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The Biology of a Marine Decapod Crustacean, *Pleuroncodes planipes* Stimpson, 1860

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Marine Biology

by

Carl Milton Boyd, Jr.

January 19, 1962

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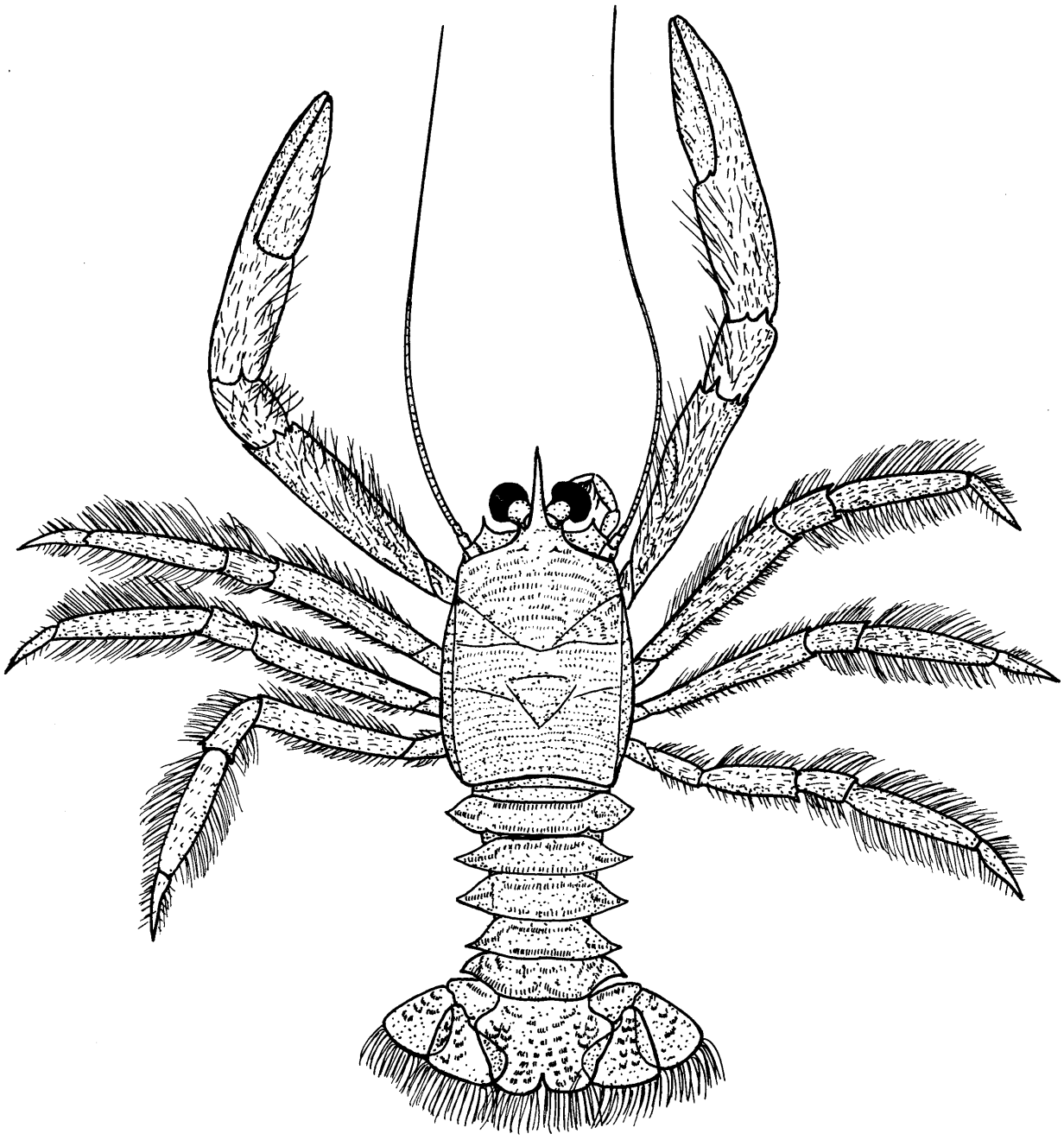
January 19, 1962



UNIVERSITY OF CALIFORNIA

GRADUATE DIVISION, SOUTHERN SECTION

ANNOUNCEMENT OF THE

FINAL EXAMINATION FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

OF

CARL MILTON BOYD, JR

A. B., 1955; M. A., 1956

Indiana University, Bloomington, Indiana

MARINE BIOLOGY

FRIDAY, JANUARY 19, 1962, 9:00 A.M., IN ROOM 1265

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"The larval stages of Pleuroncodes planipes Stimpson (Crustaces, Decapoda, Galatheidae)," Biological Bulletin, 118 (1): 17-30 (1960)

ABSTRACT OF THE DISSERTATION

The Biology of a Marine Decapod Crustacean,

Pleuroncodes Planipes Stimson, 1860

An ecological study of Pleuroncodes planipes has been undertaken to correlate the animal with its oceanic environment. The animal studied is an anomuran galatheid decapod crustacean about 9 to 11 cm long, resembling a small homarid lobster. These crabs exist in the ocean both as pelagic animals and benthic animals. In the pelagic phase the crabs range from 16° N to 37° N, and have a distribution which is typically neritic. The center of the population appears to be along the southern coast of Baja California. The distribution of the crabs in the pelagic phase is believed determined by several prevailing currents carrying them away from this population center. Dense surface occurrences are correlated with a diurnal vertical migration; the crabs are generally found in the upper 25 meters at night and descend to greater depths during the day.

The crabs are benthic as well as pelagic in certain areas, and at least sometimes alternate between the benthos and the plankton with a diurnal rhythm. In their benthic phase they are found on the continental shelf along the western coast of southern Baja California, between the depths of 75 meters and 300 meters.

The feeding habits of the crabs seem to be as diverse as their ecological range. As planktonic animals the crabs are able

to feed on phytoplankton and small zooplankton. As benthic animals the crabs have the ability to sift through the substrate with their maxillipeds and thus extract small animals living in the sediments.

The crabs play an important part in the diet of several other marine animals. Many fishes such as the skipjack tuna, the yellowfin tuna, the albacore, and various kelp bed fishes also feed heavily on P. planipes when the crabs are available to them.

The young of P. planipes pass through a series of zoeal larval stages after hatching. There are five morphologically discrete stages, and generally the larvae change from one stage to the next by molting. Larvae in Stage IV, however, may molt from four to nine times without greatly altering their basic morphology. There is evidence from laboratory culturing that the number of these sub-stages may be influenced by the temperature at which the larvae develop, with higher temperatures causing more sub-stages. The duration of the larval phase is influenced by the temperature at which the larvae were reared, and the rate follows a Q_{10} of about 1.9. The larval duration is also influenced by rearing conditions other than temperature, for the size of the larval rearing container or the presence of other larvae in the container has also been shown to influence the duration of the larval phase. A larval stage was seen in the laboratory which has not been found in nature, and it is probable

that the stage was an artifact of laboratory culturing conditions.

Growth rates of P. planipes have been determined from both laboratory and the field; the two answers complement each other and generally agree. They indicate that the young are spawned in winter months and spend the first year of life in the plankton as larvae and immature crabs. The crabs become reproductively mature in their second year of life, and exist then as both planktonic and benthic animals; toward the end of the second year they become exclusively benthic.

FIELDS OF STUDY

Major Field: MARINE BIOLOGY

Studies in Oceanography: Professors Robert S. Arthur, Norris W. Rakestraw and Francis P. Shepard.

Studies in Marine Biology: Professors Edward W. Fager, Carl L. Hubbs and Martin W. Johnson.

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Introduction and acknowledgements

This study of the general biology of *Pleuroncodes planipes* has pursued two goals: the first, to gain a knowledge of the ocean by using the animal as a "vehicle" in the study of such oceanic phenomona as the distribution of currents and temperatures, etc.; the second, to learn as much as possible about the life of the crabs in hopes that the information, in addition to applying directly to *P. planipes*, might also apply to other marine organisms.

As the crabs have proved to be relatively easy to maintain in laboratory aquaria, it has been possible to obtain parallel answers to many questions--one answer from the ocean and another from the laboratory. The two answers generally have complemented each other in a most valuable way.

Dr. Martin W. Johnson has acted as my major professor in this study, and it has been a pleasure to work with him. Dr. E. W. Fager has proved very helpful in critical appraisal of the statistical tests used; discussions with him on questions of the general philosophy of biology have served to shape my thoughts as well as my approach to marine biology. Dr. Carl L. Hubbs has, on several occasions, pointed out valuable references which he had encountered. Thanks are extended to Dr. Maurice Blackburn, who made financial support available for this study. Mrs. Dorothy Walton and Mr. John Nordback acted as technical assistants during parts of the study and their help was valuable. Mrs. Joan Stewart has read the

text of the thesis as it evolved, and her criticism, comments, and encouragement have been appreciated very much. During the week-ends and nights spent in the laboratory, as well as the months spent at sea, my wife Donita has taken the responsibilities of the family; she has always provided support when it has been needed, and her consideration is gratefully acknowledged.

History of the Genus Pleuroncodes

In March, 1859, a considerable number of specimens of a then undescribed anomuran crab were washed ashore at Monterey, California. These crustaceans, which resembled small homarid lobsters, were collected by Mr. Alex S. Taylor and sent to Dr. William Stimpson, who was then describing the crustacean material collected by the North Pacific Exploring Expedition. He described the crabs from Monterey, along with some of the same species sent from oceanic waters by another collector, as Pleuroncodes planipes; new genus and new species, and assigned it to the family Galatheidae. Stimpson used the nomenclatorial perogative to the humorists' advantage in naming the animal, for the name can best be translated as "the bulgy-sided crab with flat feet." In the new genus Stimpson also included a species from the shores of Chile described by H. Milne-Edwards in 1837 as Galathea monodon, which hence became Pleuroncodes monodon. These are the only two species assigned to the genus at present.

Initial descriptions of the two species are quite inadequate. Milne-Edwards' 1837 description morphologically fit most of the species of the genus Munida, a large genus closely related to Pleuroncodes and containing about 41 species. Milne-Edwards' figures of G. monodon, published in 1851, however, are excellent. Stimpson's description of P. planipes is only slightly better; he did not present any figures of the new species, and apparently the first figure of the species to occur in the literature was in

Schmitt's 1921 monograph of the California Decapod Crustacea. Schmitt's description is the most complete to date. For a description of P. monodon the reader is referred to Faxon (1891) and Haig (1955).

Haig listed P. monodon as ranging from Ancud, Province of Chiloe, Chile, in the south, to Lobos de Afuera Uskabdsm Peru. In stating this she conjectured that the specimens from off Acapulco, Mexico, discussed by Faxon, were not P. monodon, as Faxon identified them, but P. planipes. However, after having examined these specimens I regard it as probable that Faxon was dealing with P. monodon, which therefore probably ranges from Chiloe, Chile, to Acapulco, Mexico, and is perhaps contiguous in its northern distribution with P. planipes. The Mexican specimens examined by Faxon were considerably larger than any specimens reported in the literature or seen by myself from the Chilean coasts. If specific differences exist between the Central American form and the Chilean form, they cannot be detected with the material now available.

Members of the family Galatheidae are typically benthic when adult. Larvae of all the species are pelagic for at least a short time, and presumably the small postlarval crabs can alternate between the plankton and the benthos before they assume an exclusively benthic life. Two antarctic species, Munida gregaria (Fabricius), 1793, and M. subrugosa (White), 1847 may be either pelagic or benthic as adults, but are more commonly benthic (Matthews, 1932). The young of M. gregaria--in the so-called

Grimothea stage--are predominantly pelagic, and have been reported on several occasions as being so numerous that they color the sea bright red over large areas.

Stimpson noted in the original description of P. planipes that the crabs were washed ashore at Monterey, California--presumably from the plankton. He also reports having received animals from a Mr. Grayson, who took them at 24° N x 130° W, where the animals were obviously planktonic. Prior to the present report the animals were believed to be entirely planktonic and were not definitely known to be members of the benthos.

Swimming behavior

Pleuroncodes planipes has evolved phylogenetically from stock which is characteristically benthic during the entire phase of adult life. Like those portunid crabs that are pelagic, P. planipes owes its ability to swim to minor modifications that do not remarkably alter its form, but allow it to remain afloat with less expenditure of energy. The bulging sides of Pleuroncodes, the trait which gives the genus its name, may be a modification to decrease the settling rate of the animal. The major morphological adaptation of a pelagic life, however, is the development of dense comb-like rows of setae on the anterior and posterior margins of four pairs of walking legs. These setae approximately triple the width of the leg, with no increase in weight (see frontis). The leg itself is flattened in the dorso-ventral plane. In making use of these modifications the crab stretches out its legs, and greatly resembling a large spider, settles slowly down through the water.

These morphological modifications serve only to retard the sinking rate of the crab; in order to maintain itself in a given water layer the animal must also actively swim. This it does by holding its legs forward close to the body, and then repeatedly flexing the abdomen--an effort which moves the animal rapidly backwards and upwards. The animal alternatively slowly settles downward and then actively swims upward, and is thus able to regulate its depth.

A peculiar behavior of P. planipes was noted by Beklemishev (1960). In this pattern the crab swims to the surface of the water and inverts itself so that its legs partially protrude through the air-water interface. The inverted animal gives the illusion that it is walking on the under surface of the water. The function of this mode of swimming is unknown, but it is possible that this allows the mouthparts of the animal to contact and filter out food items floating just at the surface of the water.

Diurnal migration in Pleuroncodes planipes

There are many more catch records of P. planipes during night hours than during daylight hours in the cruises 6001 to 6008, discussed below (197 for night, and 94 for day). Stations on Scripps cruises are operated regardless of the time of the day, and the number of stations occupied in day and night hours is approximately equal--neglecting the small biasing influence due to the seasonal shift of the time of sunset and sunrise. The unequal availability of the animals to capture may result from two factors: 1) during daylight hours the crabs may see the net coming and thereby avoid it, and 2) the crabs may not be in the areas sampled in the daytime, but are there at night. Both of these factors are believed to operate; though their relative effects on the occurrence of the crabs in the plankton samples is completely unknown. There is corroborative evidence from several lines, however, that suggests that the crabs do migrate vertically at night from depths deeper than reached in the routine net hauls, and it will be assumed in this study that the sampling error induced by visual avoidance of the net in daylight hours is small and that diurnal migration accounts for the bulk of the difference in abundance in the plankton samples. A regression analysis discussed in a later section indicated a tendency for larger crabs to be caught during the daytime. This would be unexpected if crabs were avoiding the net, for larger crabs could supposedly more easily avoid the net than smaller crabs.

The number of crabs caught at each hour of the day during the cruise in March, 1960, is summarized in figure 1.. This cruise was specifically chosen because the vernal equinox is in that month and the problem of un-equal day and night hours is thereby avoided. In March, 96 crabs were caught at daytime, and 563 crabs at night. A X^2 test of the numbers of crabs caught at the hourly intervals graphed in figure 1 against the mean occurrence expected at that hour if their occurrence with time were random indicates the day-night difference in frequency is highly significant, ($P < 0.001$).

Further evidence of migration of the crabs to the surface is seen in Table 1. Samples tabulated in this table were collected in June, 1961, at the places listed on the table. Collections were made with a meter net towed horizontally at depth for one-half hour. The net at the surface was open; all others were opened only at the designated depth by the Leavitt open-closing device. Generally three nets were used on the wire simultaneously. The data from each station is a composite of several lowerings until all the specified depths had been sampled. The ship at each station followed a parachute drogue suspended at 1,000 m in an attempt to remain with the same parcel of water. During the daylight hours only one crab was caught in a total of 57 plankton tows. At night, 54 tows were made and 84 crabs were caught; all of the crabs were caught in the upper 50 meters, and most of them were caught in the upper 10 meters. The single crab netted during the daytime was caught at 75 meters. It is possible that during the day the crabs were deeper than the

Figure 1. Graph showing the numbers of crabs caught at each hour interval of the day during the CalCOFI cruise in March, 1960.

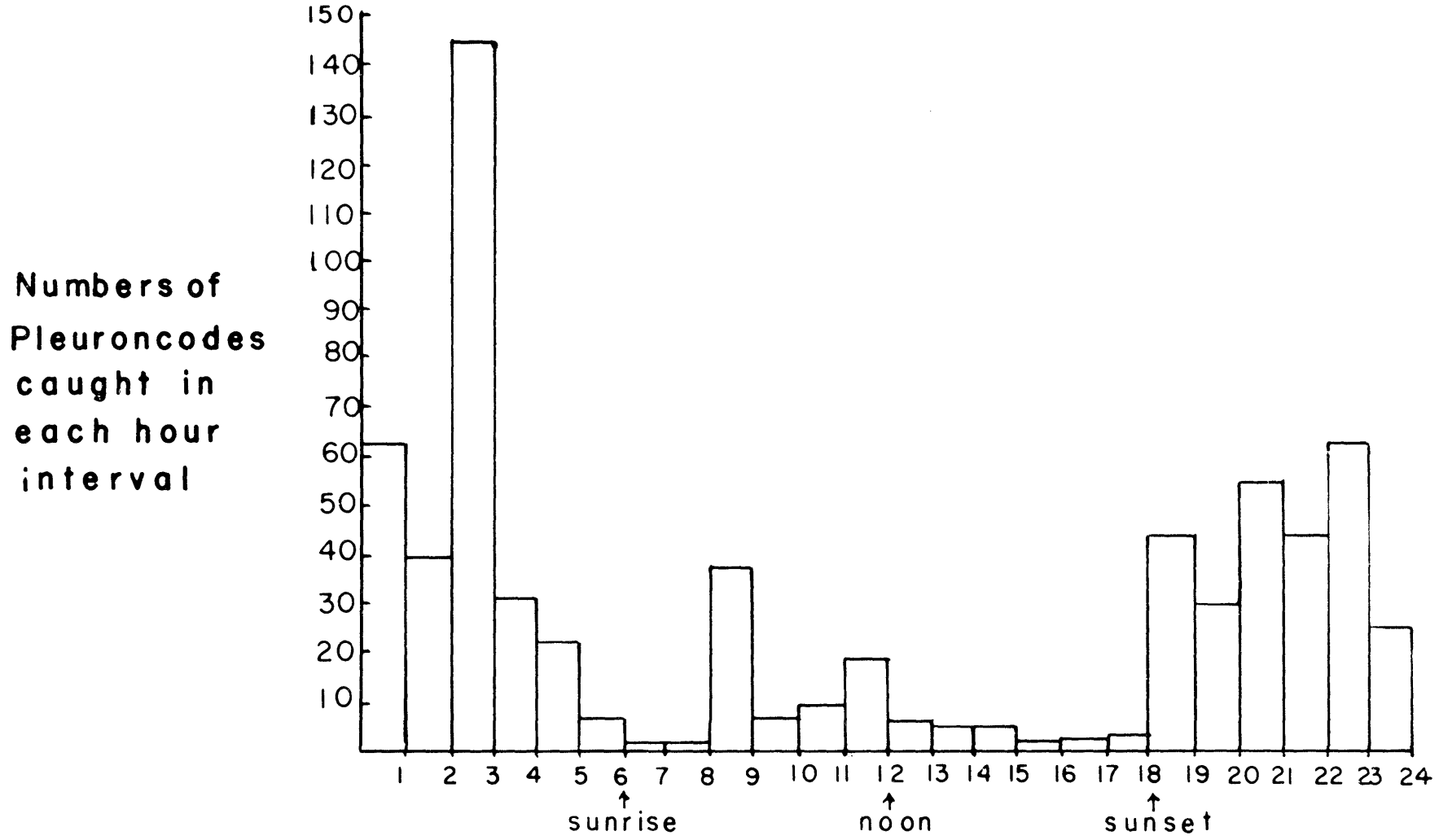

Numbers of Pleuroncodes caught in each hour interval
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
sunrise
noon
sunset
Time of Day in Hours
CalCOFI Cruise 6003, March, 1960

Table 1. Distribution with depth of *P. planipes* in the plankton in several day-night series of closing net plankton tows.

27° 14' N x 116° 34' W

27° 43' N x 115° 33' W

27° 33' N
115° 53' W

Depth in meters	11 June day	11 June night	12 June day	12 June night	13 June day	14 June day	14 June night	15 June day	15 June night	17 June day	17 June night
0	0	8	0	0		0	7	0	11	0	42
10	0	0		3		0	7	0	0	0	0
25	0	1	0	10		0	0	0	0	0	0
50	0	2	0	0		0	0	0	0	0	0
75	1	0		0	0	0	0		0	0	0
100	0	0	0	0		0	0	0	0	0	0
150	0	0	0	0	0	0		0	0	0	0
200		0	0	0		0	0	0	0	0	0
300	0	0	0	0		0	0	0	0	0	0
400	0		0	0	0	0	0	0	0	0	0
500	0	0	0	0		0	0	0	0		0
750					0				0		
1000	0										

Day

1 crab

57 tows

Night

84 crabs

54 tows

500-1,000 meters sampled in this series. An alternative solution, in many ways preferable, is that during the day the crabs were in the upper 500 meters, but were dispersed to such a degree that they were not caught, while at night they were concentrated in the upper 10 meters.

It is believed that in neritic waters of depths less than 300 m the animals settle to the bottom and assume a benthic mode of life during the day. They may or may not migrate to the surface at night. Not a single specimen of P. planipes was seen at the surface during a twelve day cruise to southern Baja California, in December, 1960, although thousands were caught in bottom trawls there. On a cruise to that same area in April, 1961, thousands of specimens were seen at the surface each night, while not a single specimen was obvious during the day.

At times great numbers of P. planipes are seen swimming at the surface of the ocean. The late Dr. Bell Shimada of the Inter-American Tropical Tuna Commission reported (personal communication) steaming through such numbers that the "ship seemed to crunch through them for at least ten miles." Numbers in excess of 100 per m^2 of water surface over broad areas have been seen and photographed. The swarms are commonly seen during the night, but also during the day, and their presence is not associated with seasonal breeding. It is believed that they are a consequence of crabs swimming up to the surface, chiefly at night, to feed in the rich surface layers. Dense aggregations, such as the record of

more than 100 per m^2 are perhaps a result of oceanic convergences; densities of from 1 to 10 crabs per m^2 are more common. The majority of the crabs in these swarms seems to be within the upper meter of water. These swarms are most often seen along the western coast of Baja California.

Occasionally large numbers of crabs are washed up on the beaches and mass mortalities result. Beach strandings have occurred throughout most of the known range of the crab's pelagic distribution. Many strandings were recorded from the San Diego area in 1958, where they had not been recorded for many years. The period of 1957 and 1958 in San Diego was remarkable for the intrusion of many species of pelagic animals from areas to the south. Strandings on the beaches south of Punta Eugenia are believed to be common.

The crabs involved in the strandings the author has observed have all been in the upper 50 cm of water in the surf zone. According to Inman (1952) there is a net transport of this surface layer of water onto a beach by breaking waves. This on-shore transport is balanced by water moving off-shore in fast-moving rip currents and also along the bottom. The beach, then, is the ultimate destination of any object floating in the near-shore surface waters. An on-shore wind and a receding tide hasten and intensify the stranding. When the crabs are once caught in the surf zone they are washed onto the beach by the up-rushing waters. When the wave recedes they soon die of dessication.

The numbers of crabs involved in the strandings may range from a few hundred specimens to many, many times that number. One report (Dr. George E. Lindsay, personal communication) from the Gulf of California notes the crabs occurring in windrows up to three feet deep and ten feet wide over a stretch of beach three to four miles long. The number of crabs involved in a stranding of this size would be astronomical.

Typically, strandings of the crabs seem to be merely cases of swarms of crabs swept onto the shore by adverse seas. One record is available, however, in which animals of other species were washed in with P. planipes in a manner suggesting a widespread mass mortality effecting several phyla. There was a "red tide" in the coastal waters at that time. This stranding occurred at San Bruno, south of Santa Rosalia, Baja California, in the Gulf of California, on March 29, 1960. Among the great windrows of crabs washed ashore was one rather large moray eel, Gymnothorax octavianus (Myers and Wade) and many ophiuroids, Ophiocoma aethiops Lutken, asteroids, Heliaster kubinjii Xantus, echinoids, Arbacia incisa A. Agassiz, and holothurians. These species characteristically live on a rocky intertidal and sub-tidal bottom (Steinbeck and Ricketts, 1941), and were presumably tossed up on the beach by the waves. The factor responsible for the death of the eel and the echinoderms was assumed to be associated with the red tide. However, the crabs were alive as they washed ashore, and it is possible that a stranding of crabs occurred coincidently with a red tide which

killed the other animals. (A series of laboratory experiments indicated that the "red tide" occurring off La Jolla in 1958 had no toxic effect on P. planipes. The principle alga in that bloom was Gonyaulax polyedra).

The distribution of Pleuroncodes planipes in the plankton

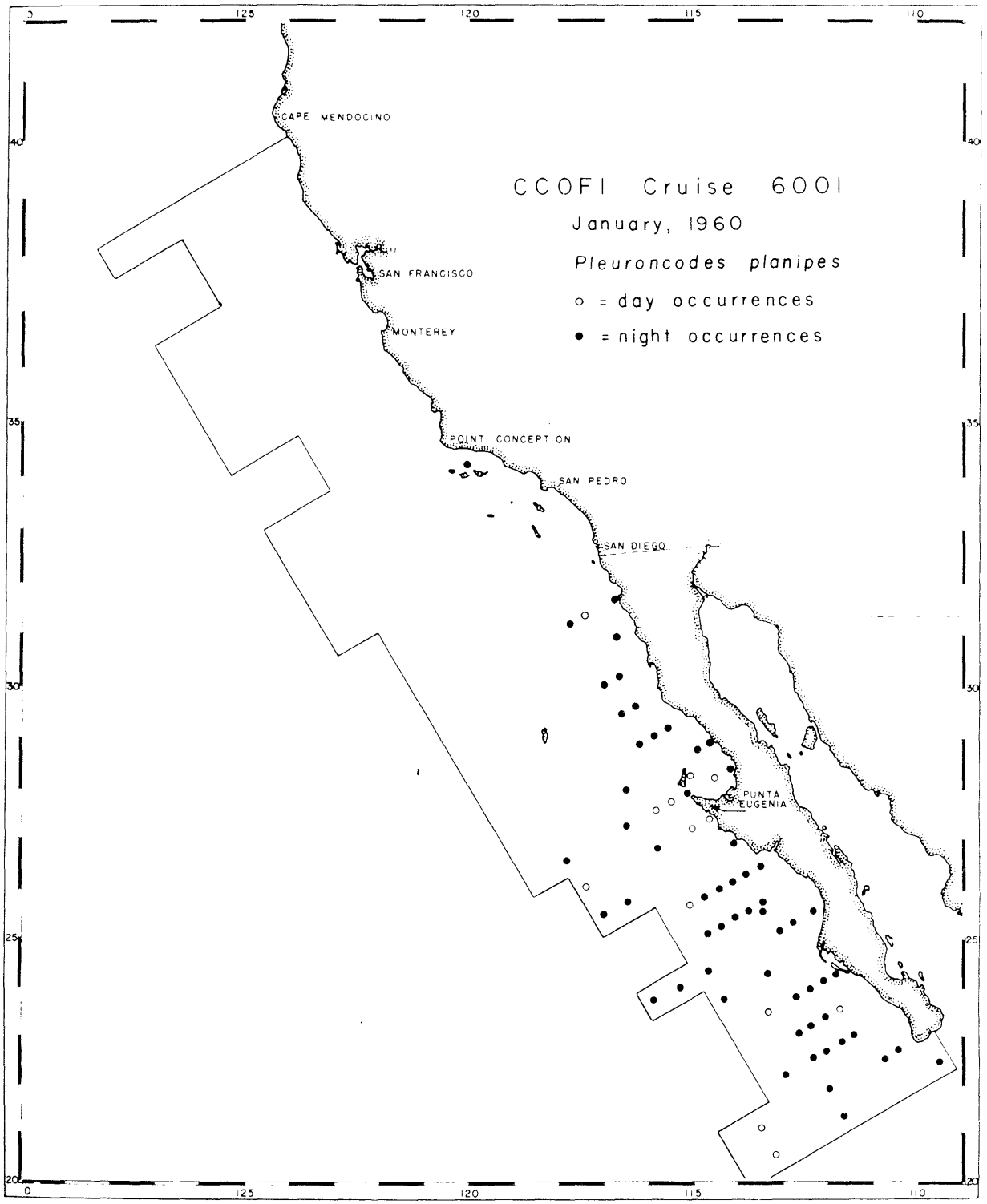
The partial distribution of adult P. planipes is shown in figures 2 through 9, based on cruises made monthly from January to August, 1960, into the California Current. The cruises were made as a part of the California Cooperative Oceanic Fisheries Investigations (hereafter abbreviated CalCOFI). The overall pattern of stations occupied during the eight months is shown in figure 10. At each station an oblique plankton tow was made with a meter net from 140 m depth to the surface, sampling about 500 m^3 of water. The boundary lines on charts 2 through 9 indicate the areas within which stations were occupied; the positions of stations in the area shown by figure 10. Only those stations at which adult crabs occurred are shown on figures 2 through 9; an open circle indicates a day-time capture, and a closed circle a night-time capture. This discussion is limited to data from these eight cruises because the sampling patterns of prior and subsequent cruises were abbreviated.

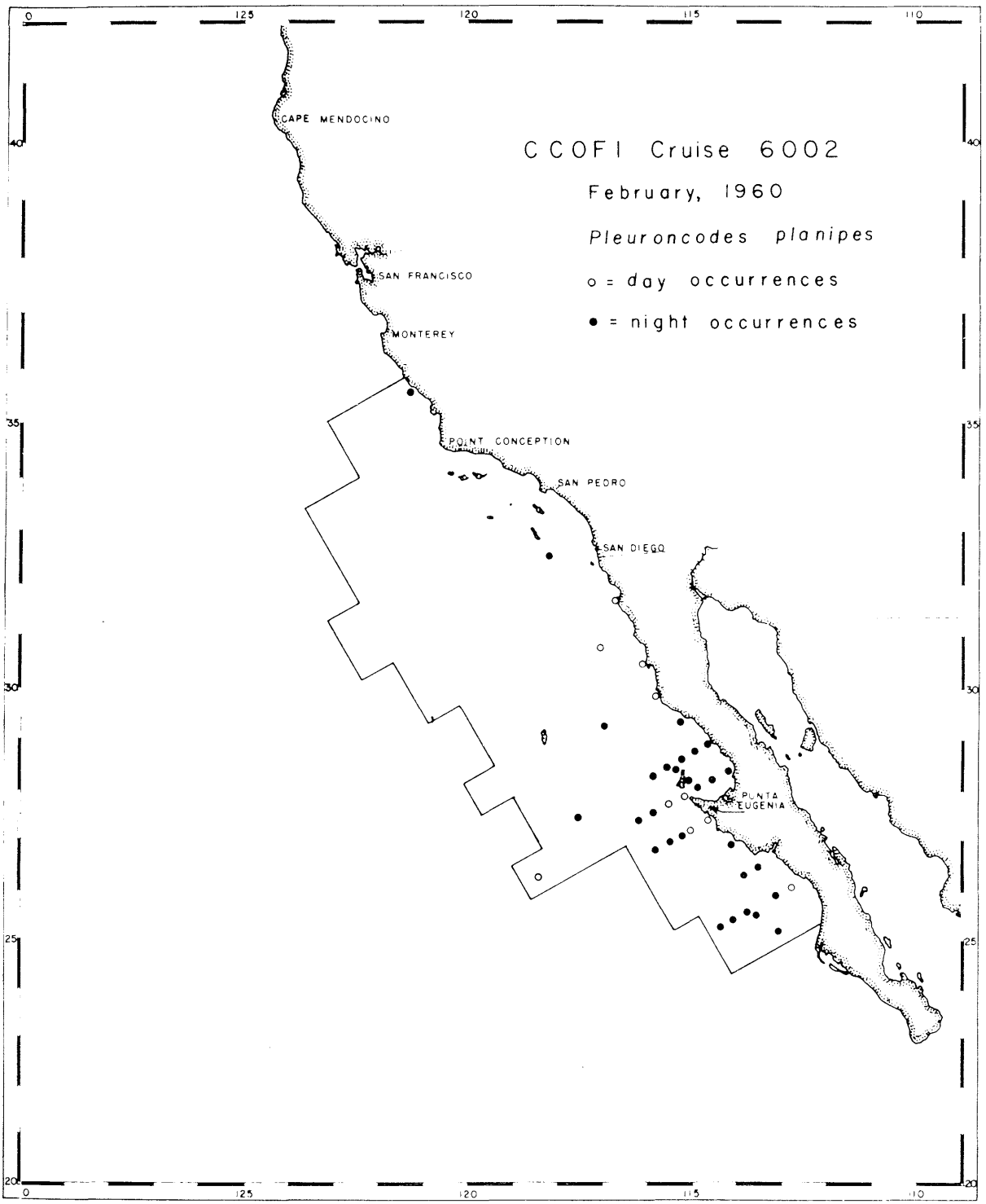
Four conclusions can be drawn from study of the distributional figures. The most obvious of these is that the center of distribution of P. planipes seems to lie on the continental shelf along the western side of southern Baja California. In that area the animals may be found abundantly swimming in the surface waters, as well as sitting on the bottom (see chapter on the benthic habitat). It is also apparent, by contrasting the numbers of open and closed circles that crabs are more often caught during the night than the day. The third item that can be seen is the isolated occurrence of

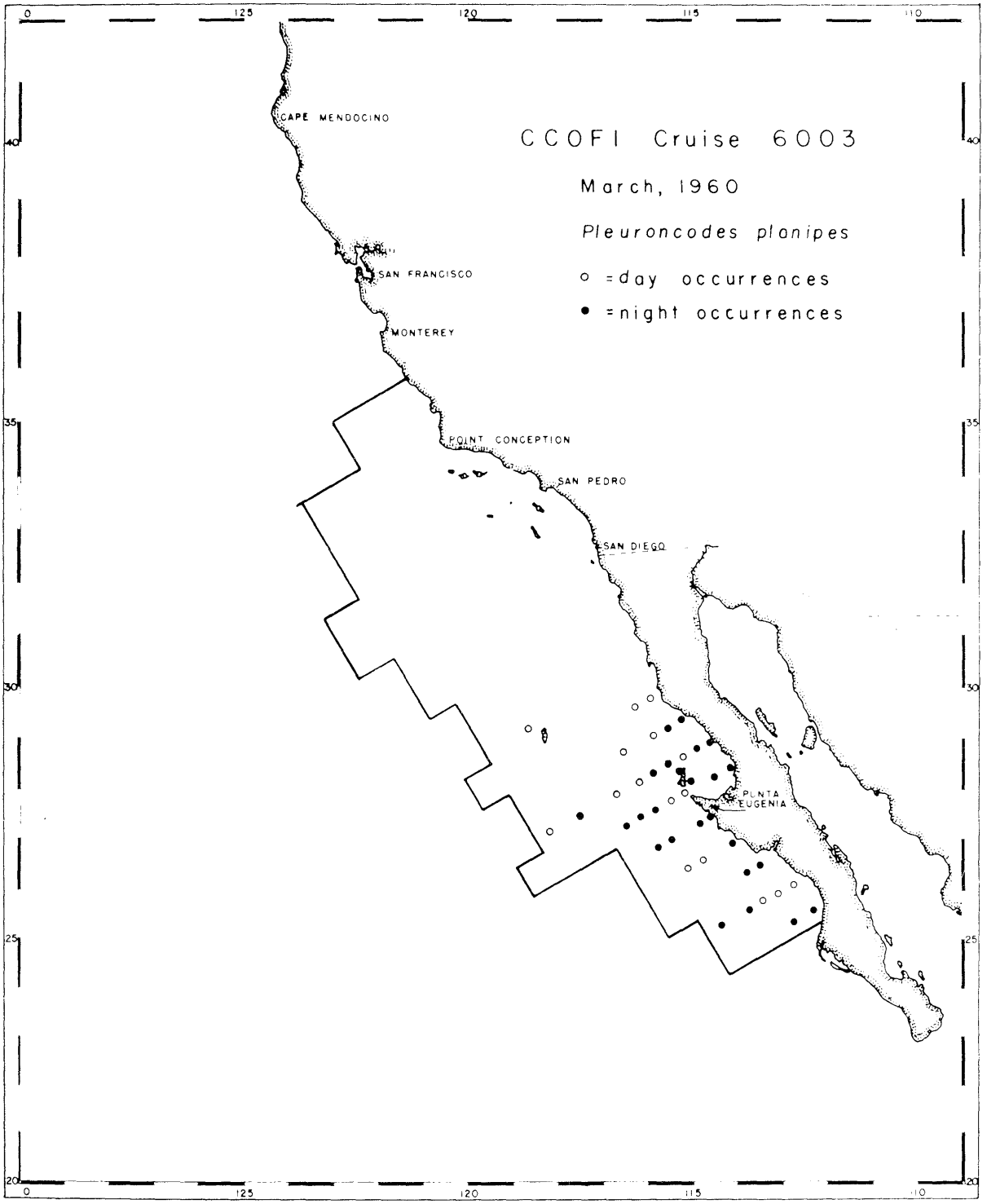
crabs in the areas off San Diego, and even north of Point Conception in cruises 6001 and 6602. These extreme northern occurrences indicate that in their pelagic mode of existence the adults are constituents of the plankton, and as such are distributed more or less according to the ocean's current patterns. It is also evident that the distribution of the crabs extends south of the CalCOFI pattern, so that the sampling to the south is open-ended.

The surface circulation along the western coast of Baja California is complex, but in general there are two currents, acting in opposite directions. The more obvious of these currents is the California Current, which sweeps in a southerly direction along the California Coast, and starts to swing westward in the latitude of southern Baja California. As it does so its hydrography and fauna gradually change, and it eventually becomes or joins the North Pacific Equatorial Current. The effect of this southwesterly swing of the California Current on the distribution of P. planipes can be seen by examining the chart of extreme records of the crabs, figure 11. All documented records of P. planipes fall within the outlined area. The westernmost record is from the original species description by Stimpson (1860), 24° N x 130° W, and is well within the North Pacific Equatorial Current. The few records from that western area indicate that the crabs are relatively scarce there. The few that have been found were probably swept away from coastal waters. These animals, caught in the Equatorial Current, must be

Figures 2 through 9. Occurrences of *Pleuroncodes planipes* in the CalCOFI cruise patterns, January through August, 1960.


CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
CCOFI Cruise 6001
January, 1960
Pleuroncodes planipes
○ = day occurrences
● = night occurrences
125
120
115
110
40
35
30
25
20


CCOFI Cruise 6002
February, 1960
Pleuroncodes planipes
o = day occurrences
● = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
0
125
120
115
110
40
35
30
25
20


CCOFI Cruise 6003
March, 1960
Pleuroncodes planipes
○ = day occurrences
● = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
0
125
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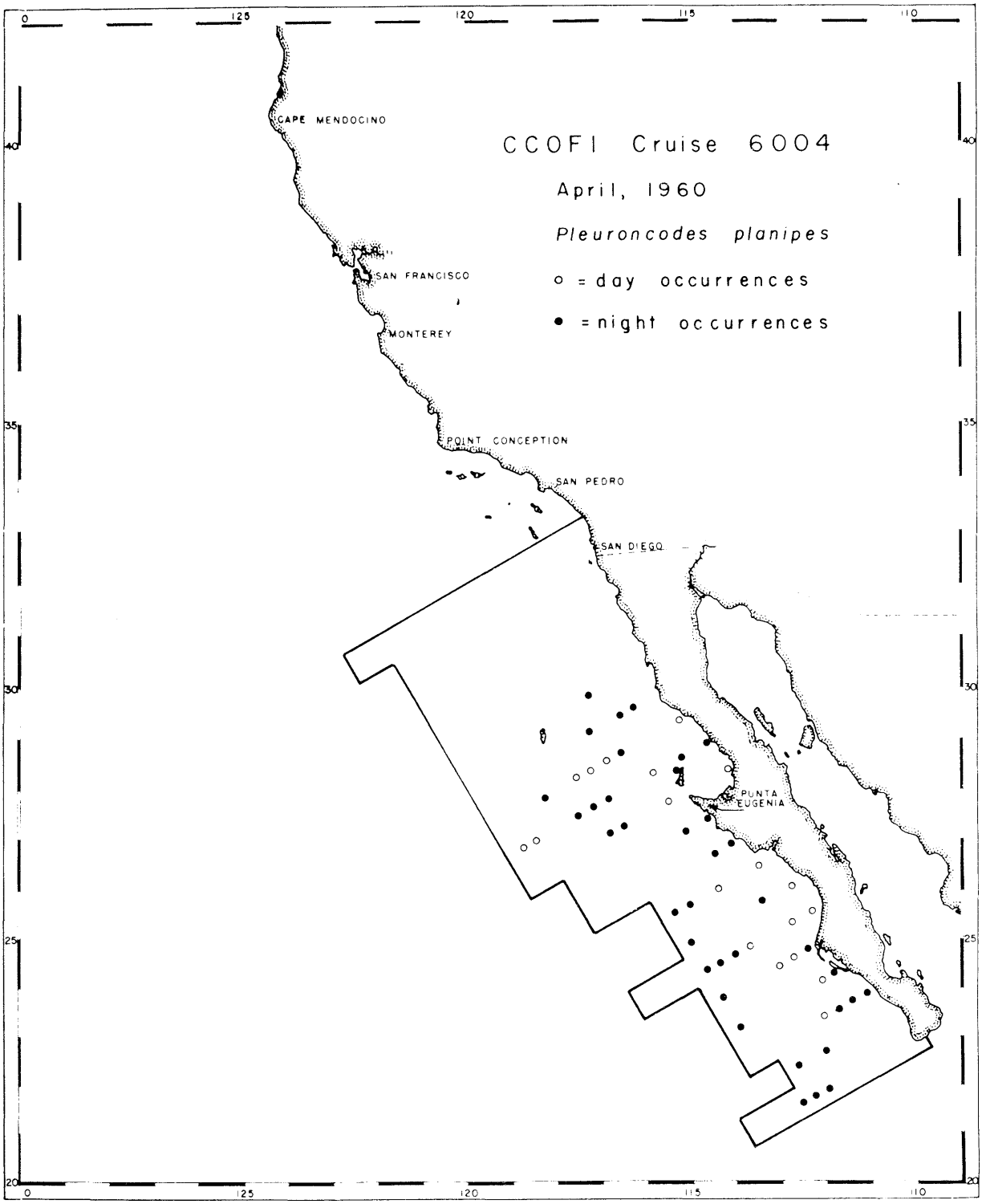
CCOFI Cruise 6004
April, 1960
Pleuroncodes planipes
o = day occurrences
• = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
0
125
120
115
110
40
35
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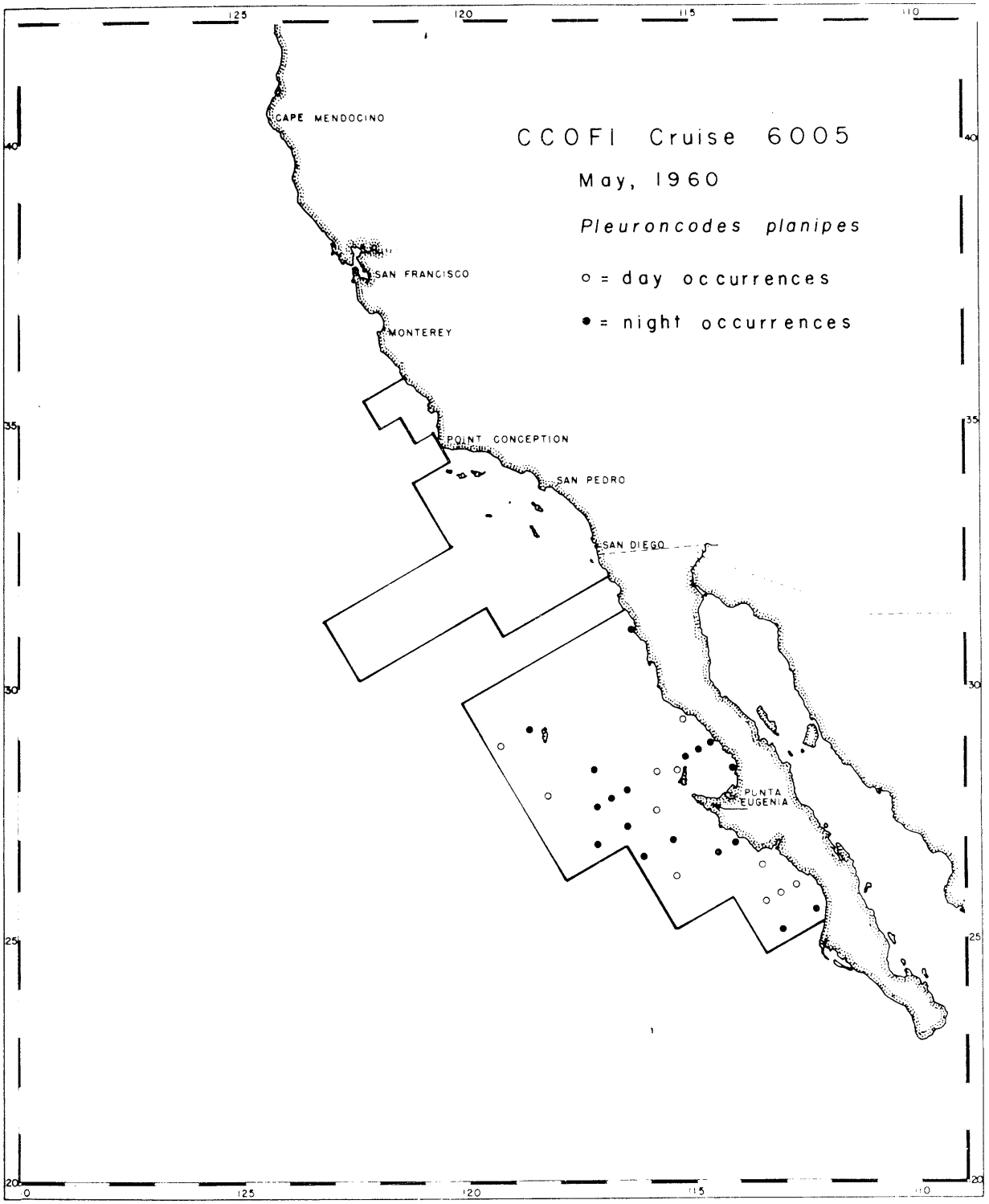
25
20


CCOFI Cruise 6005
May, 1960
Pleuroncodes planipes
○ = day occurrences
● = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
125
120
115
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20
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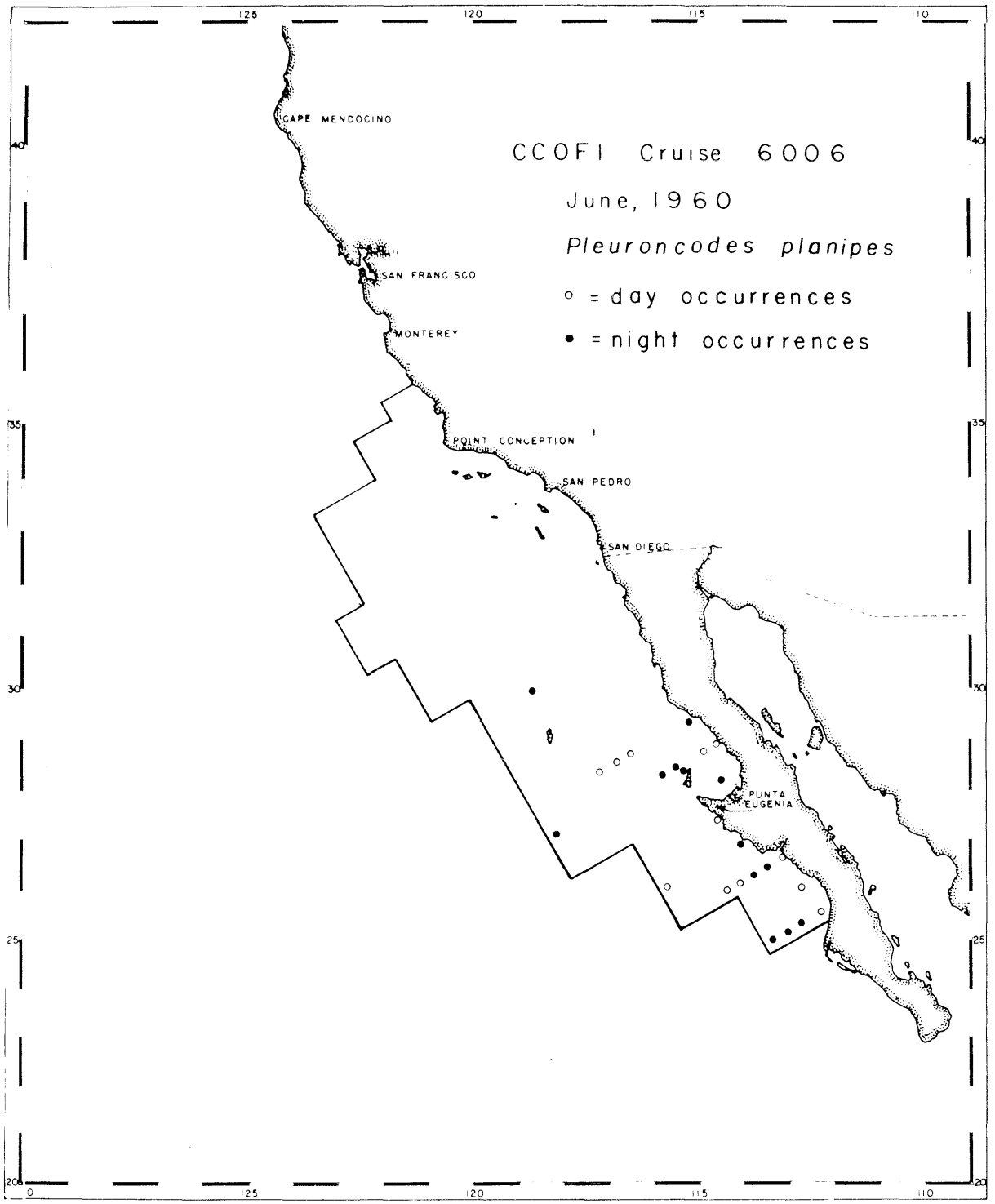
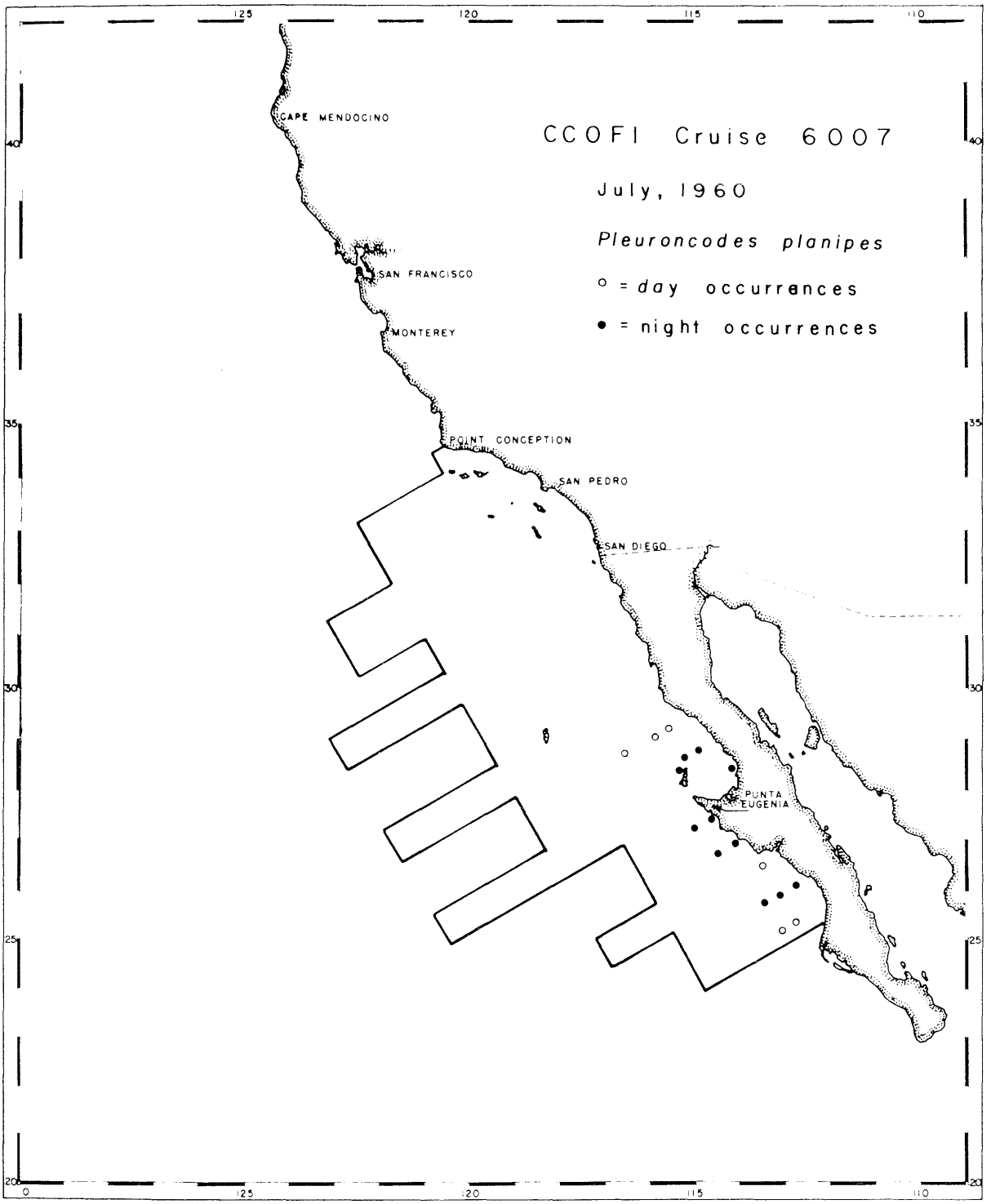

CCOFI Cruise 6006
June, 1960
Pleuroncodes planipes
○ = day occurrences
● = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
125
120
115
110
40
35
30
25
20


CCOFI Cruise 6007
July, 1960
Pleuroncodes planipes
○ = day occurrences
● = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
125
120
115
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35
30
25
20

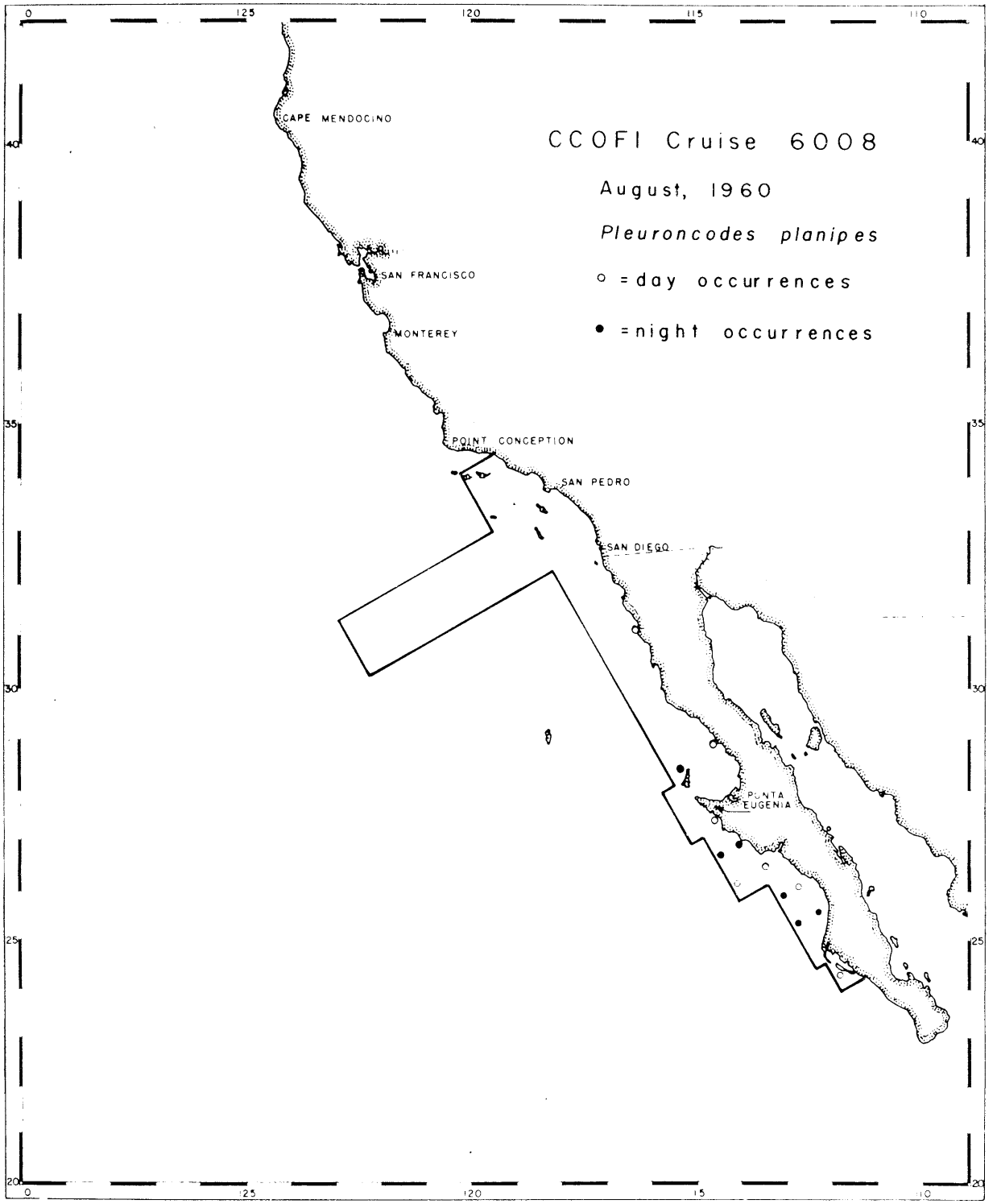

CCOFI Cruise 6008
August, 1960
Pleuroncodes planipes
o = day occurrences
• = night occurrences
CAPE MENDOCINO
SAN FRANCISCO
MONTEREY
POINT CONCEPTION
SAN PEDRO
SAN DIEGO
PUNTA EUGENIA
0
125
120
115
110
40
35
30
25
20

Figure 10. Base map of CalCOFI cruises between January and August, 1960, showing intensity and location of stations occupied.

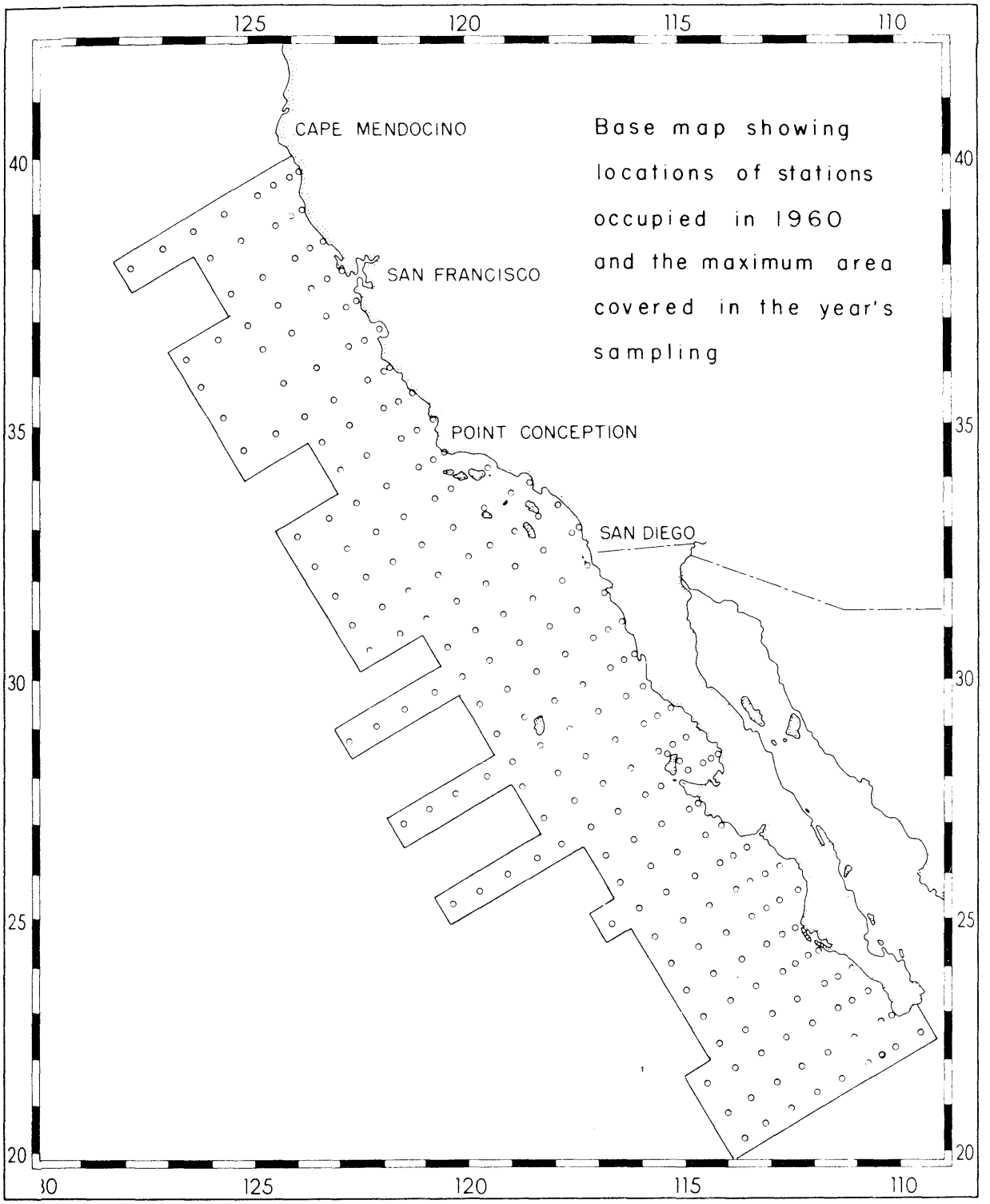
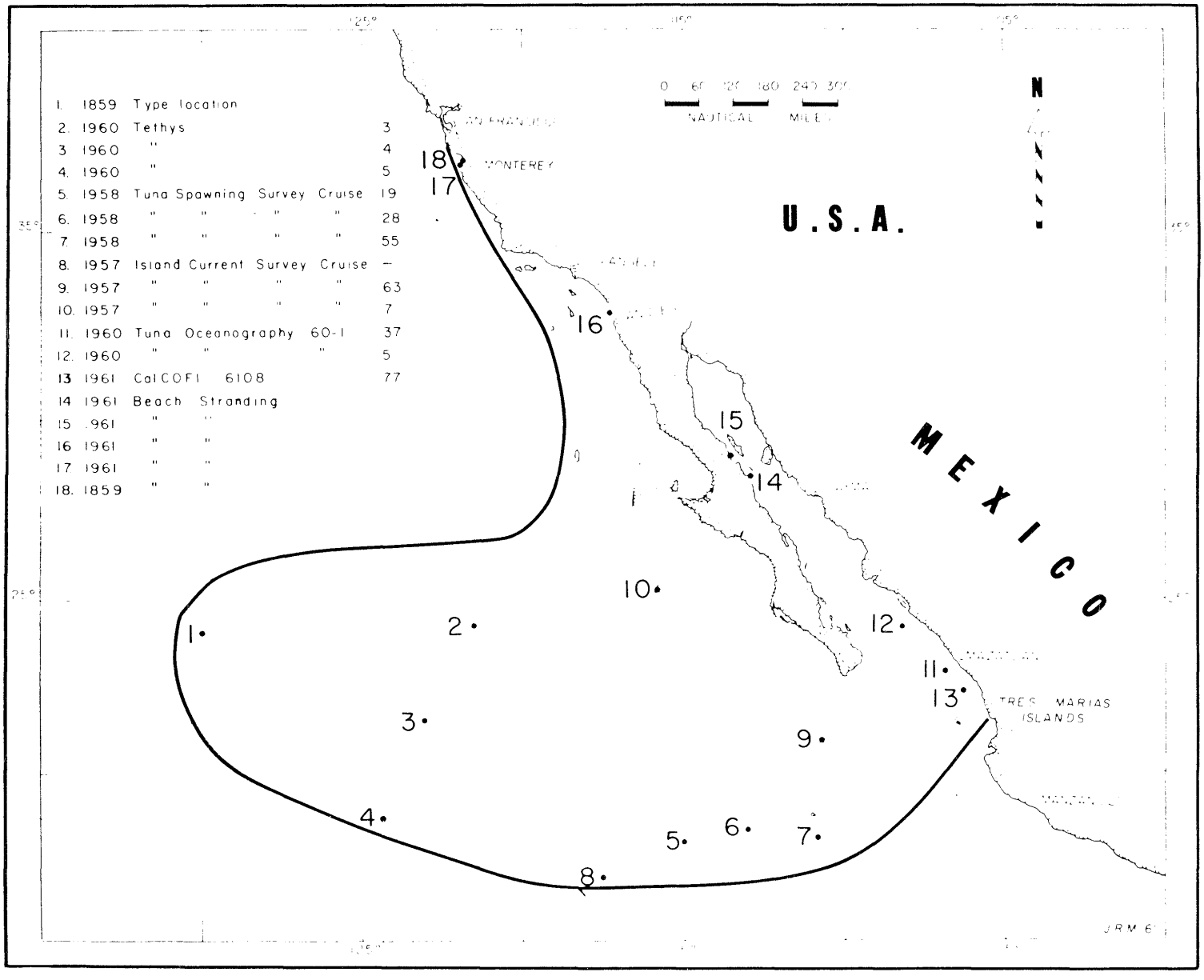

125
120
115
110
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
Base map showing locations of stations occupied in 1960 and the maximum area covered in the year's sampling
40
35
30
25
20

Figure 11. Chart of outlying occurrences of Pleuroncodes planipes and the limits of the distribution of the species. The shaded area indicates the area of greatest abundance.

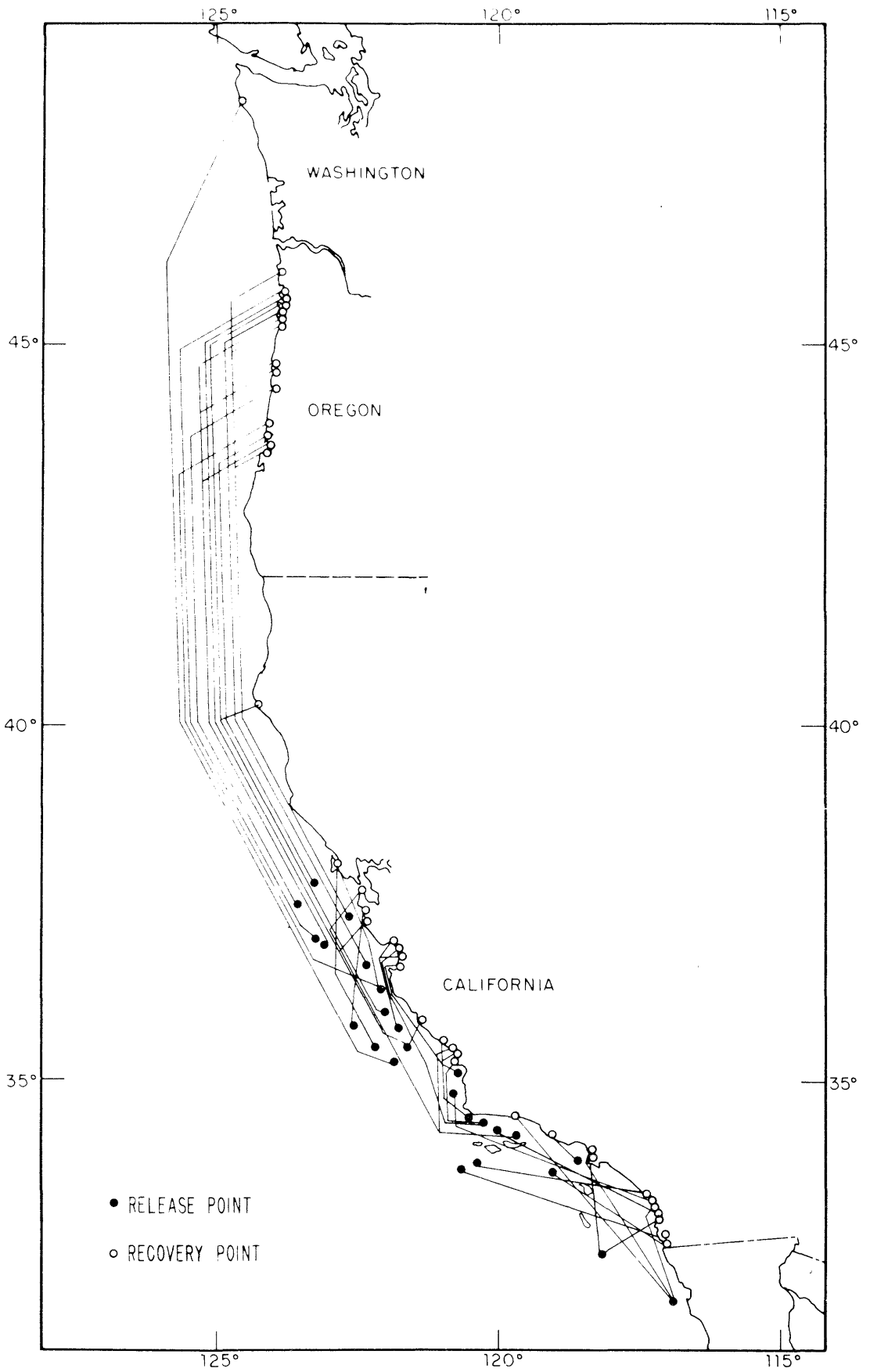

1. 1859 Type location
2. 1960 Tethys 3
3. 1960 " 4
4. 1960 " 5
5. 1958 Tuna Spawning Survey Cruise 19
6. 1958 " " " " 28
7. 1958 " " " " 55
8. 1957 Island Current Survey Cruise —
9. 1957 " " " " 63
10. 1957 " " " " 7
11. 1960 Tuna Oceanography 60-1 37
12. 1960 " " " 5
13. 1961 CalCOFI 6108 77
14. 1961 Beach Stranding
15. 1961 " "
16. 1961 " "
17. 1961 " "
18. 1859 " "
0 60 120 180 240 300
NAUTICAL MILES
N
U.S.A.
MEXICO
MONTEREY
TRES MARIAS ISLANDS

assumed to be expatriates which do not contribute further to the maintenance of the species.

The occurrence of P. planipes north of its center of distribution appears to depend upon a system of rather poorly understood northerly-moving counter-currents. This system is composed of three parts (for further discussion see Reid, 1960) which may have a common origin; 1) the Davidson Countercurrent, which flows northward very near shore between Point Conception and the Oregon-Washington area, 2) the Southern California Countercurrent, which moves nearshore waters northward from southern Baja California, evidently expanding into a gyre inside the islands off Southern California (see Johnson, 1939), and then moving northward very near to the shore around Point Conception, and 3) an under-current which transports deeper waters (at about 200 m depth) northward from Baja California. The under-current is the least understood of the three. The surface counter-currents are known to be seasonal, and have their strongest northward flow in January and February. The plot of drift bottles from the winter of 1958 shows quite well the effect these currents would have on free-floating objects (figure 12, from Reid, 1960). These counter-currents must account for the strandings of P. planipes on the beach at Monterey, California in the winter of 1859, as reported by Stimpson in the description of the species (1860), and again in 1960 as reported by Glynn (1961).

It has been assumed that the distribution of P. planipes is determined by the fluctuations of the currents, and that the animals,

Figure 12. Recoveries of some drift bottles released in January, 1958. Black squares show the release points, circles show the recovery points. (From Reid, 1960).


125°
120°
115°
WASHINGTON
45°
OREGON
40°
CALIFORNIA
35°
RELEASE POINT
RECOVERY POINT

despite their benthic affinities are at times truly planktonic. Certainly there seems to be an obvious similarity between the current pattern and its changes and the distribution of P. planipes (see figure 11). It is, however, possible that when animals are found in a new area it may be because they have actively migrated into it; the migration being possible because the currents had previously carried water with suitable temperatures, food, etc., into the area. If, however, an individual P. planipes were actively to swim from Punta Eugenia to Monterey it would take some 55 days to make the journey, at a constant velocity of 0.5 knots. Such continued swimming exertion seems unlikely for an animal that has such strong ecological ties to the benthic habitat. Probably the distribution of P. planipes in the plankton is the result of both active migration and passive transport, with the latter being the more important.

At the southern tip of Baja California there is often an oceanic front, generally tending south or southeast (Cromwell and Reid, 1956). On the western side of the front one finds the relatively cold turbid waters of the California Current; on the eastern side the water is several degrees warmer and often has the clear blue color by which some people characterize "tuna waters." This warmer water is part of a poorly defined body of water known as the Eastern Tropical Pacific water mass, perhaps a part of the larger Equatorial Pacific water mass (Roden and Groves, 1959). It extends southward to Ecuador, and tapers off to a point at about

140° West longitude. The most south-western record of P. planipes (No. 1 on figure 11) probably resulted from a transitory breakdown of the front, allowing the crabs to move into the area. Many additional plankton samples have been taken in this region, but P. planipes has been only rarely caught. The few animals found there should be considered as expatriates living under suboptimal conditions. Further to the south the conditions may change from suboptimal to lethal.

The distribution of the crabs in the Gulf of California is less well documented because the CalCOFI program sends only occasional cruises into the Gulf. The available data indicate that the crabs sometimes occur in the Gulf in abundance; large shoals of crabs have been found even in the northern half. The crabs found in the Gulf may have been swept in from areas on the western side of the peninsula as a consequence of the sporadic exchange of water between the California Current and the Gulf of California (see charts presented by Cromwell and Bennett, 1959). The alternative explanation is that the crabs are able to find areas within the Gulf which are suitable as benthic habitats even though the continental shelf there is almost completely lacking and the shoreline drops off precipitously to depths of many hundred fathoms. Certainly the occurrence of crabs in the Gulf is poorly understood, and both dredgings and plankton tows are needed to fill in the answers.

The benthic habitat

Perhaps the most interesting single question that was posed in the study of Pleuroncodes planipes was whether or not the animal was benthic at any period of its life. Certainly the animal has evolved from stock that was benthic, for of the 230 described species of the family Galatheidae only two species other than P. planipes are ever pelagic as adults--and those two only to a limited degree. (They are Munida subrugosa and M. gregaria, in antarctic waters, Matthews, 1932). P. planipes, however, has been regarded as a strictly planktonic animal since its description in 1869, which was based on specimens found swimming at the surface some 1130 km off the Mexican coast, and also from specimens washed ashore from the plankton by a winter's storm at Monterey, California.

Specimens of P. planipes freshly dipnetted from surface water immediately settle to the bottom of ship-board aquaria and assume a benthic mode of existence which is in sharp contrast to their pelagic life of a few moments earlier. Those crabs which werekept in laboratory aquaria for growth studies lived almost entirely as benthic animals. It was felt that the question of whether the crabs were benthic in nature could not be answered fully or conclusively by observations in aquaria or by experimental work, but only by evidence from the field. A dredge was therefore designed and built which would remain closed while it was being raised or lowered, thereby avoiding capturing pelagic specimens, but which would open upon contact with the bottom.

The center of the distribution of P. planipes in the pelagic phase, as discussed earlier, is off the western coast of southern Baja California. The bright coloration of the animals, their well-developed eyes and known depth distributions of other Galatheidae suggested that the animals, if benthic, were most likely to be benthic along the continental shelf rather than at abyssal depths. The bottom fauna on the continental shelf of Baja California has been essentially unsampled; the deeper waters in that latitude had been sampled in the dredging program of the "Albatross."

With these facts in mind, a cruise was planned to the shelf area in the region of 26° N latitude in November and December, 1960. On this cruise the following sampling and measuring devices were used at most of the stations occupied: (1) an closing-opening dredge with a mouth opening 1/2' x 2', (2) a 10 foot otter trawl, (3) a series of meter plankton nets which were towed horizontally, with one net close to the bottom, another intermediate in depth, and the third at the surface. The two sub-surface nets were rigged with the Leavitt opening-closing device, and were open only while being towed at their specific depths, (4) a 900 foot bathythermograph, (5) a series of seven Nansen bottles spaced throughout the water column; the water from these samplers was titrated by the standard Winkler method for dissolved oxygen content.

On November 30, 1960, at the first station, with a water depth of 58 fathoms, a 15-minute tow of the dredge collected 23 specimens of P. planipes mired within a ball of gray mud. The ten foot otter

trawl, towed on the bottom for 25 minutes at the same location, caught an estimated 300 pounds of the crabs. A 10 minute tow with the series of plankton nets caught one crab at the surface and none at the two lower depths. It seemed, then, that P. planipes was benthic, and abundantly so.

During the cruise 19 meter net tows were made (each two consisting of a single net). After sampling at the first station the plankton tows were lengthened to 20 minutes, each net sampled about 800 m^3 of water. A total of seven crabs were caught in the plankton tows. The otter trawl, with a mouth width of ten feet, probably sampled no more than five times as much water as the meter net when towed for 25 minutes. However, the difference in catch between the plankton net and the trawl was always so great it seems likely that, during this cruise, essentially all of the crabs caught in the otter trawl were benthic, even though the trawl remained open while it was being raised and lowered. This was substantiated by the opening-closing dredge which, with an opening only about 12% of that of the meter nets, caught several times as many crabs.

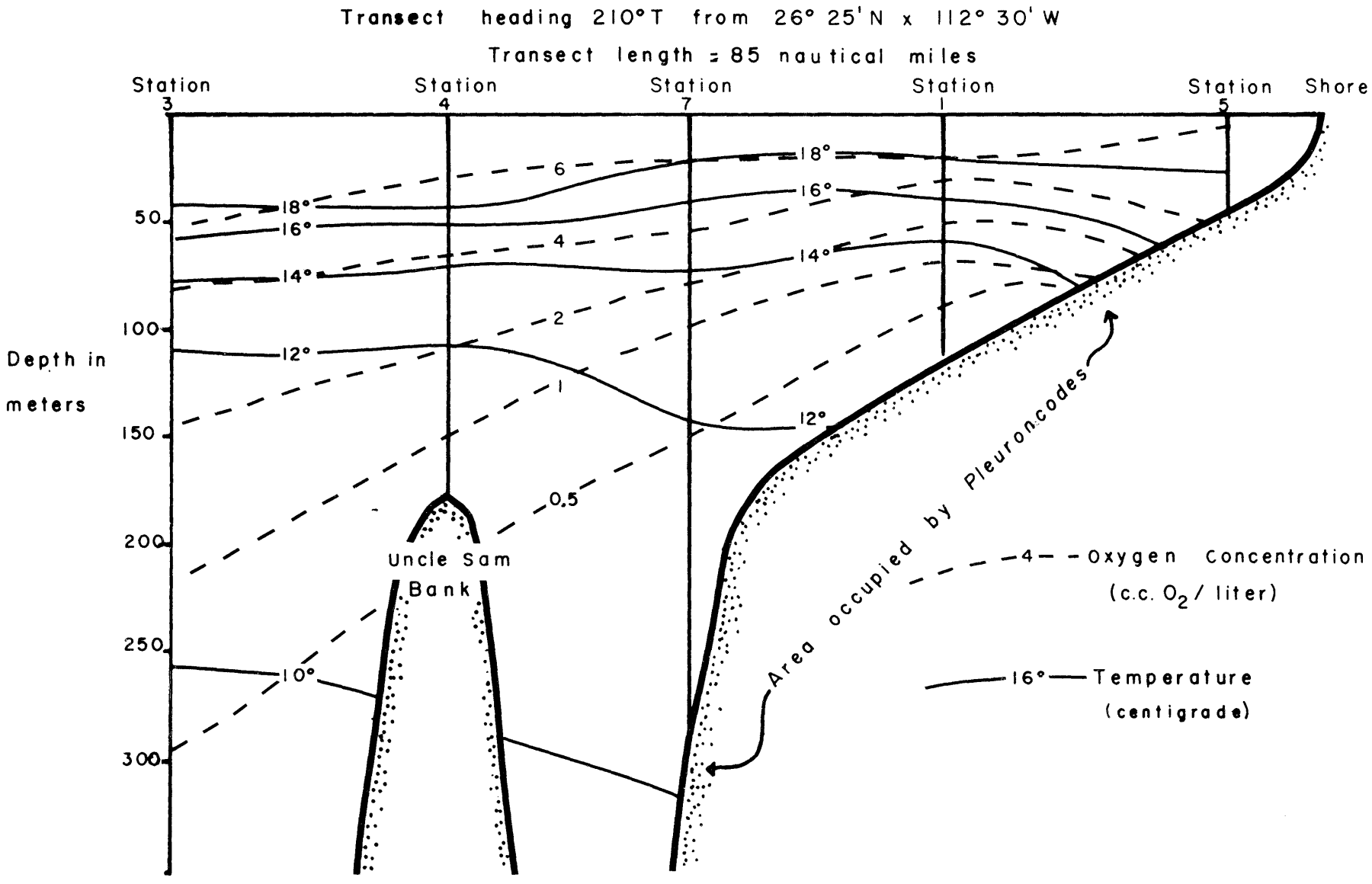
Bottom samples for P. planipes were taken at thirteen stations during the cruise. At a latitude of 26° N the crabs were found abundantly on the bottom between depths of 75 and 300 meters. The substrate at those depths ranged from a gray mud to a gray sandy mud. The edge of the continental shelf in the area is at a depth of about 200 meters. P. planipes was not found on the deeper bottoms down the continental slope where naked rock, solitary

corals, crinoids occurred. Figure 13 presents the distribution of crabs with depth, together with the hydrographic data based on five stations taken while heading on a course of 210° T, from the point 26° 25' N 112° 30' W. The western-most station was 85 nautical miles from the shore. Other stations occupied during the cruise supported the general picture. No specimens of P. planipes were caught on Uncle Sam Bank, which is quite rough and rocky. Trawls made recently at the base of the continental slope in that area, at depths of 1700 fathoms, where the sediments are again fine, also caught none of the crustaceans.

Considerable numbers of two other species of invertebrates were collected with P. planipes. One of these was a two cm long white holothurian, Cucumaria chilensis Ludwig, identified by Dr. Elisabeth Deichmann, of the Museum of Comparative Zoology, Cambridge, Massachusetts. P. planipes, which is a voracious omnivore, did not eat the holothurias when placed with them in ship-board aquaria. The other abundant invertebrate was a gastropod, Nassarius miser Dall, identified by Mr. Emery P. Chace of the San Diego Museum of Natural History. There were very few worm tubes or other animals in the bottom sediments. It is probable that the constant sifting over of the substrate by P. planipes in their search for food would reduce the numbers of any invertebrate animals having no defense against the crabs.

No crabs larger than 26 mm standard carapace length had ever been found in the plankton collections, and it had been assumed

Figure 13. Vertical profile showing temperature structure, bathymetry, oxygen concentration, and the distribution of Pleuroncodes planipes along the western coast of Baja California, Mexico, at a latitude of 26° N in December, 1960.


Transect heading 210°T from 26° 25'N x 112° 30' W
Transect length = 85 nautical miles
Station 3
Station 4
Station 7
Station 1
Station 5
Shore
Depth in meters
50
100
150
200
250
300
18°
16°
14°
12°
10°
6
4
2
1
0.5
Uncle Sam Bank
Area occupied by Pleuroncodes
4 — Oxygen Concentration (c.c. O_2 / liter)
16° — Temperature (centigrade)

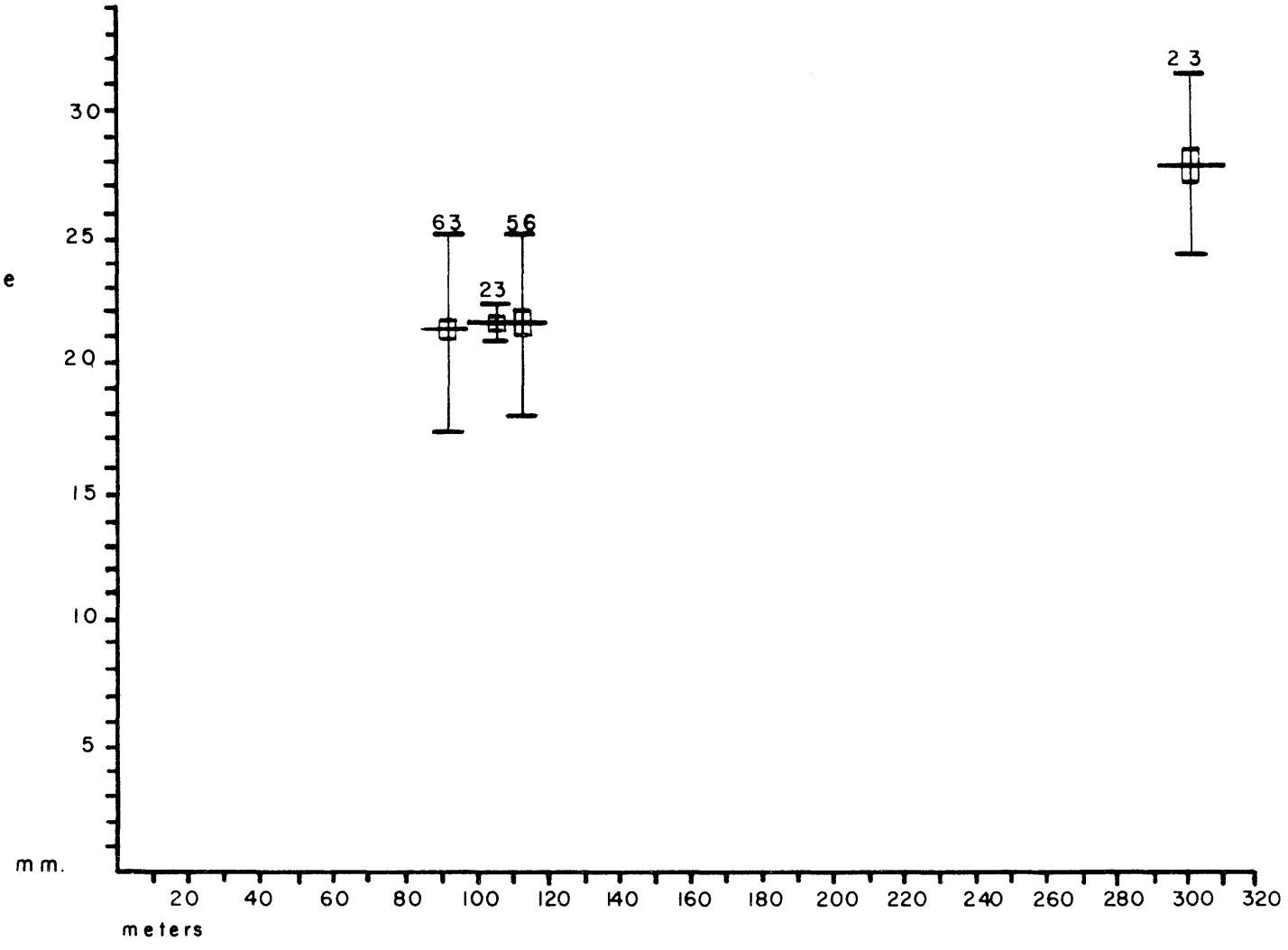
that this was their maximum size. According to the growth curve (figure 21), crabs with this carapace length would be between one and two years old. However, at the deepest station at which the crabs were still caught (300 meters) the otter trawl and the closing dredge brought up crabs of larger size; the mean standard carapace length of the crabs was 27.9 mm, and the maximum standard carapace length was 32.0 mm. The position of this size on the theoretical growth curve (circle on figure 21) suggests that these larger crabs, living along the edge of the continental shelf, constitute an older year class, and are probably in their third year of life. Since none of this size has been taken in the plankton, they are presumably exclusively benthic at this age. Figure 14 presents the lengths of the large crabs, contrasted with the other crabs caught on the same cruise at shallower depths. The means of the two categories are significantly different at the 5% level.

It appears, then, that P. planipes lives to some extent on the bottom in its first two years of life and is also found as a planktonic animal at this age. The relative amount of time that it spends in these two environments is unknown, but data indicate that there is at least a diurnal component, with crabs spending the nights in the surface waters and settling to the bottom during the day-time hours, when a suitable bottom is available.

The numbers of crabs per square meter on the bottom cannot be accurately determined from the data available. A rough estimate may be derived, however, by regarding the ten foot otter trawl as a

Figure 14. Graph showing the different size categories of *P. planipes* at varying depths of water. December, 1960.

Standard carapace length of crabs caught at each station.
28 November to 6 December, 1960



Depth of capture of *Pleuroncodes*

quantitative sampling device. At one station the trawl was towed for twenty-five minutes at two knots; it should have traversed a distance of 5080 feet, and sampled 50,800 square feet. An estimated 400 to 500 pounds of crabs were taken, no scales for weighing were available, but weight estimates by several people fell within this range. One hundred crabs of the size caught in the trawl weighed 0.956 pound. These values give an estimate of 0.8 to 1.0 crabs per square foot of bottom or 9 to 11 crabs per square meter. Estimated densities for other stations were similar.

During the December, 1960 cruise, P. planipes was limited to the west by the continental slope, and to the east by approximately the 75 meter depth contour. Samples were taken from 25° N to 31° latitude but no crabs were found north of Punta Eugenia (25° 50' N), even though the trawl was towed on bottoms which were similar in sediment and depth to those further south. Sampling on a cruise in April, 1961, showed the crabs to be present on the bottom at 24° N, to the south of our original transect. It is probable that they are found southward to the tip of the peninsula. Their benthic distribution in the Gulf of California is completely unknown but the crabs have been seen at the surface in the Gulf, and have also been washed ashore there in great numbers. It is therefore quite possible that there is a benthic population in the Gulf where the proper depth, substrate, etc. occur.

The feeding habits of Pleuroncodes planipes

The bulk of the contents of the gut of fresh specimens of P. planipes taken near the surface is a green amorphous mass which presumably is phytoplankton; a few diatom tests can be seen as well as occasional fragments of crustacean remains, such as setae, bristles, etc. To determine how well P. planipes can filter phytoplankton, several experiments were performed using cultures of known cell density of single species of algae (not bacteria-free) labeled with Carbon-14. Individual crabs were allowed to feed on the cultures for known lengths of time and then killed, and the gut with its contents were dried and assayed for radio-activity. The sample was combusted and counted as CO_2 in a vibrating reed electrometer, (Dynacon, model 6000, Nuclear-Chicago). The three species of algae used were Dunaliella salina, diameter about 10 μ; Gonyaulax polyedra, diameter about 80 μ; and Dytilium brightwellii, an elongated cell measuring about 30 μ by 70μ. Gonyaulax and Dytilium were detectable in the gut contents of the crabs when the cells were present in the cultures at densities of about 1,000 and 400 cells per ml respectively; these are densities which are common in the neritic waters of the ocean. Dunaliella, however, could be assayed in the guts of the crabs only when the density of the suspension upon which the crabs had fed was 10^5 or more cells per ml. P. planipes does, then, have the ability to filter out phytoplankton, but presumably cannot feed on the nannoplankton--of which Dunaliella is a representative--unless the cells occur in unusually

high densities. It seems probable that the bulk of the amorphous green mass in the gut contents of P. planipes is made up of the larger phytoplankton species.

P. planipes filters phytoplankton and small zooplankton by a filtering mechanism intimately associated with the respiratory mechanism used to pump water past the gills. This pumping is primarily accomplished by the scaphognathite (the exopod) of the second maxilla, which extends laterally from the mouth back into the branchial cavity. The scaphognathite, as it beats with a sinusoidal motion, draws water into the branchial cavity from the ventro-lateral margin of the carapace near the basal segments of the walking legs. The water is drawn anteriorly over the gills and is forced out at the antero-lateral margin of the carapace, near the mouth parts. This respiratory current is essentially continuous. In comparison with the maxillipeds of two near relatives, Galathea squamifera and G. dispersa, discussed and figured by Nicol (1932), the maxillipeds of P. planipes are more copiously setose. This is perhaps a partial adaptation to life as a pelagic phytoplankton feeding animal. The mouth parts which do the actual filtering of the food are the endopods of the second and third maxillipeds. These structures extend ventrally and posteriorly, and in effect form a basket of setae, with the mouth and its overlying mouth parts in the middle of it. Food particles moving forward in the respiratory current are sieved out by the maxillipeds and passed on to the mouth.

An additional current, essentially an acceleration of the respiratory current is produced intermittently by the beating of the exopods of the second and third maxillipeds. This activity can be initiated by pipetting a suspension of food particles (copepods, Artemia nauplii, algal cells, etc.) into the water around the crab. This current is quite strong; in turbid waters the effects of the jet can be seen for 12-15 cm in front of the animal.

An experiment was run to determine the rate at which P. planipes could filter copepods from the water. Four adult crabs were placed individually in 1500 ml of sea water with 750 live specimens of Tigriopus californicus, a spray-zone harpacticoid copepod. After the crabs had been allowed to feed for an hour in the dark they were removed and the remaining copepods were counted. The number eaten gave an estimate of the filtering rates of the crabs; these estimates ranged from 270 to 660 ml water filtered per hour, and had a mean value of 400 ml per hour. In the area of the ocean where the crabs are most abundant, adults and juveniles of calanoid copepods occur in the euphotic waters at densities averaging perhaps 150 per cubic meter (values probably range from 15 to 1500 per cubic meter; Dr. Abraham Fleminger, personal communication). A crab filtering copepods at a rate of 0.4 liters per hour, at these densities, would filter out about 2 copepods per day, (probable range 0.15 to 15 copepods per day). The dietary or caloric demands of P. planipes are completely unknown but this is almost certainly not enough food. Values can be computed on the basis of available respirometric data,

but they pertain only to resting crabs, and probably have little bearing on the nutritional needs of crabs swimming actively in surface waters.

The ability to filter phytoplankton and small zooplankton would be useful to P. planipes when it is swimming in surface waters where such food is available. However, the crabs spend part of their life in the benthic environment, where presumably phytoplankton and zooplankton are not abundant enough to constitute a food supply. The crabs in this habitat are able to work over the bottom sediments, sifting out the food material that is present there (e.g. nematodes, polychaetes, etc.). This method is common to many galatheids and involves the use of the endopod of the third maxilliped as a rake to lift up the sediment and pass it to the anterior mouthparts. Food material is sifted out and ingested, and the refuse is rejected.

The crabs can also use the large chelipeds and strong mandibles to feed upon organisms far larger than themselves, putting them into the broad categories of scavengers and even predators. They are highly cannibalistic in captivity. In the laboratory the crabs have been observed to eat salps, which may be a natural food. In general, P. planipes seems to be able to feed in several manners and upon a wide variety of foods.

Pleuroncodes planipes as food for other animals

Individuals of *P. planipes* are large, and often obvious, very abundant components of the plankton. Data from several sources indicates that the species constitutes a considerable proportion of the diet of many marine carnivores.

In an analysis of the food habits of the albacore (*Germo alalunga*) caught off California and Baja California, McHugh (1952) stated that *P. planipes* comprised about 11% of the total volume of the contents of albacore stomach examined in his study. Albacore caught in areas where *P. planipes* is more abundant had a higher percentage by volume of *P. planipes* in the stomach contents (13% to 43%). In a recent paper on the food habits of the yellowfin tuna and the skipjack tuna, Alverson (1962) presents charts which give the percentage composition of yellowfin tuna stomach contents in several oceanic areas. *P. planipes* constituted 78.1% of the volume of the tuna's stomach contents in the area along the western coast of Baja California (approximately the area outlined in figure 5). Around Alijos Rocks (24° 57' N, 115° 45' W) the percentage was as high as 97.5% over the several months duration of his study. *P. planipes* amounted to 34.1% of the volume of the stomach contents of all the yellowfin tuna caught and sampled in the entire Eastern Pacific Ocean, and occurred in 39% of the stomaches he examined. Presumably both the albacore and the yellowfin tuna feed on *P. planipes* when it is planktonic, for the two fishes are not known to be bottom feeders.

Quast (1962) noted that in the spring of 1959 P. planipes was commonly found in many of the fish stomachs he examined during his study of the kelp bed fishes off La Jolla, California. Among those fishes were the kelp bass (Paralabrax clathratus), the sheepshead (Pimelometapon pulchrum), various rockfishes (Sebastodes spp), the senorita (Oxyjulis californica), and the sculpin (Scorpaena guttata). P. planipes is not usually found in the La Jolla area, but in the Spring of 1959 many swarms of the crabs were swept northward from their usual southern habitat. Whenever swarms of P. planipes are swept into a region those fishes living there feed heavily on them. The yellowtail (Seriola dorsalis) and white sea bass (Cynoscion nobilis) have also been found to feed on P. planipes at the Coronado Islands, Baja California, Mexico. Bottom fishes are also known to feed on P. planipes. Mr. Paul Sund, University of Washington, reports (personal communication) that while fishing off San Diego, California, in water 330 feet deep he caught boccacio (Sebastodes paucispinis), lingcod (Ophiodon elongatus), the barber pole fish (S. rubrivinctus), and various other bottom species, all gorged with P. planipes.

The gray whale (Eschrichtius gibbosus) has also been reported to feed on P. planipes (Matthews, 1932). This whale spends most of its life in cold waters of the western North Pacific, but migrates to Baja California waters in the winter for breeding. Matthews relates information received from a whaler, Captain Fagerli, and writes "In 1926 at Magdalena Bay on the Pacific coast of Mexico

where shoals, presumably of Pleuroncodes planipes, were seen, the Sei, Humpback and Pacific Grey, but not the Blue whales, were found to be feeding on these crustacea. Captain Fagerli noticed that the blubber oil obtained from Sei whales on the Patagonian and Mexican coasts was always of a definitely yellowish colour, quite unlike that obtained from this species elsewhere. He believes that the difference in colour is produced by feeding on lobster-krill." Scammon (1874), however, writing on the gray whale, noted "To our personal knowledge, but little or no food has been found in the animal's stomach. We have examined several taken in the lagoons, and in them we found what whalers called "sedge" or "sea-moss" (a sort of sea-cabbage)...." Howell and Huey (1930) reporting on a single individual killed at Trinidad, in northern California, noted that many specimens of Euphausia pacifica were found "within its mouth and among its baleen," and conjectured that it had been feeding on the crustaceans. Trinidad, however, is considerably north of the normal distribution of P. planipes. It remains a moot point whether gray whales off Baja California feed on P. planipes; certainly the crabs are abundant there and would constitute a ready food supply.

The California sea lion (Zalophus californianus) also feeds on P. planipes, as do many birds. Among the birds that have been observed eating the crabs at the water's surface are the western gull, the California gull, Heermann's gull, Bonaparte's gull, elegant fern, and the brown pelican. This crustacean probably comprises a large part of the diet of many sea birds along southern Baja California.

Reproduction

Adult Pleuroncodes planipes females carry their eggs attached to their pleopods in the same manner as brachyuran and other anomuran crabs. Specimens in the laboratory bred and laid eggs readily; the eggs produced were carried for 6 to 22 days (generally about 14 days). During that time the eggs changed from a golden color to a dark amber, as the eyes of the embryos developed. All the larvae hatched out as swimming Stage I zoeae, and once hatching began all the eggs carried by a female hatched within about 12 hours. Females carry up to 3650 eggs (the largest number counted in this study); larger females tend to have more eggs than smaller females. Females kept isolated from males occasionally produced eggs, but these were invariably sterile, and were sloughed off from the pleopods within a few days. Records of individual females in the laboratory indicate that each female usually had two, and rarely three, broods of eggs per season. Females in the laboratory generally molted within a few days after their eggs hatched. Sexual maturity, as denoted by the ability of the females to produce eggs, was attained at a size of 14-15 mm standard carapace length. Females of that size are about 12 months old.

In the laboratory the egg bearing season lasted from November through April, with the peak in February. Table 2 shows that the egg-bearing season in the field followed a similar pattern.

The numbers of males and females caught in the CalCOFI plankton tows differed significantly from 50/50 at the 0.01 level, as tested by the signed ranks test, two tailed. The average percentage observed was 53.85% males, and 46.15% females. The reasons for this departure from the 50/50 sex ratio are not known, but the departure may result from one or more of the following: 1) more males may be hatched than females, 2) females may have a lower survival rate than males, or 3) the plankton nets may not sample males and females with equal effectiveness.

Table 2. Numbers and ratios of male and female Pleuroncodes planipes caught in the monthly CalCOFI plankton samples. The number of these females which were carrying eggs is also given.

Cruise	Number & percent males		Number & percent females		Number & percent of those females gravid		Month
5812	13	(54)	12	(46)	0	(0)	December
5901	293	(55)	241	(45)	27	(11)	January
5902	169	(51)	161	(49)	58	(36)	February
5903	16	(24)	24	(60)	0	(0)	March
5904	186	(58)	133	(42)	0	(0)	April
5905	111	(51)	106	(49)	0	(0)	May
5906	89	(52	83	(48)	0	(0)	June
5907	193	(51)	186	(49)	0	(0)	July
5908	400	(60)	291	(40)	0	(0)	August
5909	46	(52)	42	(48)	0	(0)	September
5910	140	(55)	113	(45)	0	(0)	October
5911	3	(100)	0	(0)	0	(0)	November
5912	0	(0)	2	(100)	1	(50)	December
6001	199	(59)	141	(41)	41	(29)	January
6002	168	(61)	106	(39)	59	(56)	February
6003	324	(49)	334	(51)	133	(40)	March
6004	413	(55)	341	(45)	2	(.6)	April
6005	180	(46)	208	(54)	0	(0)	May
6006	71	(52)	66	(48)	0	(0)	June
6007	106	(57)	79	(43)	0	(0)	July
6008	87	(51)	84	(49)	0	(0)	August
Total	3207		2753				

Larval development of *Pleuroncodes planipes*

In 1960 I described and figured five larval stages of *P. planipes*, based on specimens taken from the plankton in neritic waters off southern Baja California. The five stages were morphologically discrete, and it was assumed that each stage was passed through in a single molt. Since then the larvae have been reared through all larval stages to adulthood. This laboratory data supports the validity of the five stages described and adds a great deal of information concerning the larval development.

The rearing techniques used in this study are similar to those described by Broad (1957 a and b), Coffin (1958), Costlow and Bookhout (1959), and Rees (1959) who used them with other crustacean larvae. They involve the use of antibiotics to reduce the numbers of contaminating bacteria in the larval cultures, and also the use of *Artemia* nauplii for larval food. Freshly hatched larvae of *P. planipes*, taken from adult females kept in the laboratory, were pipetted into their various containers filled with sea water from the end of the Scripps pier. The water had been filtered through glass wool to remove detritus and larger animals that might prey upon the larvae.

Experiment 1; started 19 February, 1960; duration 74 days. A total of 200 freshly hatched larvae were placed ten per container in 20 one liter styrene plastic containers, each holding 500 ml of water and antibiotics. The antibiotics used were 1) 50 mg/liter streptomycin (trade name "Combistrep" by Pfizer, dihydrostreptomycin

and streptomycin sulfate, powder), and 2) 50 mg/liter penicillin, (penicillin G, by Abbot, pill form, buffered with $CaCO_3$, 928 units per mg, ground to a powder before use). This penicillin was used because earlier experiments indicated that the more readily available penicillin (a mix of 75% procaine penicillin and 5% penicillin G) was toxic to crab larvae. The containers were placed in trays of flowing sea water, which held them at temperatures ranging from 15° C in February to 18° C in June. Larvae were transferred to fresh sea water twice each week, and freshly hatched Artemia nauplii were added at that time. In the process of transferring the larvae into the fresh medium, each was drawn up into a 2 mm bore glass pipette and examined through the pipette under a low power dissecting microscope to determine its stage.

Experiment 2; started 1 March, 1960; duration 74 days. A total of 100 larvae, ten in each of ten containers, were treated similarly to the larvae in Experiment 1, except that the penicillin was omitted; streptomycin was used in concentrations of 50 mg/liter; temperatures ranged from 15° to 18° C.

Experiment 3; started 12 April, 1960; duration 108 days. Ninety-three larvae were kept individually in plastic containers in 50 ml sea water; 50 mg/liter streptomycin was added. Temperature, 16° to 19° C. Larvae were fed, transferred into new medium, and examined as in the preceding experiments. The containers were checked daily for molts, and the molts were removed and preserved in glycerine on slides.

Results of Experiments 1, 2, and 3

The experiments proved that the larvae could be reared through all larval stages in the laboratory, and gave information concerning the total duration of the larval phase. The data are summarized below:

Exp.	Shortest period to megalops	Longest period to megalops	Average	Survival to megalops
1.	54 days	68 days	61 days	7/200 = 3.5%
2.	53 "	74 "	64 "	56/100 = 56%
3.	71 "	110 "	87 "	15/93 = 16%

Each of the seven larvae to reach the megalops stage in Experiment 1 and one of the 56 resultant megalops crabs in Experiment 2 passed through a new stage, VI. This stage has never been seen in a search of hundreds of larval specimens from the plankton. It was similar in morphology to Stage V, but was larger and characterized by a tuft of plumose setae on each of the pleopods. It is probable that it was an artifact of treatment, and its presence was due either to the penicillin or to the $CaCO_3$ buffer in the pills used, for other conditions were similar. As later experiments involving mixtures of non-buffered penicillin and streptomycin did not give Stage VI larvae, it is possible that the carbonate was the cause.

It was noted in the first two experiments that Stage IV took more time than the other stages. Modal values in Experiment 2 were: Stage I, 9 days; Stage II, 8 days; Stage III, 8 days;

Stage IV, 25 days; and Stage V, 12 days. The mean durations could not be calculated because larvae were followed as a population, and not as individuals. It was suspected that Stage IV consisted of at least two molts, but the exact number of molts or the morphological differences between molts could not be determined because the history of individual specimens could not be followed. Experiment 3 was set up to make it possible to follow individual specimens through the larval stages.

Although the volume of water per larva was identical (50 ml) in each of the three experiments, and other conditions were the same in Experiments 2 and 3, the duration of the larval phase was longer in Experiment 3 than in either Experiment 1 or 2 (cf. data presented above). The three average values cannot be compared in the usual manner because the duration of the larval period in Experiments 1 and 2 is not known for individual larvae, and a variance cannot be calculated. A comparison of the ranges, however, indicates that the values for Experiment 3 differ significantly (at better than the 0.05 level) from the values for Experiments 1 and 2, but that the latter do not differ. The slightly greater temperature of Experiment 3, if it had any effect, should have caused a shortening of the larval period (see below). The only parameter in the three experiments which was known to be very different was the isolation of individual larvae in Experiment 3 versus their group rearing in Experiments 1 and 2. This difference had two components: the larvae had less total water in which to swim though the volume of water per larva was identical, and they

were not in association with other larvae. Either may have prolonged the larval phase in Experiment 3.

By following the molting sequence of individual larvae it became evident that the number of molts passed through before a larva becomes a megalops varied from larva to larva. The morphology of Stages I, II, and III in the laboratory was as had been described in the 1960 description based on larvae taken from plankton collections. Each of these stages was passed through in a single molt. Stage IV, however, was divided into a series of what can be called sub-stages, each separated by a molt, but all morphologically within the general description of Stage IV. The larva increased in size through the sequence of sub-stages, and the number of setae on some of the appendages (e.g., uropods, antennal scales) increased, but the differences between the various sub-stages of the complex were so inconsistent that a sub-stage could be identified with certainty only by knowing how many molts the larva had passed through. The number of molts within the Stage IV complex varied from four to nine. The percentage of larvae passing through each sub-stage is given below:

IVa = 100%	IVe = 82%
IVb = 100%	IVf = 65%
IVc = 100%	IVg - 59%
IVd = 100%	IVh = 29%
	IVi = 2% (died before reaching Stage V)

The mean duration of each of the larval stages and the 95% confidence limits of the sample, the cumulative elapsed time to the end of each particular stage, the number of larvae completing each stage, and the instantaneous death rate based on $N_t = N_0 e^{-dt}$ are given below:

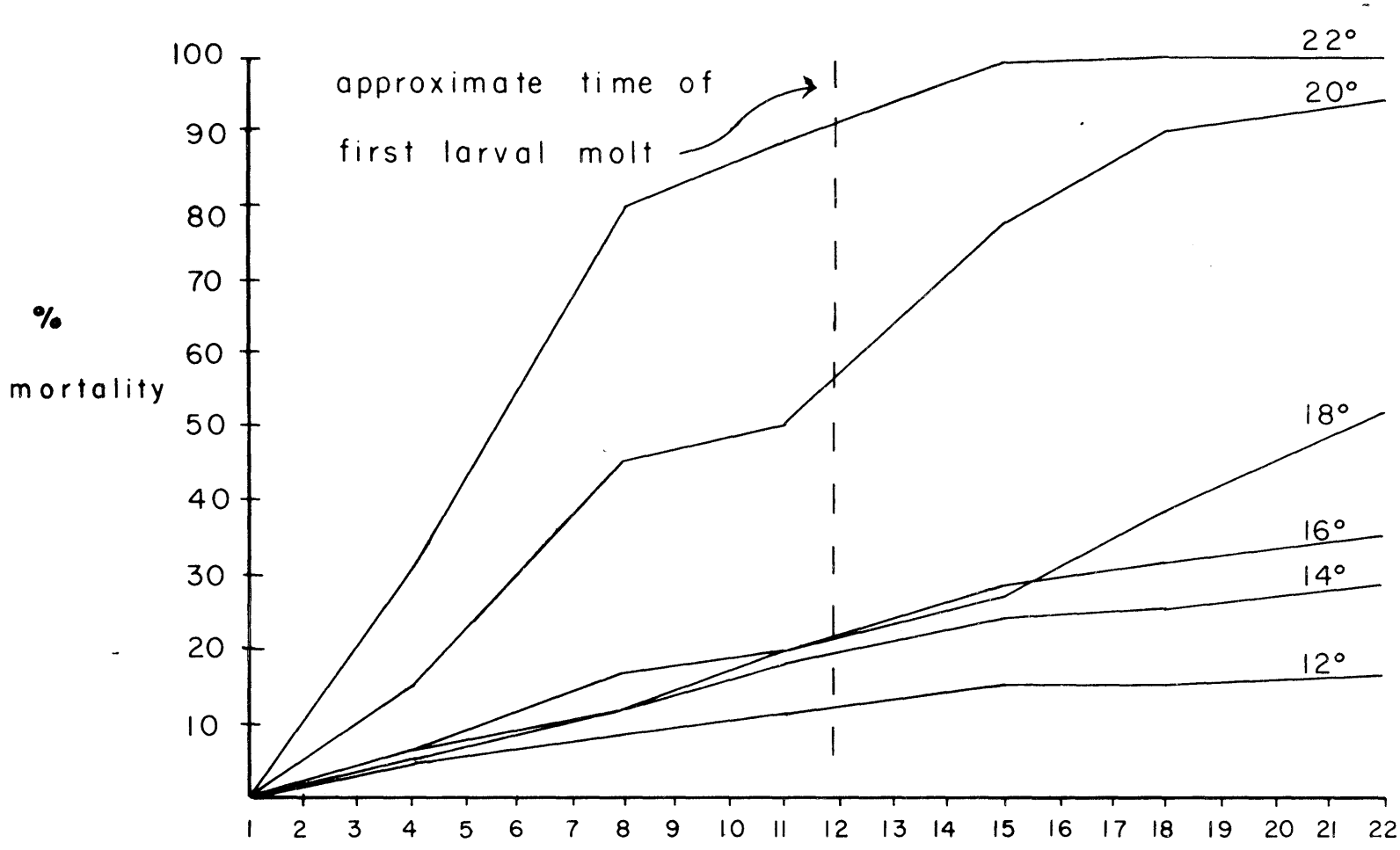
Stage	Mean and 95% limits (days)	(days)	N	Instantaneous death rate (days)
I	11.9 ± 5.7	11.9	46	0.059
II	8.0 ± 4.5	19.0	45	0.003
III	7.4 ± 5.7	27.3	41	0.013
IVa	6.9 ± 3.8	34.2	39	0.007
IVb	6.7 ± 5.9	40.9	36	0.012
IVc	7.4 ± 4.3	48.3	32	0.016
IVd	8.8 ± 5.4	57.1	28	0.015
IVe	8.7 ± 4.4	65.8	22	0.016
IVf	11.1 ± 6.6	76.9	18	
IVg	9.8 ± 4.7	86.7	16	
IVh	10.0 ± 4.0	96.7	8	
V	13.7 ± 6.6	86.9	15	0.000

The instantaneous death rate cannot be tabulated for individual stages subsequent to sub-stage IVd, for the deletion of stages is confused with mortality in the data analysis. It is evident from the table that the highest death rate occurred in the first stage, and mortality after that was essentially equal one stage to the next.

Experiment 4; started 25 April, 1960; duration, 163 days. Methods: a device was designed and constructed which maintained larval cultures at six constant temperatures. The temperatures selected were 12°, 14°, 16°, 18°, 20°, and 22° C. The two extreme temperatures selected are approximately the surface temperatures of, respectively, the northern and southern ends of the distributional

range of the adults in the spring months. Larvae were placed in sea water containing 50 mg/liter penicillin (Pfizer, penicillin G, potassium; 1,585 units/mg powder) and 50 mg/liter streptomycin (Combistrep, by Pfizer). Larvae were transferred into fresh sea water twice each week, and at that time were staged under the microscope and fed as in the previous experiments. The larvae were kept in styrene containers, each containing 18 compartments which measured 4.5 x 5.0 x 3.8 cm deep and held 50 ml of sea water. Six containers were used at each temperature; initially two larvae were placed in each compartment, giving 216 larvae at each temperature, or a total of 1296 larvae. All of these larvae were obtained from the same female over a period of about 12 hours. The extra larva was placed in each compartment because Experiment 3 had shown that mortality was highest in the first few days. It was hoped that enough to fill the tray compartments would be alive after this initial period. After 22 days the extra larvae in the 12°, 14° and 16° cultures were discarded, leaving individual larvae (108 total) in the compartments; mortality had been higher at the higher temperatures so that only 101 larvae remained at 18°; 16 larvae at 20°; and none at 22°. The mortality data for the first 22 days is shown in figure 15 : The estimated instantaneous death rates through Stage I (0-11.9 days) are: 12°, 0.011; 14°, 0.018; 16°, 0.020; 18°, 0.020; 20°, 0.074; 22°, 0.192. No larvae survived to the megalops stage in either the 20° or 22° cultures; these temperatures may therefore be regarded as lethal in this experiment.

Figure 15. Mortality of larvae of *Pleuroncodes planipes* reared in the laboratory at several constant temperatures.



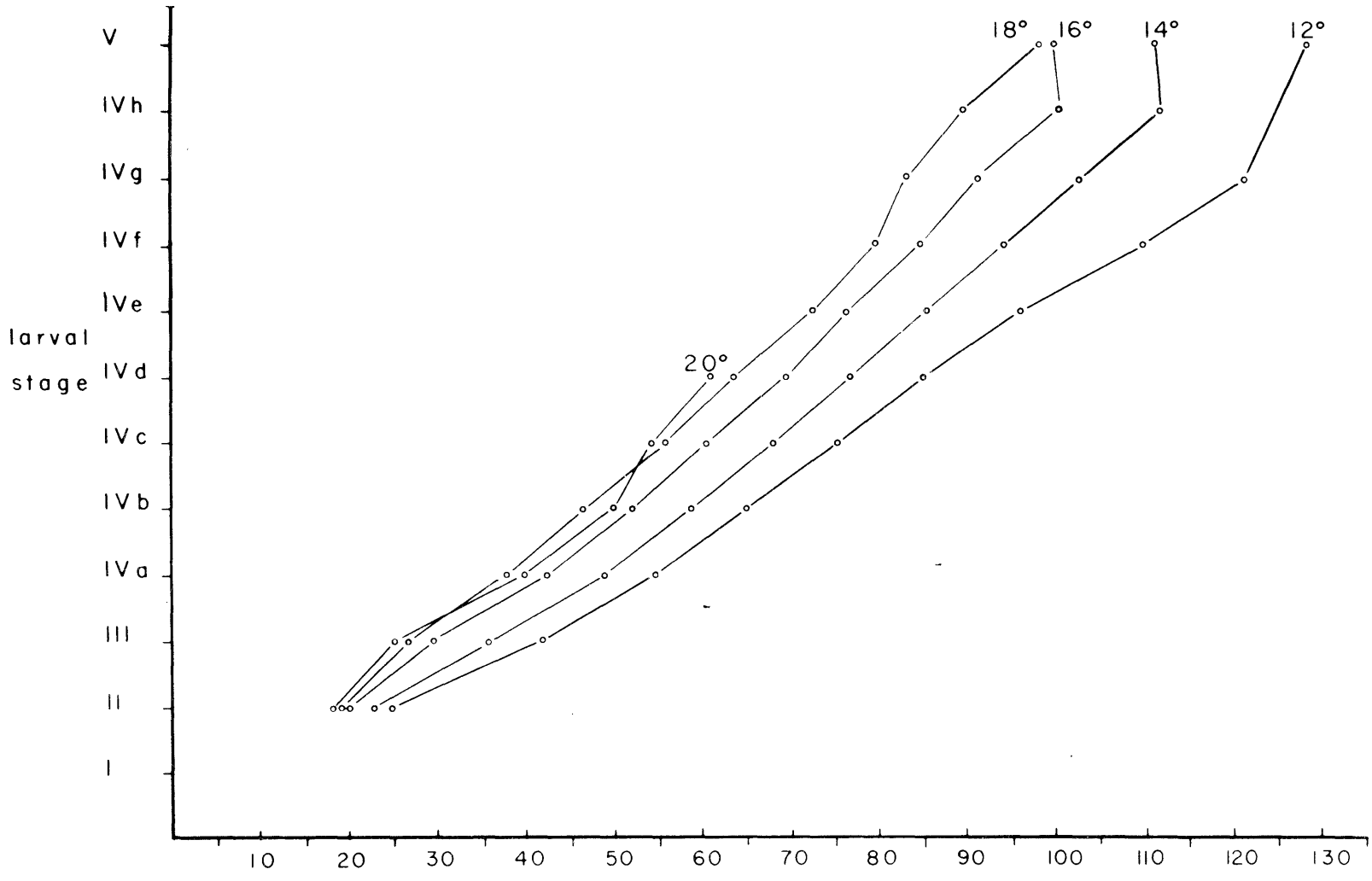
Time in days; percent mortality of larvae of *Pleuroncodes planipes* reared at several constant temperatures.

Within certain limits larval development should be faster at high temperatures; Figure 16 shows that this is true for P. planipes, at least over the range from 12° to 18° C. No data are available for the duration of Stage I because at the time the larvae were in that stage they were not kept individually. It will be noted that the mean number of days to the end of sub-stage IVh is greater than the developmental time to the end of Stage V for the 14° and 16° cultures. This is because many larvae omitted one or more of the later Stage IV sub-stages and passed directly to Stage V, thereby shortening their larval duration. The trend of the 20° line is probably correct but it is based on too few individuals to be very accurate; at the end of Stage III only 3 larvae were alive in the 20° culture. The mean duration of each stage (with the 95% confidence limits of the sample) is shown in Table 3. The values are cumulatively summed to give the average total number of days elapsed to the end of each stage.

A Q_{10} value for the rate of larval development of P. planipes can be calculated on the basis of the mean number of days of life to the end of the larval phase. The first three values, 128, 111, and 98 (for 12°, 14°, and 16° respectively) give an average Q_{10} of 1.95. The fourth value, for 18° (98), when compared with the 12° value gives a Q_{10} of 1.6. This figure is based on only three larvae at 18°, and is suspect; the correct value is probably about 1.9.

The number of sub-stages passed through in Stage IV varied from larva to larva in this experiment as it did in Experiment 3.

Figure 16. Rates of development of larvae of *Pleuroncodes planipes* reared in the laboratory at several constant temperatures.



Mean number of days to the end of each larval stage of *Pleuroncodes planipes* reared at several constant temperatures

Table 3. Mean duration of stages of P. planipes larvae reared at several temperatures. These durations are cumulatively summed and presented under the heading Σ. The number of larvae passing through each stage is presented under N.

12°

Stage	Mean duration and 95% limits	Σ	N
II		24.7	
III	16.9 ± 7.0	41.6	84
IVa	12.8 ± 5.4	54.4	71
IVb	10.7 ± 5.8	65.1	68
IVc	10.4 ± 6.7	75.5	63
IVd	9.1 ± 5.1	84.6	60
IVe	11.7 ± 5.1	96.3	56
IVf	12.4 ± 7.0	108.7	50
IVg	12.0 ± 6.7	120.7	13
IVh			
V	17.7 ± 7.9	127.5	50

14°

Stage	Mean duration and 95% limits	Σ	N
II		22.3	
III	13.2 ± 8.1	35.5	61
IVa	12.6 ± 9.6	48.1	52
IVb	9.9 ± 5.9	58.0	45
IVc	9.5 ± 6.8	67.5	42
IVd	9.3 ± 5.2	76.8	37
IVe	7.2 ± 4.0	84.0	35
IVf	9.1 ± 3.8	93.1	33
IVg	8.9 ± 3.0	102.0	15
IVh	9.0 ± 5.7	111.0	2
V	13.2 ± 4.7	110.9	31

16°

Stage	Mean duration and 95% limits	Σ	N
II		19.7	
III	9.6 ± 7.1	29.3	57
IVa	12.8 ± 6.6	42.1	51
IVb	10.0 ± 6.9	52.1	43
IVc	8.8 ± 7.0	60.9	37
IVd	8.1 ± 5.8	69.0	34
IVe	7.6 ± 4.7	76.6	32
IVf	7.4 ± 5.9	84.0	28
IVg	7.2 ± 4.3	91.2	17
IVh	8.5 ± 4.3	99.7	2
V	10.6 ± 3.3	98.4	30

18°

Stage	Mean duration and 95% limits	Σ	N
II		19.0	
III	7.8 ± 6.0	26.8	33
IVa	10.6 ± 6.5	37.4	12
IVb	8.8 ± 4.9	46.8	9
IVc	9.2 ± 4.2	55.4	5
IVd	7.6 ± 2.8	63.0	5
IVe	9.0 ± 3.6	72.0	4
IVf	6.8 ± 1.1	78.8	4
IVg	4.0	82.8	2
IVh	6.0	88.8	1
V	11.7 ± 1.7	97.7	3

20°

Stage	Mean duration and 95% limits	Σ	N
II		18.0	
III	7.0	25.0	3
IVa	14.5 ± 3.5	39.5	2
IVb	10.0	49.5	1
IVc	4.0	53.5	1
IVd	7.0	60.5	1

From Table 3 it can be seen that no larvae in the 12° culture went into sub-stage IVh; at other temperatures some larvae went through this sub-stage on their way to Stage V. Table 4 tabulates the deletion of sub-stages by the larvae. A X^2 test applied to the top set of data in Table 4 (using as columns the data from the 12°, 14°, and 16° cultures, and as rows the sub-stages IVe, IVf, IVg, and IVh) yields a probability between 0.05 and 0.10, indicating a difference between the rows of data.

A Friedman analysis of variance can be applied to the last three rows of data in the last table. This tests whether the columns of numbers come from the same population, and yields, in this case, a probability of 0.075. If one regards this value and the above X^2 value as significant, the data are evidence of a trend indicating that at higher temperatures larvae pass through more sub-stages than they do at lower temperatures. This is in spite of the fact that the total larval span in time is shorter at higher temperatures.

Discussion

Perhaps the most interesting observation to result from the culturing of larvae of P. planipes in the laboratory is that Stage IV is divided into sub-stages, and that the number of these sub-stages may vary. The data indicate that the number of sub-stages which a larva passes through may be influenced by the temperature of the environment, with higher temperatures producing more sub-stages before the molt to Stage V; that within limits the rate of

Table 4

Top) The number of larvae which molted directly to Stage V from each stage, thereby omitting late sub-stages.

Middle) The numbers above are expressed as percentages of larvae which molted from each stage directly to Stage V.

Bottom) The above data are expressed as the per cent of larvae which completed a particular sub-stage before becoming Stage V larvae.

	12°	14°	16°	18°
IVe	3	1	3	0
IVf	37	17	11	1
IVg	13	13	15	1
IVh	0	2	2	1
V	53	33	31	3
IVe	6	3	10	0
IVf	70	52	35	33
IVg	24	39	49	33
IVh	0	6	6	33
V	100	100	100	100
IVe	100	100	100	100
IVf	94	97	90	100
IVg	24	45	55	67
IVh	0	6	6	33

larval development shows a Q_{10} close to 2; and that higher temperatures cause a higher death rate.

Environmental factors other than temperature affect the duration of the larval stages. For example, temperatures were the same in Experiments 2 and 3, but there was a difference in the mean larval duration. The only known differences in conditions were the size of the rearing container and the presence of other larvae in the same container. Gurney (1942) conjectured that data concerning the life histories of laboratory-reared larvae might prove misleading when applied to larvae in the ocean. In view of the demonstrated effects of various small changes of conditions on the molting sequence and developmental duration of laboratory-reared larvae, it is quite possible that their life histories may be inapplicable to larvae in the field. The matter is further discussed by Costlow and Bookhout (1959) and by Rees (1959). In the case of P. planipes larvae, however, all of the stages, except Stage VI, seen in the laboratory, including evidence for a complex of Stage IV sub-stages, can be found in larvae from the plankton. The number and detailed morphology of the Stage IV sub-stages which larvae pass through in the ocean may well differ from the number passed through by larvae in laboratory experiments, and the number of sub-stages may even vary from one part of the ocean or one season of the year to another.

The irregularities in the number of molts in the larval phase shown by P. planipes may be found in other anomuran crabs. Sub-stages, however, are difficult to detect in morphological studies

of larvae taken from plankton collections. Johnson and Lewis (1942) found a "lower Stage IV" in the larval stages of Emerita analoga based on larvae from the plankton. This lower stage is best interpreted as a sub-stage and is an indication that sub-stages occur naturally in the field. Rees (1959) noted that larvae of Emerita talpoida reared in the laboratory may pass through either 6 or 7 molts before becoming megalops. Similar results were noted in laboratory-reared larvae of E. analoga by Dr. Ian Efford (unpublished results, personal communication). A. Provenzano (personal communication) has observed a varying number of molts in larvae of some pagurid crabs from Florida cultured by him. Costlow (personal communication), however, has observed variation in the number of larval molts in only two species of Brachyura out of a total of about 20 species that have been reared in his laboratory. In the two species -- both Portunidae -- variation occurred only occasionally and resulted in a form with reduced viability which only rarely developed to the megalops stage. Broad (1957 a and b) found that the number of larval molts varied in Palaemonetes pugio, a decapod macruran, depending on the type of food given the larvae.

Stage VI, which appeared in Experiment 1, has never been found in the plankton and appears to be the result of laboratory rearing conditions. It is possible that it may occur in nature under certain conditions. Its existence would certainly support Gurney's contention that laboratory conditions produce aberrant larval forms. Kurata (1960b) observed what may be a similar

phenomenon in the advanced stages of two lithodid crabs (*Paralithodes camtschatica* and *P. brevipes*) reared in the laboratory. These stages were intermediate between the usual last larval stage and the glaucothoe.

The temperatures in Experiment 4 (12° to 22° C) were selected because these are approximately the surface temperatures at the northern and southern ends of the crab's distribution in the adult phase. The few data available indicate that the larval distribution is similar to the adult distribution, with the greatest concentrations occurring along the western coast of southern Baja California. In that area winter temperatures may commonly be as high as 20° at the surface (see figure 13). Larvae at that temperature in the laboratory had a higher mortality rate than did those at lower temperatures. Possibly, larvae in the latitude of southern Baja California do not live at the surface but rather below the surface at a more optimal temperature. The winter breeding season may be correlated with higher larval survival in the laboratory at colder temperatures.

Because problems encountered by the larvae of the polychaetes and the decapod crustaceans are similar in that they must transform from a pelagic phase to a benthic phase, it is tempting to speculate that decapod crustacean larvae such as those of *P. planipes* may respond to environmental parameters in a way similar to that demonstrated by Wilson for various polychaete larvae (cf. Wilson, 1952). He has shown that polychaete larvae are influenced by the

nature of certain substrates so that they end the pelagic phase and become benthic. The presence of other substrates tended to prolong the larval phase. Experiments similar to Wilson's have not yet been performed on larval decapods, however, presumably because of the difficulties inherent in rearing them.

The effects of antibiotics on larvae of *Pleuroncodes planipes* reared in the laboratory

In the last decade it has become common practice to use antibiotics to reduce contaminating bacteria in the culture of aquatic organisms. Oppenheimer (1955) tested several concentrations of antibiotics to determine the optimal concentration for survival of marine fish eggs and larvae. Marshal and Orr (1958) discussed the use of antibiotics in marine physiological experimentation. They mentioned that chloromycetin in the medium sometimes inhibited the feeding of copepods. Antibiotics have been used in several of the recent studies on the larval development of marine Crustacea discussed above. These drugs in laboratory cultures of aquatic organisms certainly create an unnatural situation, but it is believed that the antibiotics tend to reduce the numbers of bacteria resulting from the already unnatural culturing techniques, and hence that their use is warranted. There has been no mention of the comparative effects of various antibiotics, or of their concentrations on the survival and developmental histories of those marine Crustacea that have been reared in cultures containing the drugs.

An experiment (number 5) was devised to test the effects of several concentrations of two antibiotics on the survival of the zoeal larvae of *P. planipes*. The antibiotics used were penicillin G, potassium, manufactured by Pfizer, assay 1585 units/mg; and streptomycin sulfate, by Pfizer. They were used singly and combined

at five concentrations: 25, 50, 75, 100, and 125 mg/liter. Freshly hatched larvae were placed individually in the compartments of clear plastic trays of the type used in Experiment 4. Thirty-six larvae were subjected to each of the 15 possible treatments, and an additional 36 larvae were used as controls in sea water without antibiotics. The trays of larvae were placed in flowing sea water, which maintained the cultures at 14-16° C. Larvae were transferred into fresh medium twice each week, at which time each was drawn into a pipette and examined quickly under a low-power dissecting microscope to determine the developmental stage. Freshly hatched Artemia nauplii were added to the new medium at this time, as food for the larvae. When the experiment was terminated after 26 days, 43% of all the larvae were alive, and most of the surviving larvae had passed through two molts.

The numbers surviving each treatment and the mean larval stage after 22 days are summarized in table 5. Survival in the presence of the antibiotics was greater than in the controls at the 0.059 level (Mann-Whitney U test; pooled values from all treatments were tested against the controls). No significant differences were indicated between the types or concentrations of antibiotics. There was no evidence that any antibiotic, in any concentration, influenced the developmental rate by lengthening or shortening the duration of the larval stages during the first 22 days (Friedman two-way analysis of variance).

The results suggest that larvae reared in the presence of

Table 5

Top. Numbers of P. planipes larvae surviving various treatments after 22 days. At start of experiment samples were paired with 18-18 larvae in each treatment.

Bottom. Mean larval stage number after 22 days.

	Concentration (mg/liter)					
	25	50	75	100	125	Control
P	6-10	7-9	8-13	10-12	9-12	
S	8-16	2-12	11-11	12-13	10-12	77
M	10-12	10-14	7-9	9-9	12-14	

	Concentration (mg/liter)					
	25	50	75	100	125	Control
P	2.4	2.8	2.9	2.8	2.9	
S	2.6	2.6	2.9	3.0	3.0	2.6
M	2.8	2.7	2.8	3.0	3.0	

P = penicillin

S = streptomycin

M = mixture of both

antibiotics may show greater survival; penicillin and streptomycin appear to be equally good, and the lowest concentration is as good as the highest. In view of the possible effects of antibiotics on the number and duration of larval stages, it would seem best to use the lowest concentration giving bacterial control.

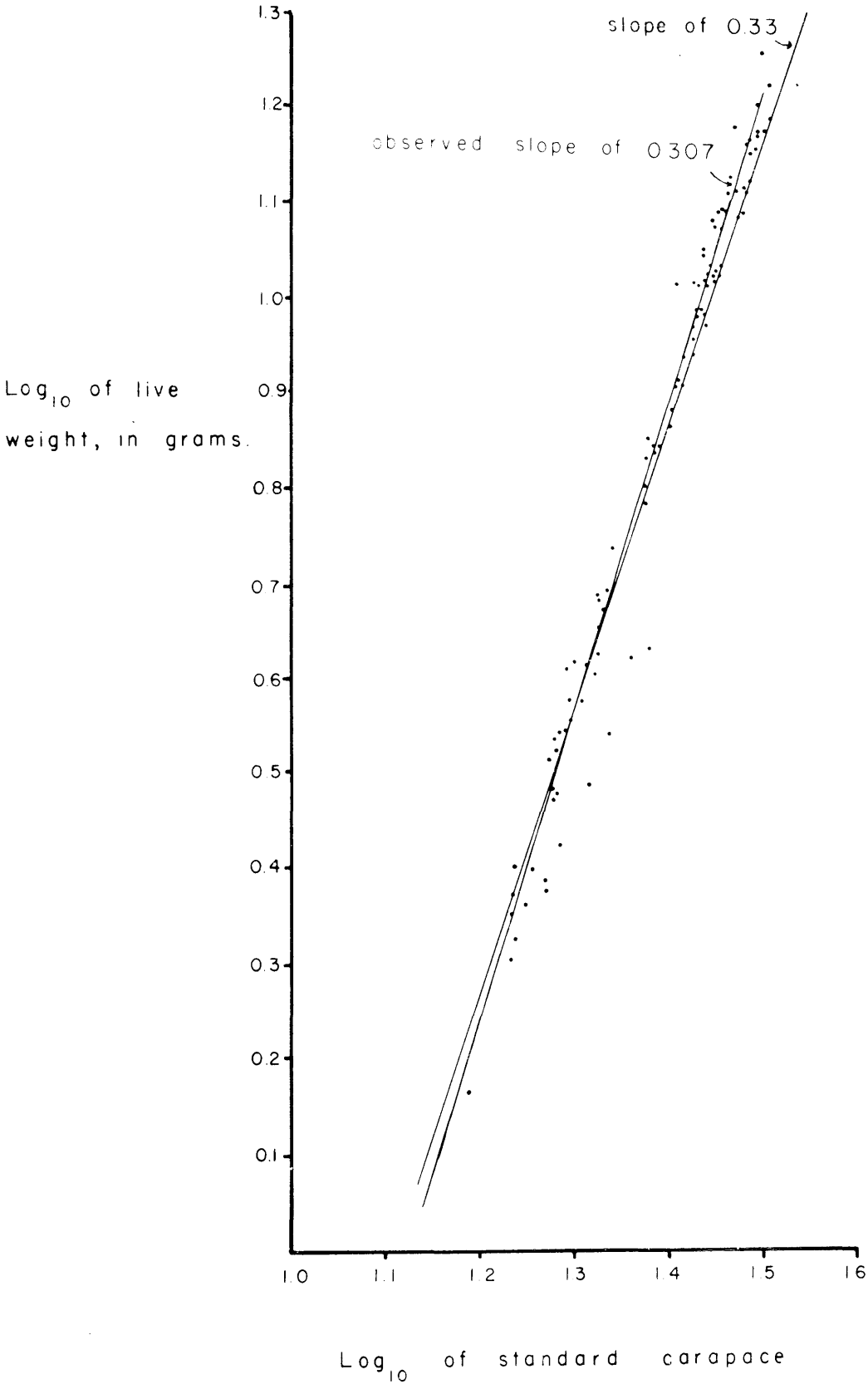
Growth rates and age structure of Pleuroncodes planipes

The measurement of crab size used during this study is the distance in mm from the notch between the rostrum and the sub-rostral spine to the posterior median margin of the carapace. This measurement, called the standard carapace length, has been found to be both more reliable and easier to take than the total carapace length or total weight. Vernier calipers have been used throughout the study; the accuracy of measurements is within 0.1 mm.

A single length measurement can be validly used as an expression of total body size only if the relationship between that linear measurement and volume or weight is constant throughout the life span. If this is so, carapace length should be related to weight by an equation of the form $\text{length} = k \cdot \text{weight}^{1/3}$, where k is a constant. On a log-log plot this relationship would follow a straight line with a slope of 0.333. The standard carapace lengths and weights of 98 specimens of P. planipes ranging from 14 to 32 mm standard carapace length, a range which covers the length of all mature specimens, are plotted on a log-log scale in figure 17. The values are best fitted (least squares) by a straight line with a slope of 0.307, k = 1.127. This slope is significantly different from 0.333 at the 0.05 probability level. For P. planipes, carapace length provides a good estimate of weight, but the relationship using the exponent 1/3 will be in error by about 5% for extremely large or small specimens.

The average relationships between standard carapace length,

Figure 17. Log-log plot of standard carapace length against live weight of 98 specimens of P. planipes. The best fitting (least squares) line has a computed slope of 0.307. The theoretical slope is 0.33.


slope of 0.33
observed slope of 0.307
Log10 of live weight, in grams.
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
1.0
1.1
1.2
1.3
1.4
1.5
1.6
Log10 of standard carapace length, in mm

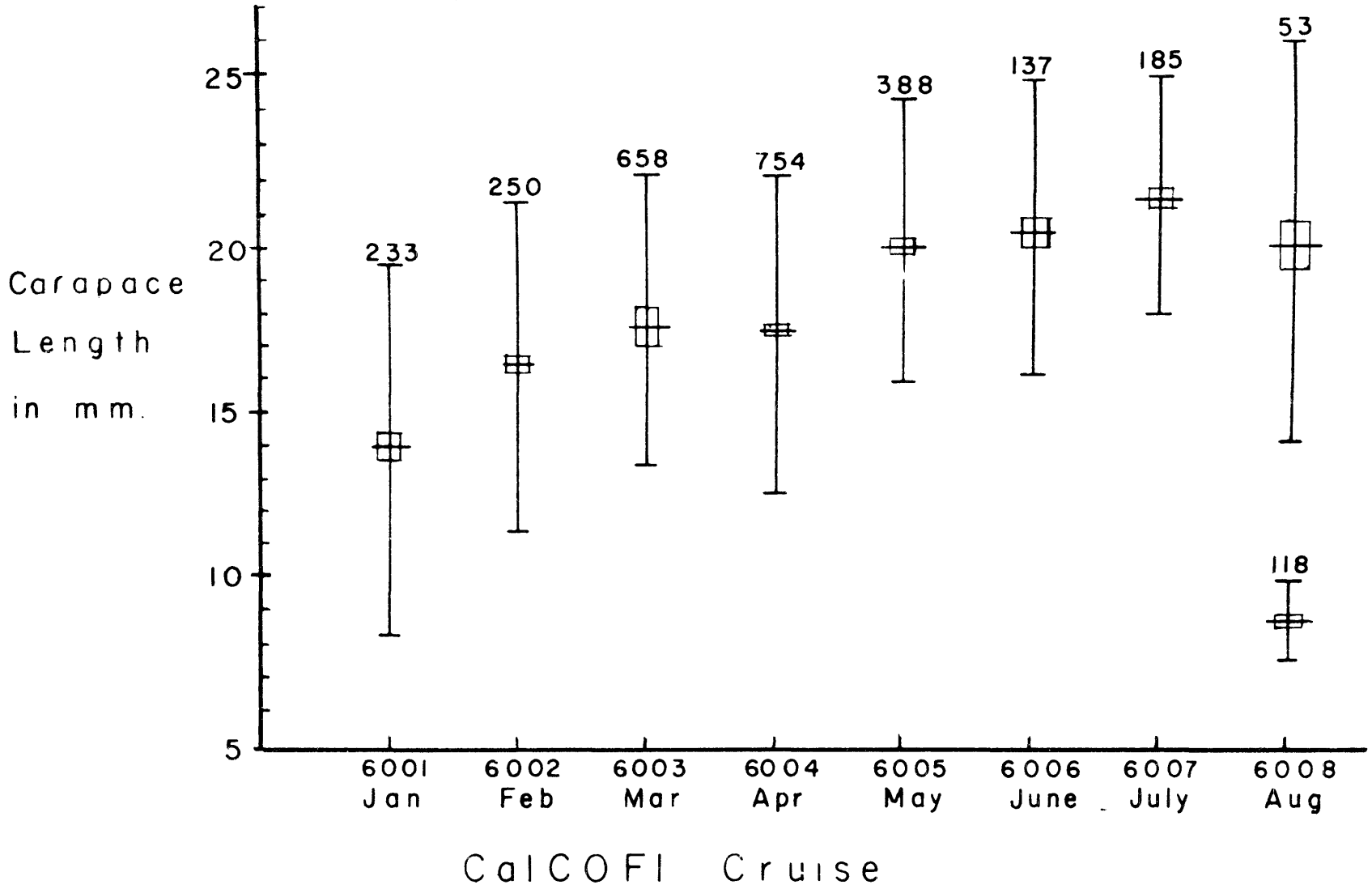
total carapace length, and total body length (measured from the tip of the rostrum to the median cleft of the telson) are as follows: s.c.l./ t.c.l./ t.b.l. = 1.00/ 1.29/ 2.45. These are based on measurements of the same 98 specimens of P. planipes.

No significant differences in standard carapace length or weight have been found between male and female specimens of any size category. Of the 98 animals represented in figure 17, 44 were males and 54 were females. There was no difference in the slopes of the regression lines of log length against log weight for the males and females treated separately ($p > 0.05$). This contrasts with the observations of several workers who have shown that size of many brachyuran crabs is a function of sex (cf. MacKay and Weymouth, 1935). No such difference was noted in P. planipes.

Growth rates in the field

All specimens of Pleuroncodes planipes (2776) which were caught on the eight monthly cruises of the Marine Life Research program of the California Cooperative Oceanic Fisheries Investigations between January and August, 1960, were individually measured and sexed. The distributional data from these cruises are presented in figures 2 through 9. Derived statistics from the measurements are plotted in figure 18; the number over each vertical line represents the number of crabs caught in each month. The total length of each vertical line represents the 95% confidence limits of the sample, the box represents 95% confidence limits of the mean, and the single centered line represents the mean standard carapace

Figure 18. Standard carapace lengths of *P. planipes* caught in the CalCOFI plankton samples between January and August, 1960.


Carapace
Length
in mm.
25
20
15
10
5
233
250
658
754
388
137
185
53
118
6001
Jan
6002
Feb
6003
Mar
6004
Apr
6005
May
6006
June
6007
July
6008
Aug
CalCOFI Cruise

length of the crabs. In August, cruise 6008, two distinct size classes of crabs were taken, and there were no crabs of intermediate size. Length-frequency plots of the earlier cruises showed no indication of more than one size class.

The trend shown by the series of means may be taken as a measure of the growth of the crabs during the eight month period. Laboratory studies indicate that these crabs are in their second year of life, and represent a single year class. The small crabs found in August are in their first year of life. The mean length of these small crabs (8.6 mm) suggests that individuals of the population sampled grow about 12 mm in that one year; from about 9 mm to 21 mm. A highly significant ($p = 0.001$) linear regression may be calculated from the lengths of the crabs from January to August as follows:

$$Y = 14.7 + 0.029\ X$$

where Y is the standard carapace length, and X is the total number of days between January 1 and the date of capture of the specimen. Data from laboratory studies discussed below indicate that this linear regression equation is probably not applicable to crabs smaller than 10 mm because of differing rates of growth.

Analysis of factors controlling size

Although the size of an animal is to a large extent a function of its age, the scatter about the means (figure 18) suggests that other factors may also be influential. In an attempt to reveal these, the field data from the same CalCOFI cruises, 6001 to 6008,

were submitted to a multiple linear regression analysis. At every station at which the crabs were found (316 stations) the following six types of data were also noted:

1) date; transformed to "age" in terms of days after 1 January;
2) temperature at 10 meters depth at station;
3) time of day of plankton tow; expressed as hours away from midnight, either before or after;
4) numbers of crabs caught in the plankton tow; transformed to log arithmetic scale;
5) latitude of the station; degrees and tenths north latitude;
6) distance offshore of the station; degrees and tenths;
7) mean standard carapace length of all the crabs caught in that plankton tow.

The program used was a multiple linear regression analysis, BIMD 06, obtained from the UCLA Medical Center, and modified for use on the IBM 7040 computer. The program tests the relation between the first six parameters (the independent variables) and the seventh (the dependent variable), here the size of the animals caught. The results were as follows:

	mean	stand. deviat.	reg. coeff.	t value	partial corr. coefficient
age	97.3	61.0	0.028	14.3	0.630
10 m temp	17.2	2.0	-0.185	-2.2	-0.125
time of day	4.9	3.3	0.080	2.3	0.128
numbers caught	2.3	1.8	0.056	0.8	0.045
latitude	26.9	2.2	0.457	5.9	0.319
distance offshore	1.0	0.8	-0.664	-4.2	-0.235
mean carapace length	17.6	3.1			

intercept of regression line = 5.96
coefficient of determination = 0.610
F value for regression, 309 and 6 degrees of freedom, 80.67 (p=0.01).

The "t" values for all the coefficients except that for numbers caught are significant at the 95% level or better. The value of the coefficient of determination (61% of the variability in carapace length is accounted for by the six independent variables) suggests that one could make a fairly good prediction of the mean length of crabs from any station for which one had "age", 10 m temperature, time of day of plankton tow, latitude, and distance offshore.

Examination of the partial correlation coefficients yields some interesting suggestions about the biology of *P. planipes*. These coefficients express the correlation between the dependent variable and one of the independent variables, the other independent variables being held at their mean values. With 300 degrees of freedom an "r" value of $\pm$ 0.113 is significant at the 0.05 level (Snedecor, 1956). As would be expected the correlation between "age" and size is a very high 0.630. The next highest partial correlation coefficient is between latitude and size, 0.319, indicating that larger crabs are found further north. Distributional data show that the bulk of the population occurs at the southern end of the sampling area. The larger crabs in the higher latitudes, then, would be on the edge of their distributional range. The partial correlation coefficient between time of day of capture and the size of animals caught is also positive and significant, indicating that larger crabs were caught during the lighter hours of

the day. This suggests that differences in the time of catch could lead to erroneous results in any size-frequency study.

The other two significant partial correlation coefficients are negative: water temperature at 10 m, -0.125, and the distance offshore, -0.235. The correlation with water temperature may be measuring the same phenomenon as the one with latitude, but does so less well. Deevey (1960) found a similar inverse correlation between temperature and size in several species of neritic copepods in the North Atlantic. The negative correlation between distance offshore and size may be related to the benthic - pelagic phases of the crab's life history; the smaller crabs being perhaps more planktonic than the heavier, larger crabs, and therefore, more likely to be found in deeper, offshore waters.

The above analysis assumes that all the crabs were hatched at a similar date, around the first of the year, and that the size difference between crabs after the date of hatching was due to environmental factors acting differentially on the growth rates of the crabs. The same sort of results in relation to latitude and temperature could, however, be obtained by assuming that the growth rates throughout the population were uniform, but the date of spawning was influenced by environmental factors. Under this interpretation those larger crabs found on the northern end of the range (or in colder water throughout the range) may be a few weeks older than the southern crabs, and hence larger. This would demand a cline of the onset of the breeding season, starting in northern

waters and progressing southward. This interpretation is corroborated by the fact that breeding occurs in the winter, simultaneously with the occurrence of colder temperatures.

Growth rates in the laboratory

Because P. planipes survives well under laboratory conditions, several experiments were performed to measure its growth rate.

Experiment 1. One hundred specimens, all taken by dip net at the surface, at the same time, off Turtle Bay, Baja California, Mexico, were kept in plastic containers filled with sea water. The majority of the crabs measured between 15 and 20 mm standard carapace length. The containers were about 12 x 16 x 11 cm deep, and held about 1600 ml of sea water. They were placed in trays with sea water flowing around them as a coolant. The temperature of the water ranged from about 12° C in winter to 22° C in summer, but varied little from day to day. The crabs were fed four times a week on shredded pieces of boiled Cervimunida johni (a galatheid closely related to P. planipes which is sold as a sea-food in local grocery stores), and uneaten food was removed before new food was added. It is believed that excess food was always present. The following table gives pertinent data on the crabs.

Number which died before molting	9
" " molted one time before dying	20
" " " two times " "	20
" " " three " " "	35
" " " four " " "	15
" " " five " " "	1
	100

mean increase in size at each molt	1.6 ± 0.1 mm
mean period between molts	63.7 ± 2.0 days

Under these conditions the growth rate is somewhat under 1 mm per month.

Experiment 2. The crabs in Experiment 1 were kept isolated from each other and were in non-circulating sea water. It was felt that these conditions might be such a departure from natural conditions that results might not be related to the growth rate in nature. A second experiment, therefore, was set up to see if results could be altered by keeping the crabs in groups in flowing sea water. Eight crabs (four males and four females) were placed together in a tray of flowing sea water. The tray measured 69 x 105 x 5 cm deep; four trays were used as a unit with sea water flowing into the first, spilling into the second, then into the third and finally into the fourth. Four such units were set up, giving a total of 128 crabs in the experiment. The food and feeding procedures were the same as in Experiment 1. In order to follow the molting history of individuals, each crab was marked by black "Opco" with a coded number on the cardiac region of the carapace. The crabs were checked daily for molts; crabs which had molted were measured and re-marked. If a crab died it was replaced by a crab of a similar size and sex. In this experiment crabs from the entire size spectrum of mature crabs were used, ranging from megalopa crabs to adults of 33 mm. The experiment lasted about 18 months, at which time 447 molts had been recorded.

On the assumption that the growth rate would not be independent of the size (age), growth rates were calculated for different size classes (3-10, 10-15, 15-20, 20-25, 25-30, and 30-35 mm standard

carapace length). The crab's length before the molt determined the size class in which it was placed. These data are presented graphically in figures 19 and 20. The method of data presentation used was discussed previously.

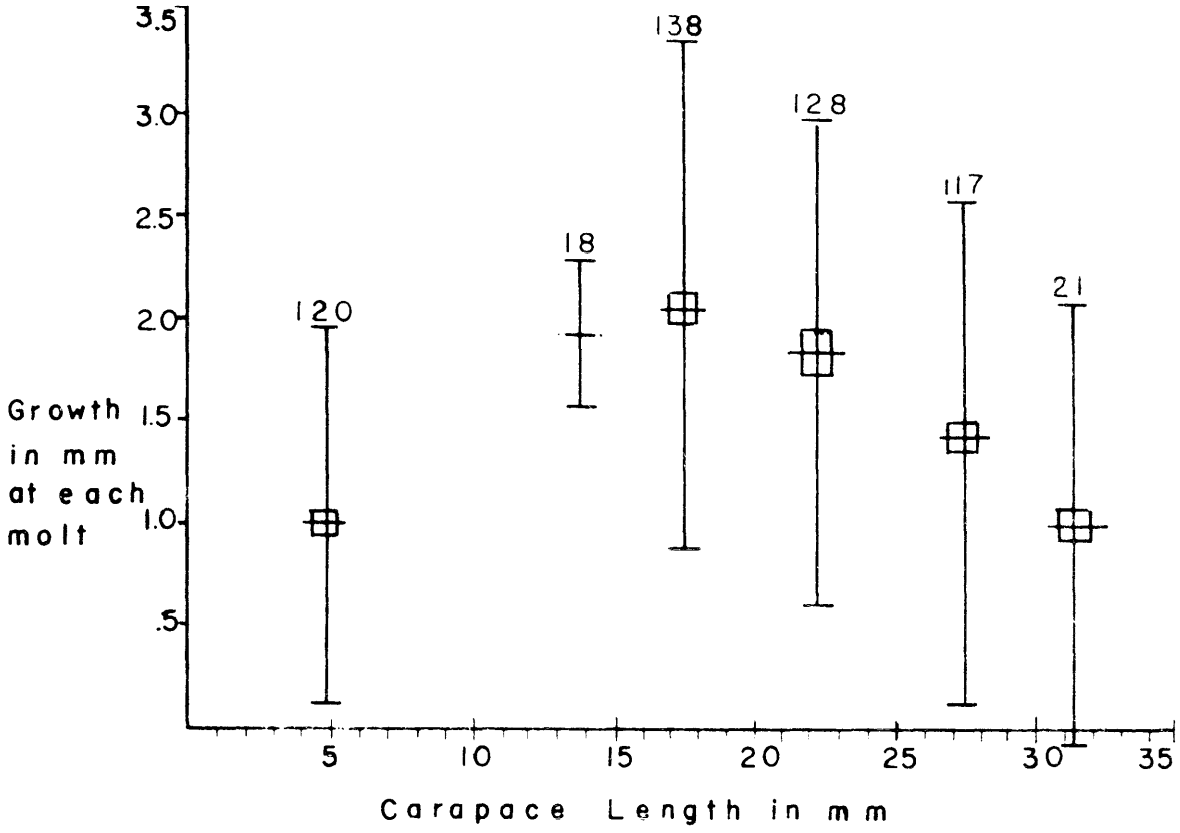
There are some data in the literature which indicate that laboratory conditions inhibit the size increase per molt and extend the intermolt period. Herrick (1909) felt that lobsters grew more rapidly in nature than when confined in glass jars in the hatchery. Hiatt (1948) notes that growth increments of Pachygrapsus crassipes were generally smaller for crabs kept in the laboratory than for crabs in nature. MacKay and Weymouth (1935), in their study of the growth of Cancer magister, report, however, that "the data at hand indicate that the increase in size per molt of mature crabs in nature does not differ significantly from that in captivity."

Work on P. planipes shows that the growth per molt and the molting frequency are definitely influenced by laboratory conditions; crabs (15-20 mm) kept in still water in 1.6 liter boxes gained 1.6 ± 0.1 mm per molt, and molted every 64 ± 2.0 days; crabs of a similar size kept in large aquaria with flowing sea water gained 2.1 ± 0.1 mm per molt and molted every 35.5 ± 3.0 days.

Not only do the crabs grow less at each molt after they have become mature, but they also molt less often (figure 20). By combining data from figures 19 and 20 a growth curve for the animals was constructed, shown in figure 21 (see also Table 6). The starting point for the curve in figure was derived from data from larval culturing experiments. Other points on the curve were

Figure 19. Size increase per molt of various size categories of P. planipes.

Figure 20. Days between molts in various size categories of P. planipes.


Growth in mm at each molt
3.5
3.0
2.5
2.0
1.5
1.0
.5
120
18
138
128
117
21
5
10
15
20
25
30
35
Carapace Length in mm

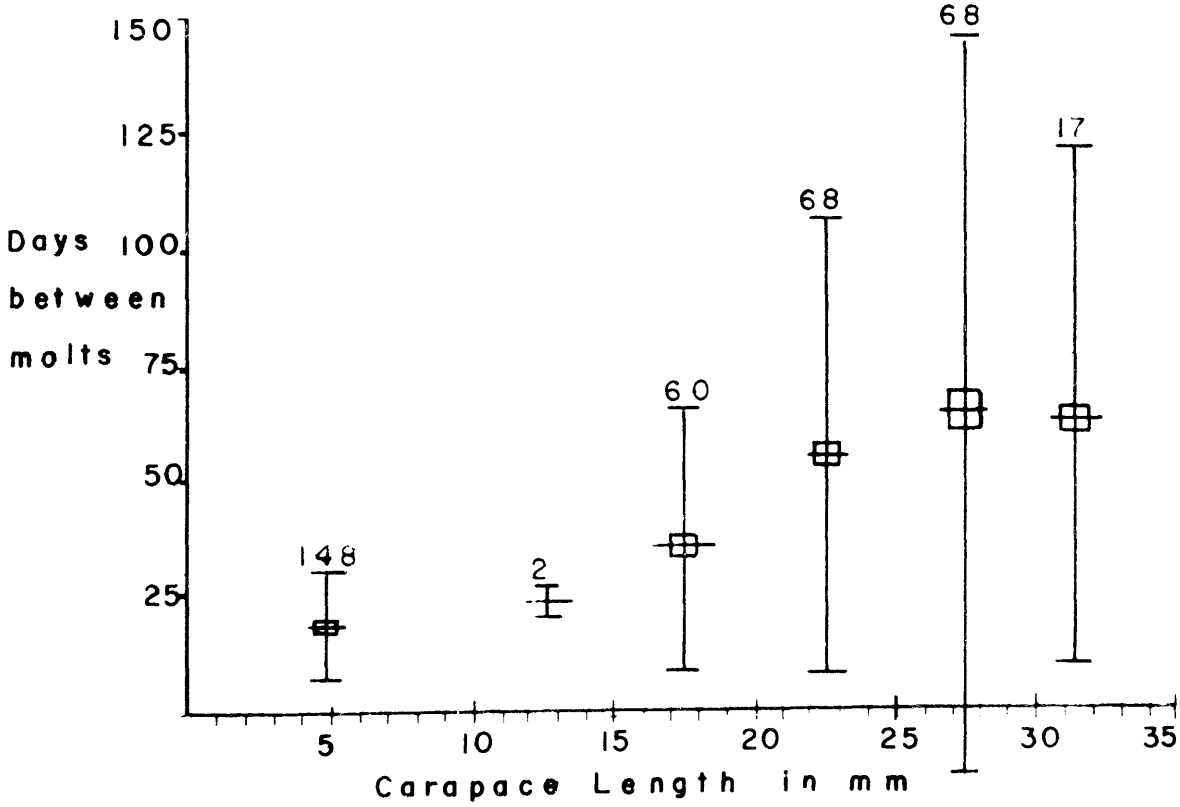

Days between molts
150
125
100
75
50
25
148
2
60
68
68
17
5
10
15
20
25
30
35
Carapace Length in mm

Figure 21. Theoretical growth curve derived from laboratory data on molting frequency and increase in size per molt of P. planipes. The two bands either side of the center line enclose the 95% confidence limits of the mean. The short vertical bars represent the mean carapace lengths and the 95% limits of the mean of specimens taken in the CalCOFI cruises from January to August, 1960; the dotted line is the regression line derived from these carapace lengths. The diameter of the circle and its location indicate the 95% limits of the mean of a group of crabs dredged off the bottom, and discussed in the chapter "The benthic habitat."

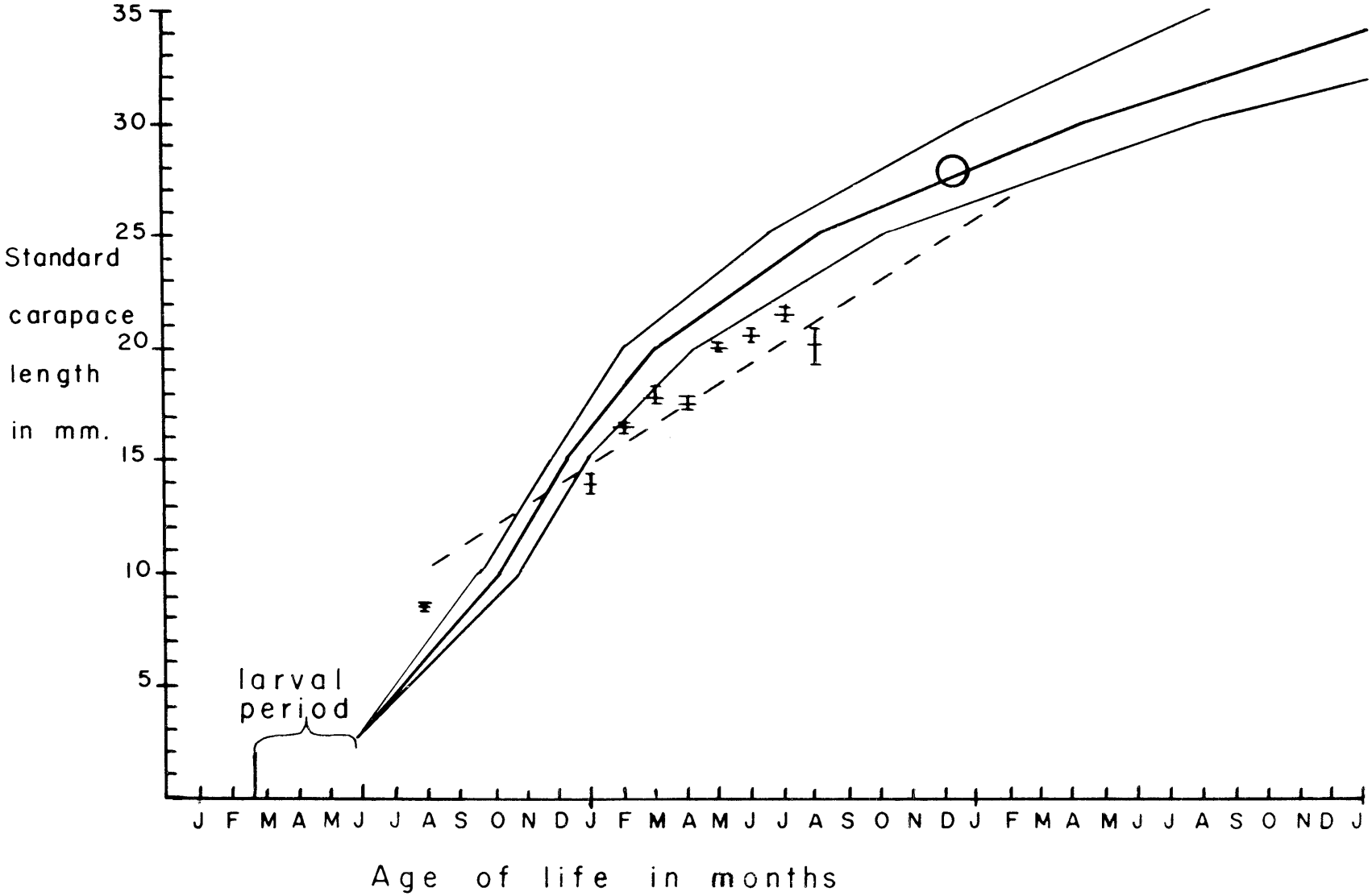

35
30
25
20
15
10
5
Standard
carapace
length
in mm.
larval
period
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J
Age of life in months

Table 6. Growth rates of *P. planipes* in the laboratory, expressed in mm per month. Means and 95% limits of the means.

Size category	Lower limit	Mean	Upper limit
post-larval to 9.9 mm	1.45	1.7	1.9
10.0-14.9	2.4	2.4	2.4
15.0-19.9	1.5	1.8	2.1
20.0-24.9	0.8	1.0	1.1
25.0-29.9	0.5	0.6	0.8
30.0-34.9	0.3	0.5	0.7

obtained as follows: the mean growth per molt for the size interval between 2.8 and 9.9 mm was 1.0 mm, and the mean time between molts was 18.8 days; the growth rate, therefore, was 1.7 mm per month; at this rate 4.2 months would be needed to grow from 2.8 to 9.9 mm. The initial slope of the line represents this growth rate. The remainder of the growth curve was calculated in a similar manner, each part using the terminal point of the preceding section for its initial point. The lines on either side of the center line were derived by similar treatment of the 95% limits of the observed mean values. The lower line was calculated using the lower limit values of growth per molt and the higher limit values of intermolt period. This combination of values gives the slowest growth curve; the fastest growth curve was calculated from the higher limit values for growth per molt and the lower limit values for intermolt period. Because of the method of calculation, these limiting lines probably represent confidence limits somewhat greater than 95%.

The means and 95% limits of the means of the measurements of field-collected crabs presented in figure 18, taken from specimens caught between January and August, 1960, are also shown in figure , as the short vertical lines on the graph. The agreement between the observed field values and the curve constructed from laboratory measurements is good, but not perfect. The laboratory specimens apparently grew faster than those taken from nature. Perhaps this was because in the laboratory the crabs had excess food present at all times. Temperature may also have had an effect, for the

regression analysis showed that larger crabs were found in colder water. If this is a result of different growth rates, the crabs reared in the laboratory at La Jolla might be expected to show a higher growth rate, because the water at La Jolla is several degrees colder than in the area 500 miles southward, where the majority of the field collections were made.

Several workers have attempted to express crustacean growth mathematically. Generally these expressions deal only with the growth of a crustacean at each molt, and do not consider the time period between molts. The first of these presentations was that of Brooks (1886), who suggested that stomatopod larvae increase their length at each molt by a quarter of their length. Many workers since Brooks have generalized that many Crustacea and larval insects molt when they have doubled their body weight, and then should increase linearly by a factor of $\sqrt[3]{2}$, or 1.26, very close to the figure suggested by Brooks. Kurata (1960a) reviewed molting histories in several Crustacea, and indicated that a constant factor of increase was generally not warranted. The data on the growth of adults of P. planipes do not substantiate a constant geometric increase, but indicate that the growth rates vary according to the phase of life of the crabs (cf. figure 19).

Respiration of *Pleuroncodes planipes*

The ocean off the western coast of southern Baja California is peculiar in that it is one of the few areas in the world where the oxygen-minimum zone warps upward almost to the surface (cf. figure 13). In the North Pacific Ocean this minimum zone is usually found at a depth of about 1,000 meters (Sverdrup, Johnson, and Fleming, 1942). Off Baja California specimens of *P. planipes* at a depth of 75 m. were living in waters containing as little as 0.5 cc O_2/liter of water.

The problem of anaerobiosis and near anaerobiosis in some freshwater and terrestrial invertebrates has received a great deal of attention (cf. Von Brand, 1946). The effects of varying oxygen concentration on marine Crustacea, however, are poorly known, although Von Brand noted that decapod Crustacea generally show little resistance to experimentally induced anaerobiosis. Because *P. planipes* was living in waters that were almost oxygen-free, it was decided to measure the respiratory rate of the crabs in the laboratory under different concentrations of oxygen to see what influence, if any, the oxygen content had on the metabolism of the crabs.

Methods

The Scholander respirometer (Scholander and Iverson, 1958) was used during this study. This volumetric device measures the volume of oxygen used by the animal per unit of time. It is dependent upon the establishment of an equilibrium between the

gases dissolved in the water in the chamber in which the animal is placed and those above the water. The oxygen extracted from the water by the animal is replaced by the oxygen from the air above the water, and this decrease in volume measured by the respirometer is related to the respiratory rate. These chambers measured 6.8 cm inside diameter and were 2.5 cm deep. They contained 85 cc of water and had an air-water interface of 36.3 square cm. A slight modification of the apparatus made it possible to run experiments with water of any desired oxygen content in the chamber. This involved inserting and sealing into the orifice of the respirometer a six inch long fine polyethylene tube (.030" i.d., .048" o.d.). This tube acted as a diffusion barrier between the respirometer and the chamber and allowed one to inject pure oxygen from the respirometer through the fine tube into the atmosphere of the chamber. A 20% solution of KOH on a paper wick was used to absorb CO_2 in the gas phase. Analyses of the oxygen content of the water before and after the experiment were made in duplicate on samples taken from the chamber through a vaccine stopper with a hypodermic syringe. Analyses were made with the Scholander microgasometric water analyzer (Scholander et al., 1955).

Normally the chamber and the attached respirometer are shaken to assure a rapid exchange of gas through the air-water interface. In this experiment the chamber and the animal were not shaken because the motion gave rise to abnormally high and variable respiratory rates. The rates given in this report, therefore,

pertain to animals resting quietly in individual chambers.

It was initially thought that the ratio of water surface to water volume would be great enough to ensure equilibrium between the two phases by simple diffusion, aided by the water-mixing action of the crab as it pumped water past its gills. However, the equilibrium was not attained. It was found, however, that when crabs were placed in the chamber in water initially saturated with oxygen (about 6 cc O_2/liter) and held there for three hours, the oxygen content dropped to 1 to 2 cc O_2/liter. If equilibrium had been established this drop would not have occurred. The respirometer readings noted during this three hour period by reading the respirometer indicated that some oxygen diffusion from air to water was occurring, but this amounted to only about 75% of the actual amount of oxygen respired -- the balance being accounted for by the drop in the oxygen content of the water. The failure of the water and air in the respiratory chamber to establish equilibrium was disconcerting, but, as will be seen below, revealed a respiratory mechanism of the crabs which would not have been found otherwise.

In order to study the influence of the ambient oxygen content on the respiratory rates of the crabs, aliquots of water having known, lowered oxygen concentrations were prepared. This was done by bubbling nitrogen gas through an aerating stone at the bottom of a tube two meters long and five cm in diameter, filled with sea water. Water flowed into the tube at the top and was drawn out at

the bottom. Analysis of the water drawn from the tube yielded oxygen levels identical to water that had been boiled for thirty minutes, indicating that the nitrogen had removed all the detectable oxygen from the water. The scrubbing method could produce oxygen-free water at a rate of about one-half gallon per minute. The de-oxygenated water was then mixed with water of known oxygen content to produce water having, within limits, any predetermined oxygen concentration. The actual oxygen concentration of the mixture was measured by the Scholander water analyzer.

Twenty-four hours before respirometry measurements, crabs were placed individually in three-gallon jars in water of the same oxygen concentration as that to be used in the experiment. The jars were sealed with no air space, and placed in a 12° C cold room. The 24 hour period allowed the crabs to adjust to the lower temperatures and to the lower oxygen concentrations. The crabs used were those being kept for laboratory growth rates (discussed above). They were normally kept in water at about 16° C.

At the time of measurement the crabs were placed individually in the respiratometry chambers in fresh sea water with the predetermined oxygen concentrations. The chambers were sealed, and flushed with an air mixture having the proper ratio of oxygen to nitrogen for that concentration of oxygen in the water. This mixture was prepared volumetrically in a 100 cc syringe. The respirometer was then attached and the apparatus placed in a 12° C water bath. All measurements were made at 12° C; the temperature

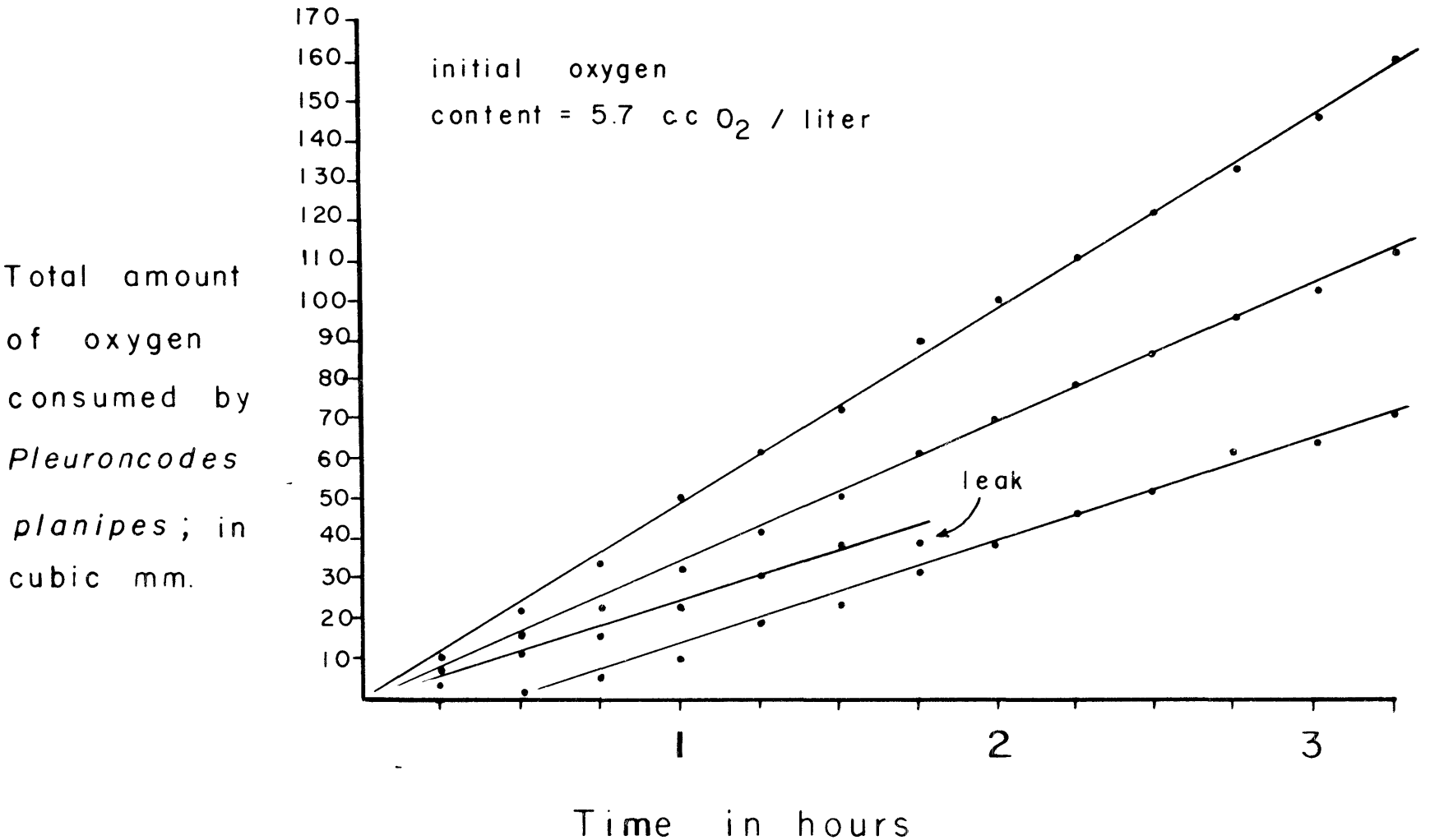
at which the crabs were found on the bottom in nature (see figure 13). Five respirometers were used in each experiment; four had individual crabs and the fifth was used with water only, for a control. Readings of each respirometer were taken every 15 minutes, usually over a period of three hours.

Results

The results of an experiment made at an oxygen concentration of 5.7 cc O_2/liter are shown in figure 22. The cumulative values for oxygen consumption were taken from the respirometer; they do not include the oxygen which was consumed from the water but not replaced from the air volume. The readings from the control respirometer have been subtracted from each of the four sets of data. The significant thing shown by this figure is that the oxygen consumption is essentially linear (i.e., the rate is constant) for any crab, throughout the three hour period. During this period the crabs maintained a constant rate even though the oxygen content of the water dropped from near saturation to a low in one case of 0.9 cc O_2/liter. There is, then, a phase of the respiratory mechanism that is independent of the ambient oxygen concentration.

A similar experiment, performed with crabs which had equilibrated for 24 hours in water with 0.9 cc O_2/liter, showed that the respiratory rates were much lower than those of crabs started in oxygen-saturated water. The mean respiratory rates at three oxygen levels were as follows:

Figure 22. Oxygen consumption of four specimens of Pleuroncodes planipes; initial oxygen content of the water, 5.7 cc O_2/liter.


Total amount of oxygen consumed by *Pleuroncodes planipes*; in cubic mm.
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
initial oxygen content = 5.7 cc O_2 / liter
leak
1
2
3
Time in hours

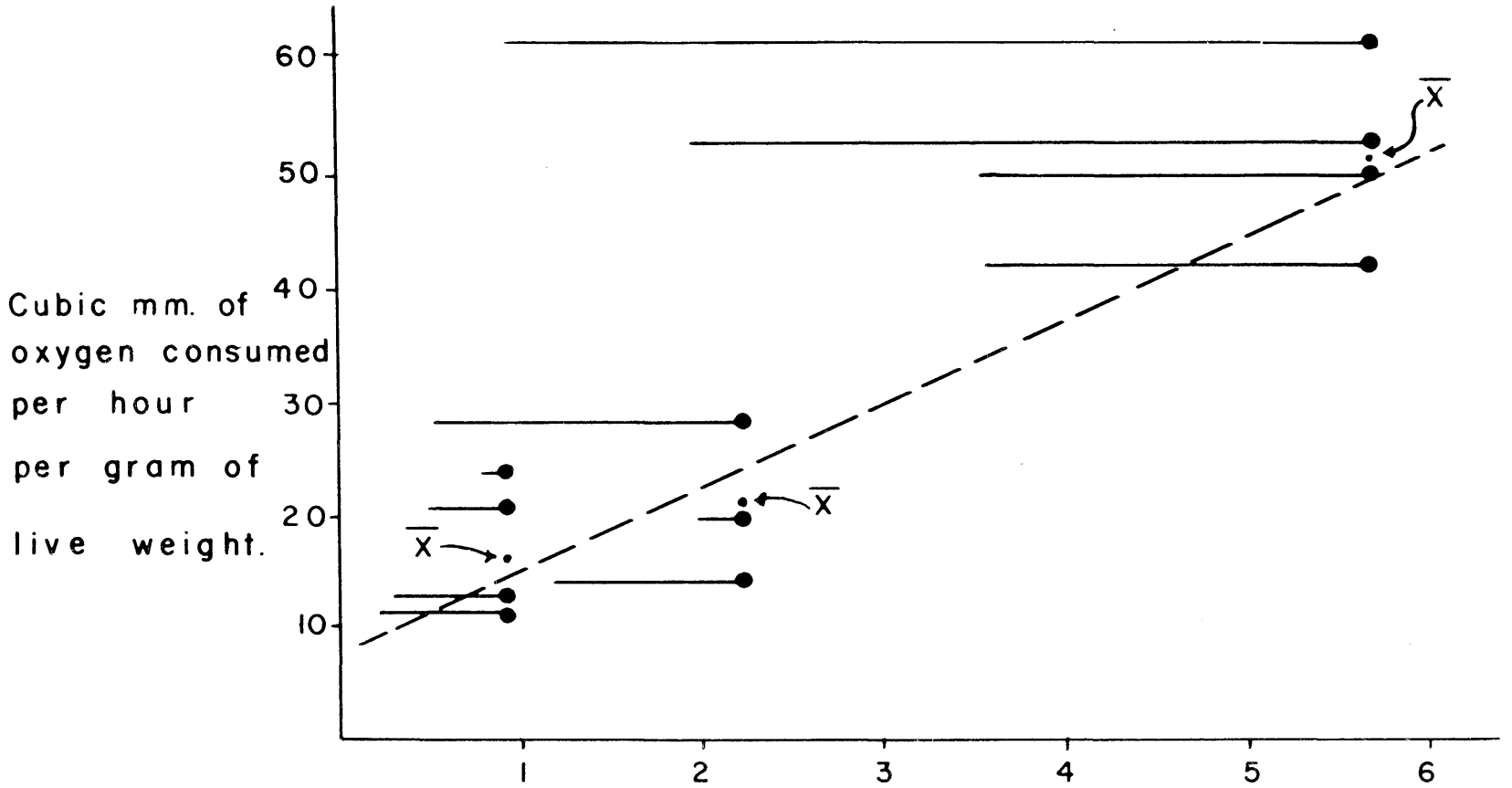
Initial oxygen content	Respiratory rate
5.7 cc O_2/liter	51.4 mm^3 O_2/hour/gram body weight
2.2 "	20.6 "
0.9 "	17.7 "

These data are presented graphically in figure 23. The length of the horizontal lines indicates the drop in the oxygen content of the water in each chamber, resulting from failure to establish equilibrium. During the 24 hours of adjustment the crabs reduced their oxygen consumption to a level commensurate with the ambient oxygen concentration. This adjustment takes more than three hours time but less than 24 hours, and presumably, if the experiment shown in figure 22 had been continued longer than three hours, the slopes of the lines would have altered to a new, lower level.

Discussion of respiration

In applying these results to animals in nature, one must keep in mind that the observed rates pertain to animals sitting quietly on the bottom of an experimental chamber. Certainly when the crabs are swimming the respiratory rates would be considerably higher. It is difficult to understand the function in nature of the first phase of respiration, which allows the animals to maintain a high rate of respiration for a short time when placed in waters of low oxygen concentration. This evidently involves an increase in efficiency of extraction of oxygen from the water. It cannot be continued for longer than 24 hours in resting animals; if the activity of the animals is increased, it probably would be continued

Figure 23. Graph showing a lowering of the respiratory rate of P. planipes as influenced by the oxygen content of the water in which the crabs had been held for 24 hours prior to the time of the experiment. Horizontal lines indicate the degree of depletion of oxygen in the respirometry chamber. Mean consumption at each initial oxygen concentration is shown by $\bar{X}$.



Respiratory Rates of *Pleuroncodes planipes*

for even less time.

If one can use respiratory rate as an index of such functions as mobility, growth, food demands, etc., then crabs sitting on the bottom in waters with less than 1.0 cc O_2/liter would have rates which are about 1/3 the rates in oxygen-saturated water. If, superimposed on this, there is a halving of the respiratory rate caused by a negative response to the 10° C. temperature drop from top to bottom, the crabs would indeed be lethargic in their benthic habitat.

This response of respiratory rates to ambient oxygen concentrations is probably widespread in the Crustacea. It was found in Homarus vulgaris by Thomas (1954), and more recently in Synchelidium sp., a littoral amphipod (Enright, 1962). These two, quite dissimilar, species are probably never found in waters with extremely low oxygen concentrations, but the mechanism still exists in them. It may also operate in the many species of Crustacea which migrate diurnally from deep, cold waters with low oxygen content to the warmer, oxygen-saturated surface waters. The adaptation of these species to their two environments is completely unknown, and represents one of the fascinating biological problems of the Pacific Ocean.

Summary

An ecological study of Pleuroncodes planipes has been undertaken to correlate the animal with its oceanic environment. The animal studied is an anomuran galatheid decapod crustacean about 9 to 11 cm long, resembling a small homarid lobster. These crabs exist in the ocean both as pelagic animals and benthic animals. In the pelagic phase the crabs range from 16° N to 37° N, and have a distribution which is typically neritic. The center of the population appears to be along the southern coast of Baja California. The distribution of the crabs in the pelagic phase is believed determined by the prevailing currents carrying them away from this population center. The crabs have been taken from the plankton 1500 km from the coast in the latitude of southern Baja California, and they were presumably carried there by the California Current as it swings to the west. The occurrence of the crabs to the north is a result of the transport of the countercurrents--the Southern California Countercurrent and the Davidson Countercurrent. These near-shore currents are responsible for the reports of the crabs along the Southern Californian coasts, and also to points north of Point Conception.

The crabs have evolved from typically benthic stock and owe their swimming ability to modification of their basic morphology. Rows of comb-like setae along the anterior and posterior margins of the walking legs are the major adaptations; these retard the sinking of the animals as they settle down through the water. The animals also actively swim by abdominal flexure. The crabs have been observed

swimming at the surface in dense aggregations of more than 100 per square meter over broad areas; densities of from 1 to 10, however, are believed more common. These surface occurrences are correlated with a diurnal vertical migration; the crabs are generally found in the upper 25 meters at night and descend to greater depths during the day. At times the dense surface aggregations are washed on to the shore, and mass mortalities result. A report from the Gulf of California notes the crabs occurred in windrows a meter deep and three meters wide over several hundred meters of beach.

The crabs are benthic as well as pelagic in certain areas, and at least sometimes alternate between the benthos and the plankton with a diurnal rhythm. In their benthic phase they are found on the continental shelf along the western coast of southern Baja California, between the depths of 75 meters and 300 meters. They have also been found on the bottom off the Mexican mainland in the area around the Tres Marias Islands, at similar depths. It is not known whether they live as benthic animals in the Gulf of California

The feeding habits of the crabs seem to be as diverse as their ecological range. As planktonic animals the crabs are able to feed on phytoplankton and small zooplankton. As benthic animals the crabs have the ability to sift through the substrate with their maxillipeds and thus extract small animals living in the sediments. They can also feed as scavengers or as cannibals by using their chelipeds and heavy mandibles. It is believed that the bulk of the diet is phytoplankton filtered out by the crabs as they swim at the surface.

The crabs play an important part in the diet of several other marine animals. The yellowfin tuna feeds on the crab to a large extent. In that part of the tuna fishery where the crabs occur, they amounted to about 78% of the tuna's diet in 1960. Many other fishes such as the skipjack tuna, the albacore, and various kelp bed fishes also feed heavily on P. planipes when the crabs are available to them.

The young of P. planipes pass through a series of zoeal larval stages after hatching. There are five morphologically discrete stages, and generally the larvae change from one stage by molting. Larvae in Stage IV, however, may molt from four to nine times without greatly altering their basic morphology. There is evidence from laboratory culturing that the number of these sub-stages may be influenced by the temperature at which the larvae develop, with higher temperatures causing more sub-stages. The duration of the larval phase is influenced by the temperature at which the larvae are reared, and the rate follows a Q_{10} of about 1.9. The larval duration is also influenced by rearing conditions other than temperature, for the size of the larval rearing container or the presence of other larvae in the container has also been shown to influence the duration of the larval phase. A larval stage was seen in the laboratory which has not been found in nature, and it is probable that the stage was an artifact of laboratory culturing conditions.

Growth rates of P. planipes have been determined from both laboratory and the field; the two answers complement each other and generally agree. They indicate that the young are spawned in winter months and spend the first year of life in the plankton as larvae and

immature crabs. The crabs become reproductively mature in their second year of life, and exist then as both planktonic and benthic animals; toward the end of the second year they become exclusively benthic. Data are available which indicate that the size of adults in nature is influenced by the temperature of the water in which they are found, for crabs are larger in colder water.

When the crabs are benthic in the area off southern Baja California they live in oxygen-poor waters, with the oxygen content being less than 10% saturation values. Laboratory experiments testing the influence of these low oxygen waters on the metabolism of the crabs indicates theat when the crabs are in oxygen-poor water their metabolism is reduced to about 1/3 the values at oxygen saturation. This may indicate that crabs in their benthic phase have lowered growth rates and food demands.

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