	-0.01	0.13	0.48	0.001	110	0.10-0.16
EL	Males	-0.28	0.15	0.53	0.001	86	0.05-0.15
	ISFs	-1.47	0.38	0.65	0.001	33	0.10-0.27
	MSFs	-2.24	0.57	0.74	0.001	27	0.28-0.40
	PFs	-3.16	0.70	0.55	0.001	13	0.10-0.32
	SFs (pool)	-3.86	0.69	0.83	0.001	60	0.10-0.40

bear pinnate setae involved in shaping the incubation chamber that holds the egg mass in position.

The ovary occupies the same anatomical position as the mature testis of males. In resting females it is ivory in color and both lobes extend to the sides and from the first to the second abdominal segment. In pre-spawning females, it becomes green and granulated in appearance, expanding posterior to the third pleonal segment, fully occupying the thoracic cavity. A pair of lateral oviducts extends from the anterior-medium portion of the ovary to the gonopores, which are located between the articulation of the coxa of the third pair of pereiopods and the thoracic sternum. The ovary is covered by connective tissue. The epithelium, composed of follicular cells, surrounds the oögonia and oöcytes.

Ovigerous females that released larvae in the lab ($n = 17$) molted afterwards, and the ovigerous setae were replaced by spur-like projections. In all cases, the ovary was white. Other females were brought from the field with spur like projections, but the ovary was either green ($n = 5$) or white ($n = 7$). After molting, females with green ovaries developed ovigerous setae and females with white ovaries kept the spur-like projections for a second time. Isolated mature females ($n = 24$) showed no successive spawnings in the tanks.

Growth in Captivity

Growth through successive instars was described with the model

$$CL_{i+1} = a + bCL_i + \varepsilon \quad [1]$$

where ε is an error term distributed as $\varepsilon \sim N(0, \sigma)$, CL_i and CL_{i+1} are pre- and post-molt carapace length, and a and b are estimated parameters. The model assumes that all the variability is due to process error. ANCOVA showed no significant difference between sexes ($F = 0.42$; df : 1,84; $P > 0.5$), and so data were pooled (Fig. 6A). The estimated parameters (sexes pooled) were $\hat{a} = 1.77$ and $\hat{b} = 0.91$ (MSE = 0.132; $R^2 = 0.95$; $n = 89$). Relative size increments at molt (expressed as a percentage of pre-molt CL) decreased with size from 30-32 % for small shrimp (~5 mm CL) to 3-5 % for large shrimp (~11 mm) (Fig. 6B). The average increment in the length of the endopod of secondary immature females was 0.6 mm (SD = 0.02, $n = 15$).

Molting frequency decreased with size. Time between molting events increased from 15-25 days for small shrimp

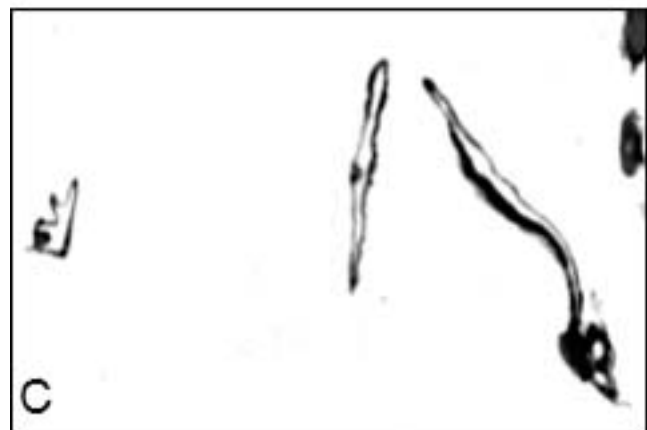
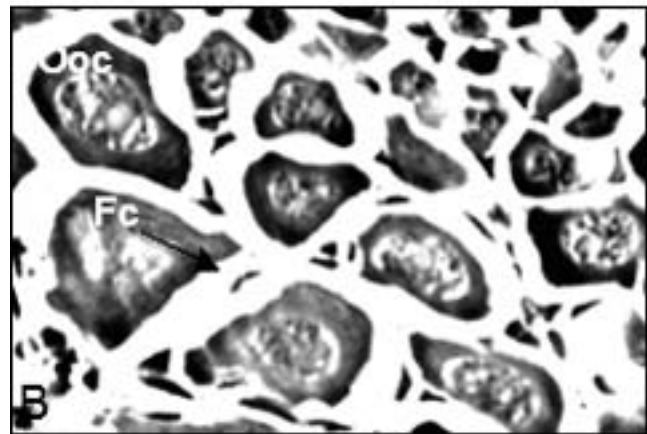
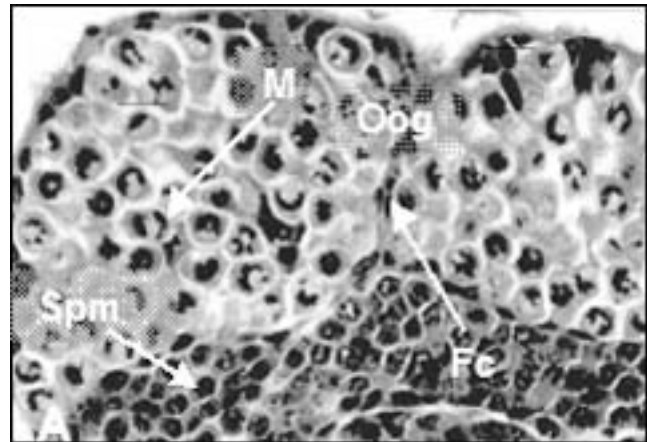


Fig. 4. *Crangon franciscorum*. Histological sections of the gonad. A) Transitional individual with spermatogonia (Spm) on one side and ovary in early stage of development. Follicular cells (Fc) start surrounding oögonia (Oog). Mitosis (M) is observed in oögonia. B) Ovary of immature secondary female of 8.3 mm (CL) that underwent sex change in the laboratory. Oöcytes (Ooc) are in stage 1, with follicular cells (Fc) surrounding them. C) Atrophied vas deferens of the same individual.

(CL ~ 7-8 mm) to 30-40 days for large shrimp (CL ~ 10-14 mm). The data were insufficient to compare molting frequency between males and females, or to model its size-dependence. Besides, molting frequency is expected to be highly influenced by temperature and so will vary

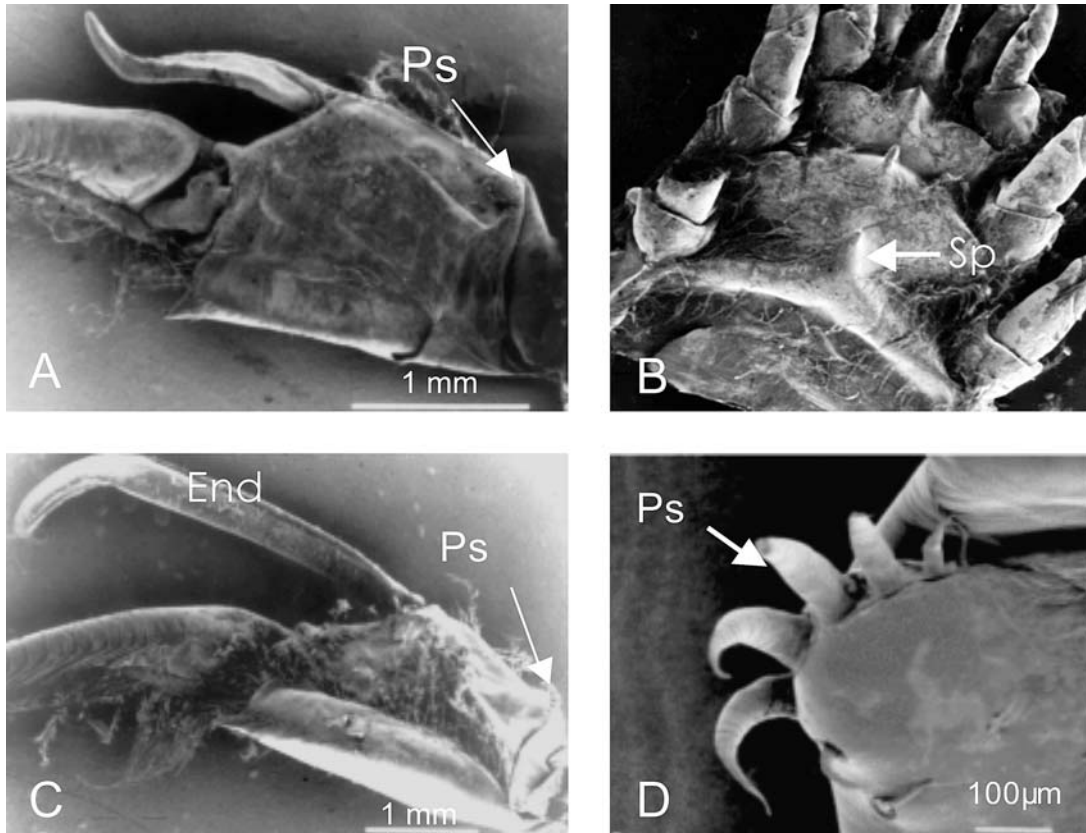


Fig. 5. *Crangon franciscorum*. Female secondary sexual characters, SEMs. A) First pleopod of immature secondary female showing enlarged area corresponding to primordial setae (Ps). B) Sternal pereion of a mature female showing the subtriangular shape of the fourth medial spine (Sp) and the round shape of sternites. C) First pleopod of a mature female with enlarged area of the spur-like projections setae (Ps). D) Enlarged area of setae (Ps).

seasonally. Our laboratory data could not possibly capture these important components of variation.

Population Studies

Monthly Size Frequency Distributions (Period 1980-81).—Size frequency distributions constructed with the data from Hoeman's (1982) study are dominated by the 1980 year-class (Fig. 7). Two other year classes were briefly represented in the samples: the remains of the 1979 year class in June of 1980, and incipient recruitment of the 1981 year class in May of 1981 (Fig. 7). In particular, of the two modal groups observable in the female sample of June 1980, the largest (average CL 12.6 mm; range: 10-16 mm) corresponds to members of the 1979 year-class, all of which were ovigerous. None of the females of the 1980 year-class (average CL 7.1 mm, Fig. 8) were ovigerous at that time. Only a few large, ovigerous females (presumably the last survivors of the 1979 year class) were observed during July and August. By that time some large females of the 1980 year-class (CL > 8 mm) were ovigerous; few were ovigerous from September through December 1980. The bulk of the females of the 1980 year-class carried eggs between January and May 1981 (when sampling ended), and presumably continued doing so into June if they followed the pattern observed for the 1979 year-class. Eggs carried by females between January and June generate the recruits (CL ~ 5 mm) that started to appear in the samples

in May. Females are likely to spawn repeated times during a given reproductive season, but the frequency of spawning could not be assessed with our data.

Average size increased linearly in both males and females from June through October (Fig. 8). ANCOVA shows significant differences between sexes in apparent growth rate ($F = 463.3$; df : 3,1533; $P < 0.001$). While females continued growing through January 1981 ($CL_{January}^{female} = 13.2$ mm), average male size started to decrease in November, after reaching maximum size in October ($CL_{October}^{male} = 10.9$ mm), a trend that continued through May 1981 ($CL_{May}^{male} = 9.2$ mm).

Samples Obtained in 1992-1993.—A single year class was represented in each monthly sample (Fig. 9). The 1991 year-class (8.2 mm average CL, Table 4) was still present in March, 1992, but had vanished by next July, when smaller individuals corresponding to the 1992 year class had been already recruited. Males grew during the summer (July-August); subsequently, mean size of males declined gradually between August 1992 and February 1993. Individuals larger than 12 mm were never observed during the sampling period. Recruitment of the 1993 year-class was clearly observable in June 1993, by which time males of the 1992 year-class had already vanished from the population.

The age composition of the female samples was similar (Fig. 9), with the exception that in June 1993, the 1992 year-

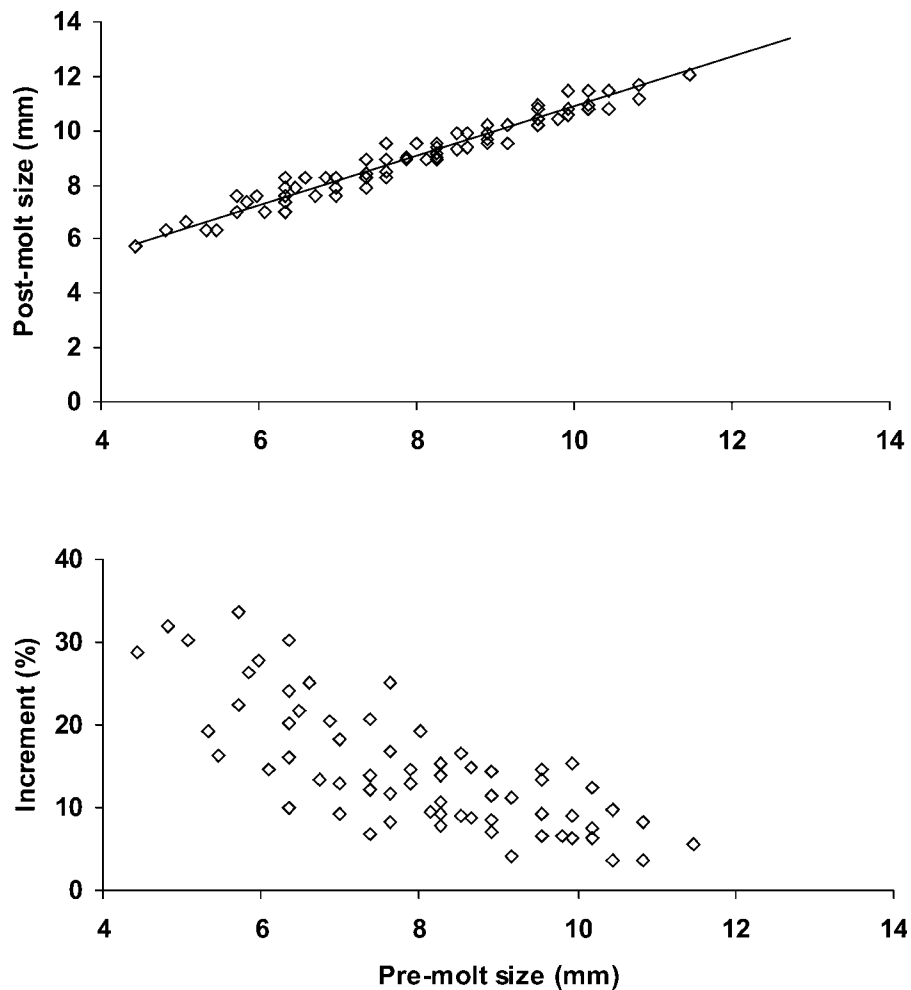


Fig. 6. *Crangon franciscorum*. Growth increments after molt in captivity. A) Hiatt diagram. B) Relative increment (as a percentage).

class was still present, and so two year-classes coexisted (immature recruits of 1993, and mature females of 1992). ISFs of the 1992 year-class (always smaller than mature females on average, Table 4) were already present during the summer of 1992, and showed up in samples through the next winter (January-February, 1993). Ovigerous females, present in all the samples, were largest (average CL 10.1-10.7 mm) during the winter and spring of 1993.

Consistency Between Growth Parameters, Survey SFDs and Morphometry of Secondary Sexual Characters.—The variance of sizes at instar projected from growth model [1] are, after Nicholson (1979),

$$\theta_i = \sigma \sum_{j=1}^i b^{2(j-1)}, \quad [2]$$

where σ is estimated by the MSE of [1]. In order to make growth projections we used a reference initial size (CL_0) of 7.1 mm, the mean CL of year-class 1980 observed in June 1980. Mean projected size after i molts (\overline{CL}_i) was calculated using [1], and the corresponding variance (θ_i) using [2]. One molt would be required to take an average individual from $CL_0 = 7.1$ mm in June to $CL_1 = 8.2$ mm (θ_1

$= 0.24$); that figure falls just between $\overline{CL}_{July}^{male}$ (7.5 mm) and $\overline{CL}_{August}^{male}$ (8.8 mm). After three molts ($CL_3 = 10.2$ mm) an average individual would be near the maximum average size reached by a male in that cohort ($\overline{CL}_{September}^{male} = 9.5$ mm; $\overline{CL}_{October}^{male} = 10.9$ mm; Fig. 10). An average individual would reach the maximum observed average size of females in the cohort ($\overline{CL}_{max}^{female} = 13.2$ mm; January-March 1981) after 7 molts counting from June 1980 ($CL_7 = 13.2$ mm). The male to female transition, occurring at a wide range of sizes, was centered in the fall.

The EL/CL ratio varied among the various stages present in the population, as shown in Fig. 3. A combination of estimated size increments-at-molt and stage-specific relationships in the EL/CL ratio permits the reconstruction of plausible life-history pathways (Fig. 10), including the male-to-female transition. IPFs need to molt two times (on average) to grow from the last juvenile stage (5-6 mm) to morphological maturity (MPF), and three times to reach minimum ovigerous size. The male-to-female transition must take, on average, two molting events in order to accommodate observed morphometric relationships (EL versus CL for mature males and females) and increments-at-molt in the CL and EL of ISFs. The size range of males and MSFs can accommodate approximately 5 instars. Field data

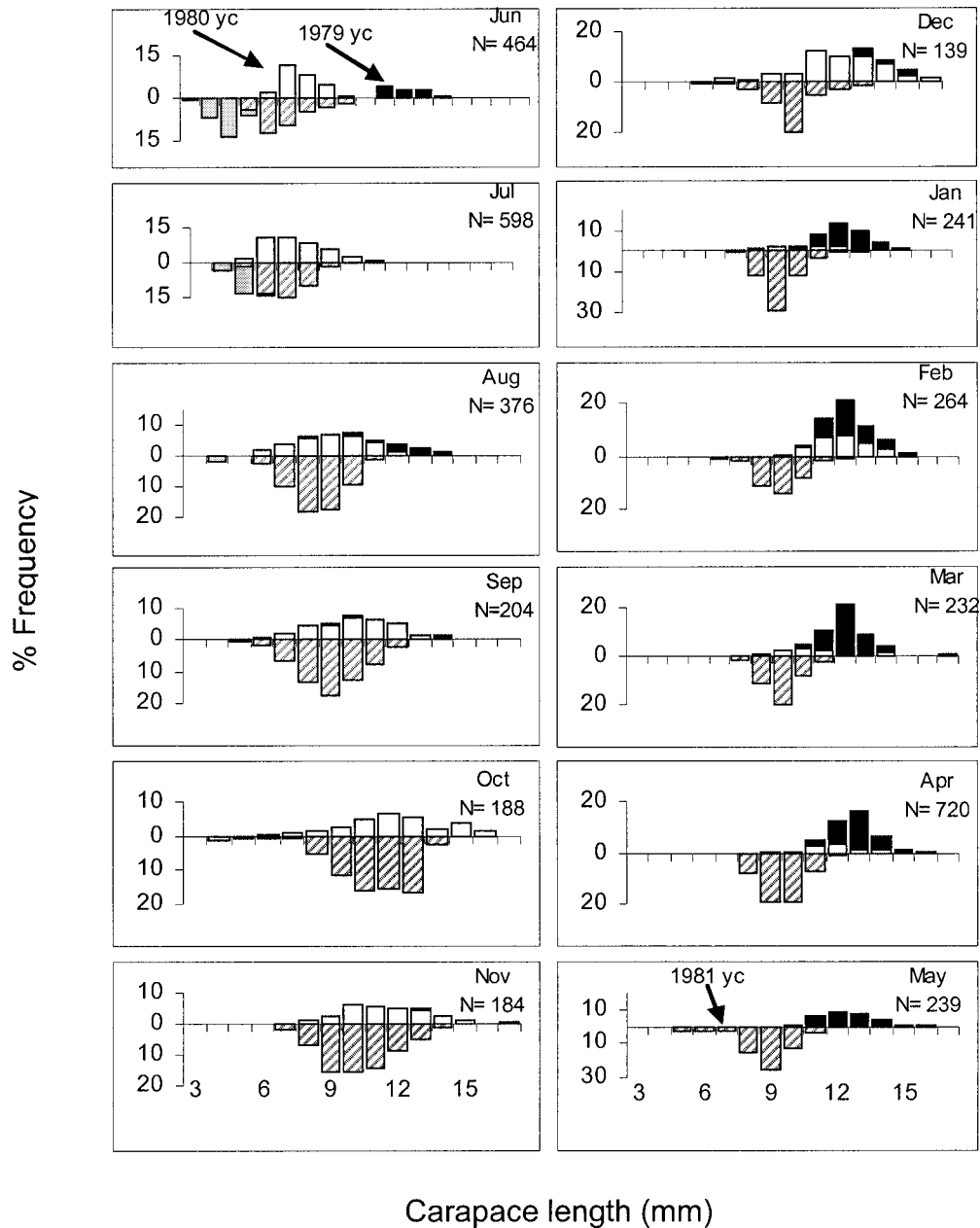


Fig. 7. *Crangon franciscorum*. Size frequency distributions of juveniles (gray), males (hatched), non-ovigerous females (open bars) and ovigerous females (black). June 1980-May 1981.

indicate that the male-female transition can be initiated over the entire range of male sizes, resulting in considerable variability in plausible life-history paths.

DISCUSSION

The life history of *Crangon franciscorum* had been previously investigated in three populations, well spread-out over its range of distribution along the west coast of North America: San Francisco Bay in California (Israel, 1936), Yaquina Bay in Oregon (Krygiel and Horton, 1975), and Grays Harbor estuary in Washington (Hoeman, 1982). These studies, all of which assumed that *C. franciscorum* is

gonochoristic, revealed a recurrent pattern: males are always smaller than females; their average size starts to decline during the fall of the first year of life, while females of the same age keep growing. By late spring of the cohort's second year of life males vanish from the population, while females (mostly ovigerous) continue to be present through early summer. Thus, males appear to have a shorter lifespan than females (approximately 1 versus 1.5 years, respectively). The observed reduction of mean size towards the end of a male cohort's life was attributed to death or emigration of the largest individuals. Krygiel and Horton (1975) concluded that males probably spawn once and then die. Reproductive females were split into two cohorts

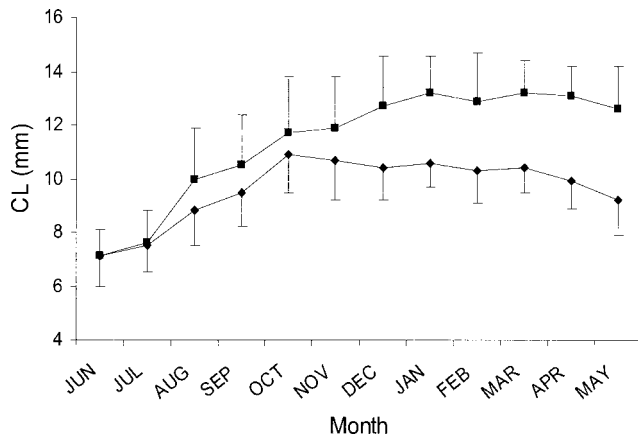


Fig. 8. *Crangon franciscorum*. Mean carapace length of males (◆) and females (■), in the 1980 year class from June 1980-May 1981. Vertical lines represent standard deviation.

evidenced by two recruitment peaks and different growth rates. Similar results were reported for *C. franciscorum* in Grays Harbor (Hoeman, 1982).

Alternatively, in this study we hypothesized that *C. franciscorum* has a sexual system of the type known as “protandry with primary females” (Bauer, 2000) or “partial protandric hermaphroditism with primary females” (Correa and Thiel, 2003). The data on population structure presented by previous authors can be also explained if the population includes both primary and secondary females. Largest males would reproduce and then change sex during the fall and winter, this resulting in the observed decrease of mean size.

We present three pieces of evidence that support the alternative hypothesis:

1. Dissection and histological examination of males collected in the field showed variable degrees of ovarian development, starting at the anterior portion of the gonad.
2. Females often showed atrophied vas deferens, a condition that has been considered evidence of them being secondary females (Jargersten, 1936; Charniaux-Cotton, 1958; Hoffman, 1972; Frechéte et al., 1970; Suzuki, 1970; Boddeke et al., 1991).
3. Two males changed sex while being held in captivity.

The reproductive system of *C. franciscorum* had not been examined before. Gonadal modification starts at the anterior end (while the vas deferens are still full of sperm) before atrophy of the androgenic glands, as is also the case in *C. crangon* (Martens and Redant, 1986; Boddeke et al., 1991). Transitional males of *C. franciscorum* retain all the external male secondary sexual characters, similarly to what has been reported for *Argis dentata* (Frechéte et al., 1970), *Pandalus platyceros* Brandt, 1851 (Hoffman, 1972), and other carideans. Charniaux-Cotton (1958), Carlisle (1959) and Hoffman (1969) demonstrated experimentally that the androgenic gland is responsible for the retention of male secondary sexual characters, which disappear only after the androgenic gland has been removed, even if the gonad has already undergone partial transformation. The default hypothesis (gonochorism) had been substantiated by

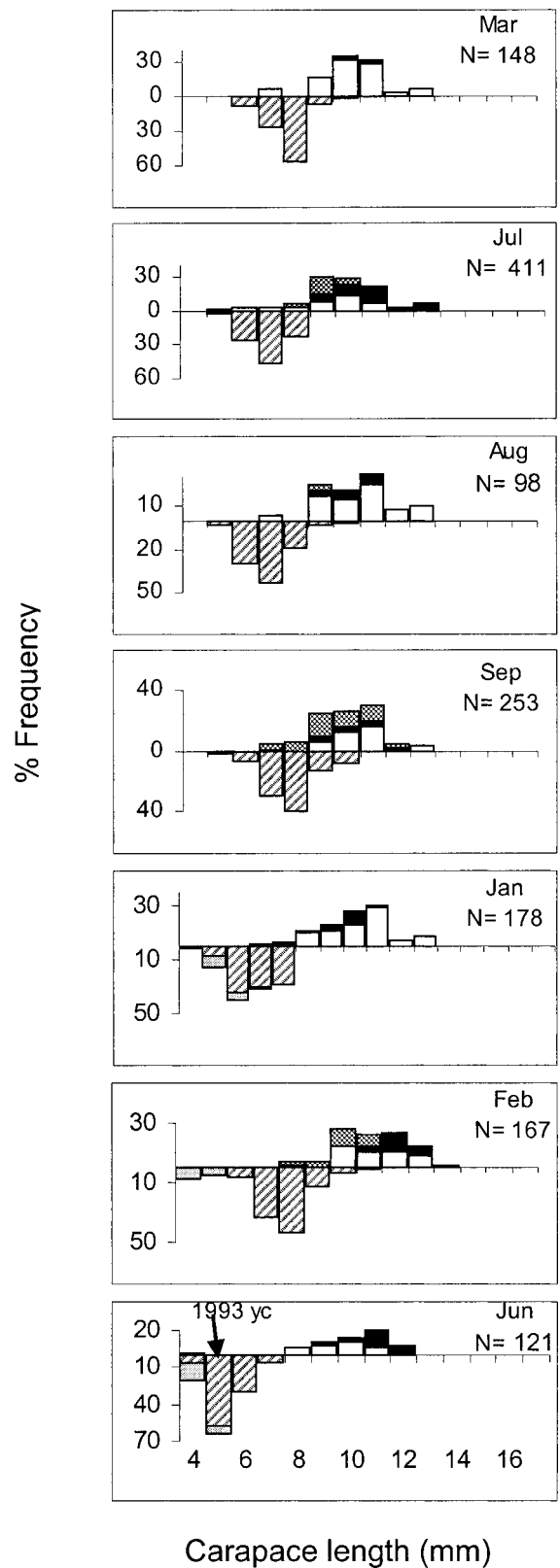


Fig. 9. *Crangon franciscorum*. Size frequency distributions of juveniles (gray), males (hatched), immature secondary females (spotted), mature non-ovigerous females (open bars) and ovigerous females (black), 1992-1993.

Table 4. *Crangon franciscorum*. Mean carapace length (mm) of females and males from Grays Harbor during the sampling period 1992-93. SD: standard deviation, N: number of individuals.

Year	Month	Total females			Ovigerous females			Immature secondary females			Males		
		Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
1992	March	9.9	0.9	29	—	—	—	—	—	—	8.2	0.7	118
	July	9.4	1.5	85	9.7	—	34	8.4	1.9	22	7.5	0.9	322
	August	10.1	1.3	27	9.9	0.6	6	—	—	—	8.5	0.8	69
	September	10.7	1.4	114	11.1	0.9	14	10.3	1.5	55	8.4	1.5	141
1993	January	9.7	0.9	38	10.6	0.6	10	7.6	0.6	3	7.3	1.1	86
	February	10.6	1.2	62	10.7	0.5	14	8.4	0.8	17	8.4	0.9	85
	June	10.1	0.8	24	10.4	0.7	13	—	—	—	5.9	0.6	48

examination of the AM in comparison to protandric pandalids (Israel, 1936; Krygier and Horton, 1975). Different from pandalids, however, the AM of crangonids is lost in a single molt rather than gradually through a sequence of molts.

Gonochorism versus protandry hypotheses have been also a subject of debate in the case of *C. crangon*. Early morphological studies (Havinga, 1930; Lloyd and Yonge, 1947; Tiewes, 1954) and the results of rearing 20 males from the third larval stage to final size of 55-60 mm length during 14 months, and not observing any sex change (Meixner, 1966), were taken as indication of gonochorism by Tiewes (1987). On the other hand, Boddeke (1966), Martens and Redant (1986) and Boddeke et al. (1991) argued in favor of protandry, basing their conclusions on morphological and histological evidence. Sex-reversal is known to occur in two other crangonids, *Argis dentata* (Frech ette et al., 1970) and *Sclerocrangon boreas* (Phipps, 1774) (Bernier and Poirier, 1981), although it was suggested that the latter species is gonochoristic based on the analysis of SFDs (Birkely and Gulliksen, 2003).

C. franciscorum shares the same basic sexual system with *C. crangon* and *Argis dentata*. Primary and secondary females occur in the three species, the latter being recognizable by the presence of atrophied vas deferens, which are absent even in immature primary females. A similar pattern is exhibited by protandrous hermaphroditic carideans of other families (Suzuki, 1970; Charniaux-Cotton, 1958, 1965; Jargersten, 1936; Hoffman, 1972; Bauer, 1986; Bergstr om, 2000). As mature *C. franciscorum* females grow larger (more than 9 mm CL, EL/CL > 0.30), the atrophied vas deferens become proportionally thinner and may go unnoticed, or break as a result of manipulation of the enlarged gonad. This introduces some uncertainty in the distinction between mature primary and secondary females, as already pointed by Frech ette et al. (1970).

The size range of ISF is broad, suggesting that sex change does not occur at a specific size. The size of the smallest mature male and the smallest ISF were the same, 6.5 mm CL, and so it is unlikely that the latter could be derived from post-reproductive males. One possible explanation might be that these individuals started developing as males but never reached sexual maturity as such. Instead, they might have continued their development as females, with presence of immature ovary and atrophied vas deferens. This has been described for populations of *Pandalus montagui* Leach, 1814, in which males reverse sex either before sexual maturity or very late in their life cycle (Charniaux-Cotton

and Payen, 1985). The observed size range of males can accommodate at least five instars, and the size range of IPFs and MPFs suggest that the male-female transition can be initiated at any point within that range. Such variability has been documented also among pandalids (Bergstr om, 1997, 2000).

Some results on sex determination in caridean shrimp have highlighted the value of the experimental study of functional aspects, such as the influence of the social environment on primary sex determination, the initiation of sex change in protandric species, and (related to the latter) the size at which sex change takes place (Baeza and Bauer, 2004; Bauer, 2002a; Bergstr om, 2000; Fiedler, 2002). At the beginning of our study it was our intention to explore this phenomenon, but based on external characters it was impossible to discriminate males that had and had not initiated the male-female transition, which precluded the required experimental design. Besides, species that live in open shelf areas (the case of several commercially important protandric pandalids) or that migrate from estuaries to shelf habitats (the case of *Crangon*) do not lend themselves to experimental studies, which is the case for small, tropical or subtropical reef-dwelling carideans that are easily kept in aquaria (Bauer, 2002a; Fiedler, 2002). Given the focus of our study (support for two alternative hypotheses explaining a recurrently observed life-history pattern), elucidation of the functional aspects of sex change is not a necessary requirement. This interesting problem deserves further inquiry.

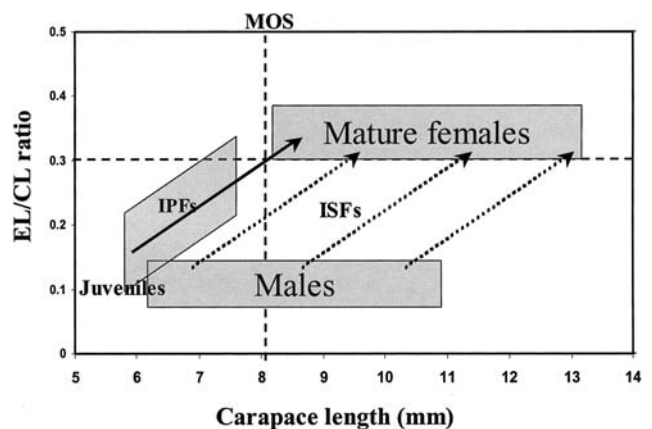


Fig. 10. *Crangon franciscorum*. Schematic of life history pathways (see Table 1 for definition of terms). MOS: minimum ovigerous size.

Only four categories of individuals are usually recognized in studies of crangonid populations: juveniles, males, and non-ovigerous and ovigerous females. Our survey of external and internal characters made it possible to refine the separation of life-history stages in *C. franciscorum* (Table 2), as is also the case for pandalids (Bergström, 2000). Characters include:

1. Shape and setation of sternal spines of the pereion, which are easy to observe, may prove useful in the sexing of large samples. Separation of males and females has been traditionally based on structures in the first and second pairs of pleopods (Butler, 1980), although morphological changes of sternal spines in some species of *Pandalus* are correlated with sexual stages (McCrary, 1971; Bergström, 2000).
2. Presence of spur-like (short) or ovigerous (long) setae on the bases and endopods of females, long used by morphologists and taxonomists to separate reproductive from non-reproductive stages (Ehrenbaum, 1890; Gurney, 1923; Sollaud, 1923; Høglund, 1943; Yonge, 1955), has not been emphasized in studies of sex change. Ovigerous and pinnate setae are secondary sexual characters (Sollaud, 1923), which in carideans can be permanent (they persist after reaching sexual maturity, e.g., Palaemonidae) or periodic (they appear only during the egg-carrying intermolt, e.g., *Leander*, *Hippolyte*). In *C. franciscorum*, we determined that they are periodic characters, correlated with ovary color.
3. EL/CL ratio of the first pleopod, which has been used in studies of other protandric hermaphrodites (Boddeke et al., 1991; Gherardi and Calloni, 1993). The index is useful to separate males from females and immature from mature secondary females when the carapace is longer than 8 mm.
4. Internal characters: The presence of atrophied vas deferens for recognizing secondary females has been extensively used in studies of protandrous hermaphroditic species (Boddeke et al., 1991). These structures are easy to observe in fresh and fixed specimens. In mature females, external examination of ovary color indicates reproductive condition (Butler, 1980), and is correlated with stages defined by setation, i.e., breeding versus non-breeding "dress" (Bergström, 2000).

Crangonids are unique among caridean shrimp in that the second pleopod lacks the appendix interna, and the AM is a relatively small structure (Butler, 1980). Thus, it is not possible to use the relative length of these two structures to assess stages in the male-female transition, as is often done in the case of protandric pandalids (Butler, 1980).

Improved staging can expand significantly the scope of the information obtained from survey samples of crangonid populations. In the population of Grays Harbor, for example, we were able to identify juveniles, primary females, males, and secondary females. Our results on *C. franciscorum* lead to reexamination of the model currently accepted for its life history. We suggest that the "disappearance" of large males during the second year of life reflects sex change rather than emigration or mortality, as was proposed in earlier studies (Israel, 1936; Krygier and Horton, 1975; Hoeman, 1982).

Our conceptual model of the life history of *C. franciscorum* in estuaries and coastal embayments is as follows (see Figure 10):

1. Young males start reaching sexual maturity by late spring, as evidenced by the presence of sperm in the vas deferens of individuals as small as 6.5 mm CL. Females mature at a larger size, minimum ovigerous size being 8.0 mm.
2. The wide size overlap among males, TMs and ISFs indicates that sex change does not occur at a specific size. Some of the ISFs are so small that they cannot possibly have passed through a reproductively mature male size, i.e., they must have changed from immature male to ISF.
3. Mature males gradually become TM during the summer, fall and winter, then molt two or three times (ISF₁ and ISF₂) before maturing as secondary females and becoming part of the ovigerous population during the winter and spring of the second calendar year of life.
4. Apparent "shrinking" of males during fall and winter reflects progressive, size-selective protandry.

The fate of females after spawning in coastal bays and estuaries is uncertain. While some authors suggested that they might die, the presence of very large females in offshore areas has led others to speculate about an ontogenetic migration leaving the estuaries and bays during the summer of the second calendar year of life (Hatfield, 1985; Siegfried, 1989). Emigration to offshore areas would be, in fact, the final stage of a process that starts with recruitment in the upper reaches of estuaries (even in nearly fresh water) and is followed by migration into progressively more saline waters (Siegfried, 1989). Our data cannot resolve this subject.

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